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ONTOGENY AND EVOLUTION IN THE MEGAPODES (AVES: GALLIFORMES)[1]

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INTRODUCTION

Unlike all other birds, megapodes of Australia and the Pacific Islands incubate their eggs in mounds or holes by heat from fermentation, sun, or volcanic activity. Furthermore, megapodes are unique among birds in being able to fly weakly on the day of hatching and in having no parental care for young.

These and other reptile-like aspects of megapode reproduction have been interpreted in two contradictory ways. Some authorities (e. g. Portmann, 1938, 1950, 1955) have maintained that megapodes are the most primitive of living birds, while others (e. g. Pycraft, 1910) have stated that the similarities of megapodes and certain reptiles are due to convergent evolution. A related and also unresolved problem has been the primitiveness of mound-building megapodes relative to those laying their eggs in holes (cf. Frith, 1962).

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Despite their anomalous nidification and precocity of young, megapodes as adults are structurally similar to other members of the Order Galliformes (e. g. pheasants) as exemplified by the overlap in adult osteological proportions (cf. data of Verheyen, 1956). Morever, the family Megapodiidae and the New World gallinaceous family Cracidae (chachalacas, guans, curassows) are particularly difficult to separate at the family level on a morphological basis (cf. Miller, 1924). Megapodes and cracids have been classified as the two most primitive gallinaceous families (Huxley, 1868; Peters, 1934).

Unlike the megapodes, most other species of Galliformes have a simple nest on the ground, but some pheasants, cracids, and the highly aberrant hoatzin (*Opisthocomus*) nest in trees. Since avian development often varies in accord with nidification, it was anticipated that the study of megapode embryos and juveniles would reveal clues pertinent to the analysis of megapode phylogeny.

Prior to this study, the only detailed accounts of structure of embryonic or juvenile megapodes were based on the genus *Megapodius* (cf. Pycraft, 1900; Friedmann, 1931; Becker, 1959). These previous investigations had led to contradictory conclusions on the homologies of the early plumages (cf. Nice, 1962) and on the phylogenetic origins of the family (cf. Frith, 1962). The object of the present study was to attempt to resolve the controversy over the phylogeny of megapodes through examining the morphology of embryos and juveniles representing several genera of megapodes.

MATERIALS AND METHODS

Specimens. Thirty embryos of the megapodes *Talegalla jobiensis* and *Leipoa ocellata* were studied (Tables 2, 3). The 11 *Talegalla* embryos were collected for this investigation in New Guinea during 1959-60 by E. T. Gilliard and S. D. Ripley in separate expeditions. The 19 *Leipoa* embryos were collected by me during 1960 in the mallee about 25 miles north of Griffith, New South Wales, Australia; the collecting area was favorable in having an unusually high density (Frith, 1959) of active *Leipoa* mounds which were as frequent as one per 50 acres in the limited suitable terrain. The eggs of *Leipoa* were marked as found and allowed to incubate in the mounds. Subsequent collections provided accurate ages for three embryos and minimal ages for certain others (Table 2). The temperature is ordinarily relatively uniform for *Leipoa* eggs together in a mound (Frith, 1959), and the time between egg layings by a hen is usually four or more days (Frith, 1959, and a few cases in this study). Thus when actual or minimal age of one embryo was known, minimal ages of progressively larger embryos in that mound were estimated by adding four more days for each. Since the first eggs were probably laid on September 4 or later, as judged from previous years (Frith, 1959), some specimens (Nos. 12, 16, 19, 1195, of Table 2) could be assigned presumed maximal ages; smaller embryos from the same mounds could also be assigned maximal ages, again using the hypothesis of four or more days between egg layings in a mound.

Eighty-two juvenile specimens (including 79 study skins) of megapodes were examined at the American Museum of Natural History and Yale Peabody Museum (YPM). Among these were the following species (with numbers of each): *Megapodius freycinet* (59), *M. laperouse* (5), *M. pritchardii* (1), *Macrocephalon maleo* (1), *Aepypodius arfakianus* (2), *Talegalla cuvieri* (2), *T. fuscirostris* (4), *T. jobiensis* (4), *Alectura lathami* (3), and *Leipoa ocellata* (1). More than 140 embryonic and juvenile specimens representing 22 genera of non-megapode Galliformes were used for comparison.

Methods. Characters were chosen for interspecific morphological comparisons according to 1) potential accuracy of description or measurement, as determined by reproducibility in repeated examinations, and 2) potential phylogenetic significance demonstrated by the extent of intergeneric variation and its possible phylogenetic interpretations.

Measurements. Measurements, selected for their applicability over a wide range of sizes, were:

WING: folded and flattened, with a rule from the anterior edge of the wrist to the end of the manus, or, in feathered specimens, to the most distant tip of a remex. Due to the distal shriveling of the ensheathed remiges of embryonic megapodes, wing lengths over 20 mm (Tables 2, 3, 5) were rounded to the nearest 5 mm.

TARSUS: with Vernier calipers from the posterodorsal surface of the ankle along the tarsometatarsus to the level of the proximal surface of the base of the hallux.

CULMEN: with calipers from the tip to the most posterior unfeathered point on the dorsal midline.

HUMERUS; RADIUS: respective maximal lengths with calipers.

THIRD (MIDDLE) DIGIT: straightened, with a rule from the tip to the most distal point of webbing connecting with an adjacent toe.

Megapode embryos Nos. 1, 20, and 21 (Tables 2, 3) were too immature to measure by these criteria.

Values in the Tables (2, 3, 5) are means of two measurements, each of which, unless otherwise noted, was rounded to the nearest millimeter. Estimated maximal ranges of variation in measuring were ± 1 mm for dimensions of 2 to 10 mm and up to ± 3 mm for dimensions of 150 mm; these maximal estimates were derived from the ranges in duplications of more than 500 measurements. Among the factors possibly affecting the accuracy in measuring were 1) unavoidable errors in aligning and reading calipers and rule, 2) structures changing in shape as well as length, 3) variations in the positions of parts of specimens at fixation, and 4) (for anatomical specimens) rate of fixation with 10 per cent formalin.

Weights (Tables 3, 5), recorded by collectors in the field, are given only for fresh specimens, as weights of preserved specimens would be unreliable. The weights and their cube roots were plotted on arithmetic and double logarithmic graphs against the various linear dimensions; if any one of the weights for *Talegalla* were grossly in error, this would have been seen as a point lying relatively far from the plot for the other points. Factors possibly influencing accuracy in weighing include uneven removal of the yolk sac of embryos before weighing, uneven drying of surface moisture on the feathers of embryos, and variations in the contents of the digestive tract of juveniles.

MORPHOLOGY OF EMBRYOS AND JUVENILES

Time in embryonic development. Young embryos of the megapode *Leipoa* developed slowly compared with embryos of phasianids (e. g. *Gallus*, *Phasianus*, *Coturnix*), as shown by the much later occurrence of the first gross appearance of egg tooth, feathers, labial groove, etc., in *Leipoa* (Table 1). Through the first 20 days, these *Leipoa* embryos attained a much smaller absolute size than did embryonic chickens (domestic *G. gallus*) as illustrated by comparing linear dimensions of *Leipoa* and chickens (Fig. 1; Tables 2 and 3). As an example, after 20 days of incubation the wing of an embryonic *Leipoa* was less than 50 per cent as long as that of a chicken (Fig. 1).

The normal incubation period of *Leipoa* is generally at least twice as long as that of known phasianids or turkeys (cf. Table 1; see also Frith, 1959, on *Leipoa*, and Romanoff, 1960, on phasianids). This lengthy incubation period of *Leipoa* is

TABLE 1. Time of certain gross morphological changes in embryos of the megapode *Leipoa* and of phasianids. Age in days after laying of the egg.

	Leipoa age	*Phasianus* age	*Coturnix* age	*Gallus* age
Egg tooth formed	21-22	9	5-6	6½-7
Labial groove formed ..	21-22	?	?	10
Feathers appear	11-21	9	5-6	6½-7
Toes are first separated	11-21	10-12	7-8	8-9
Scales appear on legs ..	29-54	13	8?-9	11-12
Eyelids come together ..	29-61	15	10-11	13
Labial groove lost	29-61	?	?	19
Hatching	60-73	23-24	16	20-21

Sources of data: *Leipoa ocellata*, specimens of this study; *Phasianus colchicus*, Fant, 1957, and Westerskov, 1957; *C. coturnix japonica*, Padgett and Ivey, 1960; domestic *G. gallus*, Hamilton, 1952.

related to both the slow early development and the large size at hatching (see p. 27 for discussion of the effects of incubation temperatures).

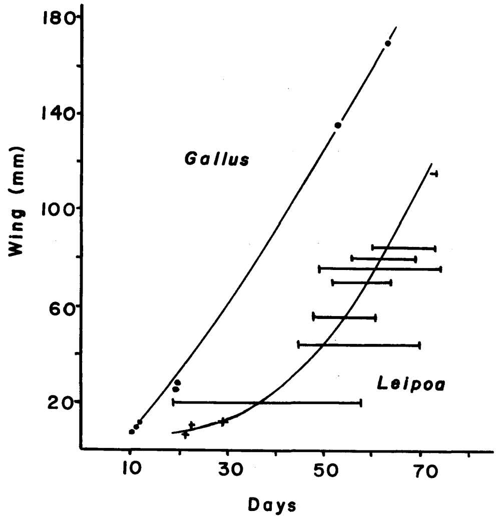

Figure 1. Chronological growth of the wing in *Leipoa ocellata* and domestic *G. gallus* (data from Tables 2 and 3). Curves showing length against time were fitted by inspection and should not be considered as quantitatively accurate.

Relative proportions and growth. At hatching *Talegalla* and *Leipoa* are about two to 15 times heavier than other newly hatched Galliformes of the genera *Coturnix, Colinus, Phasianus, Gallus,* and *Meleagris* (Lyon, 1962; Westerskov, 1957; Romanoff, 1960; see also Table 6). It is of interest that *Leipoa* and *Talegalla* at hatching have proportions and size like those of adult *C. coturnix japonica* (Table 5). The genus *Megapodius* is intermediate in hatching weight (Table 5) between *Talegalla* and phasianids or turkeys.

As a means of comparing changes in proportions during the growth of different species of the Order Galliformes, arithmetic and double logarithmic plots (e. g. Figs. 3, 4, 5) were prepared using the linear measurements of embryos and juveniles (data of Tables 2, 3, and 5). Such proportional growth was described approximately in certain cases by using the conventional allometric equation, $Y = AX^B$, or the equivalent form, $\log Y = \log A + B \log X$, where X and Y are the values of two dimensions. A and B (Table 4) were calculated using Bartlett's method as described by Simpson, Roe, and Lewontin (1960). B values for different species were compared using a modified t-test (Simpson *et al.*, 1960). Correlation coefficients for the sets of data expressed as B values in Table 4 were all significant at the 0.001 level.

To compare growth of linear dimensions relative to total body size in different species, the cube root of weight was used as one criterion for body size (see Amadon, 1943, for the

TABLE 2. Data for specimens of *Leipoa ocellata.* All are embryos except 1195. For procedures of measuring, see text. All lengths in millimeters. Estimated ages in days. Symbols: S, specimen number; W, wing length; T, tarsal length; C, culmen length; H, humerus length; R, radius length; Td, length of third digit; m, male; f, female;—, observation could not be made.

S	W	T	C	H	R	Td	Sex	Age
1	—	—	—	—	—	—	—	11-?
2	7	3	3	5	3	3	—	21-22
3	9	6	5	6	6	4	—	22
4	12	8	7	10	10	6	—	29
5	13	8	8	10	9	7	—	?-54
6	20	12	9	13	13	11	m	19-58
7	20	13	9	13	12	10	m	?-55
8	25	14	10	16	14	12	f	?-59
9	25	15	10	17	18	13	m	?
10	40	19	12	20	20	15	m	?
11	45	20	11	23	20	15	m	?-62
12	45	21	12	22	21	15	m	45-70
13	55	22	12	22	23	16	f	48-61
14	70	24	14	28	26	19	m	?-63
15	70	23	13	27	25	17	—	52-64
16	75	25	14	28	27	18	m	49-74
17	80	26	13	28	29	20	f	56-69
18	80	24	14	31	28	20	f	?-67
19	85	26	14	29	30	20	f	60-73
1195*	115	28	—	38	37	24	—	?-73

* This specimen, found dead in the field, was lacking its head.

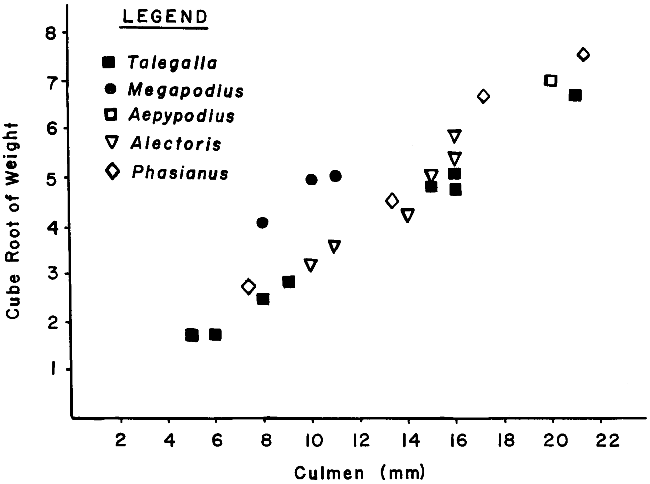

Figure 2. Relationships of the cube root of body weight in grams to the culmen length in the megapodes *Talegalla jobiensis, Aepypodius arfakianus, Megapodius freycinet* and the phasianids *Alectoris chukar* and *Phasianus colchicus*. All data from this study except that for *Phasianus*, for which mean values for males were taken from Westerskov, 1957. See text for discussion.

explanation of this procedure). Since weights were unknown for most specimens, a linear criterion for body size was also chosen. As the culmen length had a relatively direct relationship to the cube root of body weight over a fifty fold range of weights for eight specimens of embryonic and juvenile *Talegalla jobiensis* and for six juvenile specimens of the phasianid *Alectoris chukar* (Fig. 2), culmen was selected as a convenient linear measure for body size in these specimens. Moreover, similar analyses revealed that culmen is a relatively good measure for body size in embryonic chickens (10-21 days; matched lengths from figures of Hamilton, 1952, with weights from Romanoff, 1960) and in juvenile *Phasianus colchicus* from zero to nine weeks posthatching (Westerskov, 1957; see also Fig. 2 of this study). Since the culmen is a less sensitive and less accurate indicator of body size than is the cube root of body weight, certain interspecific differences have possibly gone undetected due to the use of culmen as a major standard for body size.

The scales for the cube root of weight in Figs. 3, 4, 5, are calculated from a mean value of 3.24 for the ratio of culmen length to the cube root of body weight in grams for the eight weighed specimens of *Talegalla jobiensis*. Due to the relative imprecision of culmen measurements (compared with weights)

TABLE 3. Data on specimens of *Talegalla jobiensis* and domestic *G. gallus*. Nos. 1196, A, B, C, S, T, U, V, W are posthatching specimens. For procedures of measuring, see text. All lengths are in millimeters. Weights in grams. Ages in parentheses are estimated from stages in Hamilton (1952). Symbols: S, specimen designation; W, wing length; T, tarsal length; C, culmen length; H, humerus length; R, radius length; Td, length of third digit; m, male; f, female; —, observation could not be made.

Talegalla:

S	W	T	C	H	R	Td	Sex	Weight
21	—	—	—	—	—	—	—	3.5
22	9	6	5	6	6	4	—	4.7
23	11	6	6	8	7	6	—	5
24	12	9	6	9	8	7	—	—
25	18	13	8	11	12	9	m	14.3
26	20	15	9	14	12	11	m	22
27	45	23	12	20	19	15	—	—
28	80	30	16	29	28	24	—	101
29	100	30	15	31	29	24	f	108
30	100	33	17	34	33	27	—	—
1196	115	38	16	38	35	28	—	—
A	115	35	16	—	—	—	f	125
B	160	47	21	—	—	—	m	292
C	164	49	18	—	—	—	—	—

Gallus:

S	W	T	C	H	R	Td	*Age (days)*
N	8	5	5	5	4	4	(10-11)
O	10	8	7	7	6	6	(11-12)
P	11	9	6	8	7	7	(12)
Q	25	17	10	12	10	16	(19)
R	27	19	10	13	11	17	(19-20)
S	85	26	15	29	25	24	—
T	110	36	18	35	33	30	—
U	135	44	21	40	36	35	53
V	170	51	24	47	44	42	63
W	160	54	24	50	46	41	—

Note: Specimens A, B, C are study skins.

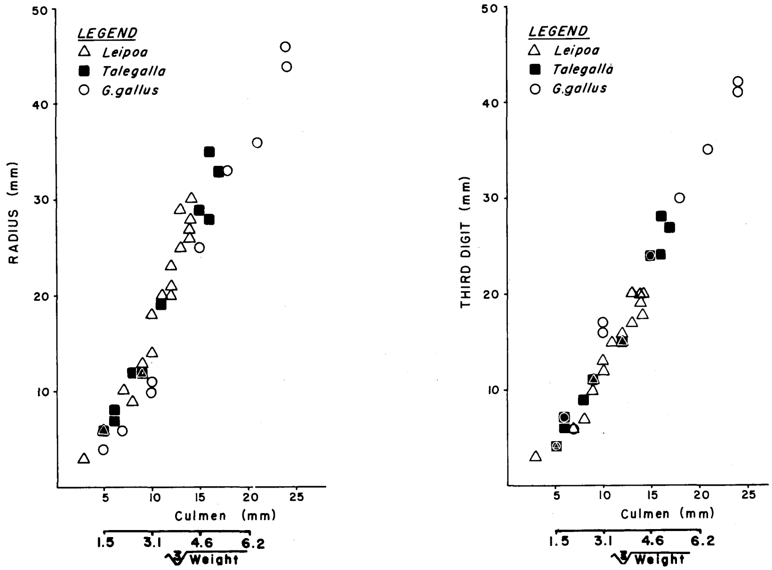

Figure 3A. (Left) Growth of the radius relative to the culmen in *Leipoa ocellata, Talegalla jobiensis* and domestic *G. gallus* (see also Fig. 4). B. (Right) Growth of the third digit relative to the culmen in these three species (see also Fig. 4).

Cube roots of weights in grams calculated by the method indicated in text (p. 9).

and probable interspecific variations in the mean ratio of culmen to the cube root of body weight, the cube root values in Figs. 3, 4, and 5, are probably not precise for individual specimens shown on the graphs; nevertheless, these cube roots of weights help to indicate, in an approximate way, the relative growth of the different species.

As shown by either arithmetic (e. g. Figs. 3, 5A) or logarithmic plots (Fig. 4), growth of linear dimensions relative to culmen in the two species of megapodes is generally similar to that of *Gallus* (see also Table 4). It should be emphasized, however, in view of the necessarily small sample sizes and inherent limits of accuracy in measurement, that these analyses tend to mask certain differences in relative growth. For example, in embryonic chickens the radius (Fig. 4A) and humerus temporarily have lower rates of relative growth followed again by higher rates (this study); the data of Romanoff (1960: 1146) show that the slow growth of these structures in chickens occurs about 14-17 days of incubation. As a consequence, the radius and humerus of chickens near hatching are a few millimeters shorter than those of similar-sized embryos of *Talegalla* or *Leipoa* (data in Tables 2, 3). In addition, measurements of three juveniles of the phasianid *C. coturnix japonica* revealed for this form also a slow mean rate of embryonic growth of radius and humerus relative to other dimensions followed by increased relative rates after hatching. The relatively short radius and humerus of *Gallus* and *Coturnix* in older embryos and at hatching are possibly adaptive in preventing premature flying of the young birds; such an adaptation would be analogous to the retarded development of remiges in juveniles of forms such as petrels and hawks. No trace of a relatively slow embryonic growth of radius and humerus was found in the megapodes.

Culmen measurement in the utilized samples covers a relatively small range (less than 20 mm), but this handicap is offset somewhat by the utility of this measurement for study skins. The culmen is measured linearly over a curved surface but nevertheless is empirically useful. In measuring the culmen of

TABLE 4. Interspecific comparison of allometric growth of dimensions relative to culmen. None of the interspecific differences in exponent is statistically significant. See text for details.

Dimension	Species	Exponent (B) with 95 per cent confidence interval	Coefficient (A)	Size of sample
Tarsus	*Leipoa*	1.6 ± 0.2	0.24	18
"	*Talegalla*	1.5 ± 0.3	0.20	13
"	*Gallus*	1.4 ± 0.2	0.18	10
Humerus	*Leipoa*	1.5 ± 0.4	0.19	18
"	*Talegalla*	1.4 ± 0.2	0.15	10
"	*Gallus*	1.4 ± 0.2	0.19	10
Radius	*Leipoa*	1.6 ± 0.2	0.26	18
"	*Talegalla*	1.4 ± 0.2	0.17	10
"	*Gallus*	1.5 ± 0.2	0.27	10
Third digit	*Leipoa*	1.5 ± 0.3	0.24	18
" "	*Talegalla*	1.5 ± 0.2	0.23	10
" "	*Gallus*	1.5 ± 0.2	0.20	10

late embryonic and juvenile chickens (*Gallus;* Table 3), the presence of the comb necessitated estimating culmen lengths in eight specimens through the projection of lines from the postero-lateral margins of the horny bill dorsally to the midline; however, this approximation did not alter the interpretations as shown by using other combinations of dimensions. At hatching in *Gallus*, *Leipoa*, and *Talegalla*, the culmen may lose up to 1 mm in length through loss of periderm, but this small change does not affect the interpretations of relative growth.

Analogous to the shorter culmen after hatching are reductions (about 5 mm) in wing length of juveniles of these species through loss of natal downs and also the decrease (less than 1 mm) in length of the third digit through loss of the claw pad at hatching. Here again the interpretations of relative growth were not affected.

Relative and proportional growth of gallinaceous wings was too complex to permit adequate representation in a simple equation, but, as shown by graphs (e. g. Fig. 5), relative growth of the wing in *Talegalla*, *Leipoa*, and other Galliformes was similar within the size range considered. The proportional growth illustrated in Fig. 5B suggests possible interspecific differences which, however, are not especially striking. Data for the Jungle Fowl (*G. gallus*) were used in Fig. 5 to provide a larger sample, but data for chickens (domestic *G. gallus;* Table 3) gave similar results.

Juvenile *Megapodius* have an unusually short culmen contrasted with those of juveniles of other megapodes or other Galliformes; the mean ratio of culmen length to the cube root of body weight for three *Megapodius freycinet* (Fig. 2; Table 5) was 2.1, compared with 3.24 for eight *Talegalla jobiensis.* Young juvenile *Megapodius* (Table 5) also differ from young juveniles of *Talegalla* in having a longer wing relative to the cube root of body weight.

Measurements of wing, tarsus and culmen of more than 110 other juvenile specimens representing 22 genera of non-megapode Galliformes (cf. Table 5) were plotted on graphs and compared. These species generally appear to have proportional growths similar to those of *Talegalla*, *Leipoa*, and *Gallus.* However, a juvenile *Crax rubra* of the cracids (Table 5) was exceptional in having a relatively short wing (shown also by figures of young *Crax globicera* (= *rubra*) in Heinroth, 1931). The shorter wing at hatching in *Crax* is apparently associated with the generally less well-developed feathers (p. 24). Forms such as ducks (e. g. *Anas*) which have delayed formation of juvenal remiges show plots of alar growth quite unlike those of Galliformes.

These analyses, although necessarily based on small samples, indicate that embryonic megapodes undergo proportional and relative growth analogous to that occurring up to several weeks posthatching in phasianids. Certain forms such as *Megapodius* and *Crax* show interesting deviations from the general gallinaceous conditions. Larger samples might reveal additional interspecific differences and possibly intraspecific variations according to individuals, sex or locality.

Some qualitative comparisons of embryos and juveniles. Embryos of *Leipoa* (e. g. Nos. 2 and 19) and of chickens shortly prehatching behaved similarly when taken from the shell, i. e. the embryos gaped and kicked. Even *Leipoa* embryos

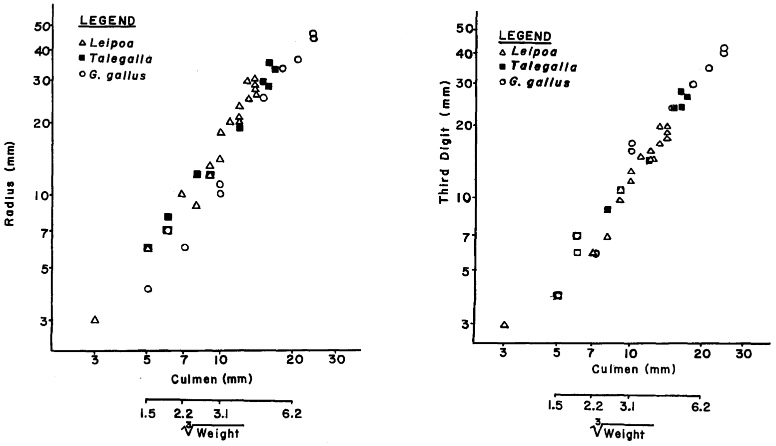

Figure 4A. (Left) Double logarithmic plot of growth of the radius relative to the culmen in *Leipoa ocellata, Talegalla jobiensis* and domestic *G. gallus*. B. (Right) Double logarithmic plot of growth of the third digit relative to the culmen in these three species.

Cube roots of weights in grams calculated by the method indicated in text (p. 9).

Table 5. Comparison of dimensions of some juvenile Galliformes. Specimens arranged by increasing tarsal length. For procedures of measuring, see text. Lengths in millimeters. Symbols: W, wing; T, tarsus; C, culmen; m, male; f, female; g, grams.

	W	T	C
Numida meleagris (f)	20	17	10
Chrysolophus pictus	20	18	7
Phasianus colchicus	30	19	8
Opisthocomus hoazin	40	19	12
Gennaeus leucomelanos	50	19	10
Syrmaticus mikado	30	20	8
Chrysolophus pictus	26	20	7
Phasianus colchicus	35	21	10
C. coturnix japonica	90	22	12
Alectoris chukar (m; 73 g)	95	22	14
Phasianus colchicus	85	23	13
Meleagris gallopavo	45	24	10
Ortalis wagleri	45	24	10
Ortalis vetula	70	24	12
Megapodius freycinet (f; 63.6 g)	100	24	8
Numida meleagris (m)	110	24	14
Megapodius laperouse	95	25	8
Alectoris chukar (m; 121 g)	115	26	15
Meleagris gallopavo	55	27	9
C. coturnix japonica (adult)	100+	27	13
Penelope purpurascens	105	27	12
Megapodius pritchardii	85	28	6
Gennaeus leucomelanos	105	28	15
Chrysolophus pictus	115	30	14
Alectoris chukar (f; 154 g)	120	30	16
Tragopan temmincki	130	30	14
Ortalis wagleri	110	31	15
Alectoris chukar (f; 198 g)	130	31	16
Mitu tomentosa	85	32	14
Talegalla fuscirostris	120	32	15
Alectura lathami	105	33	15
Phasianus colchicus (f)	110	33	18
Francolinus gularis	120	33	15
Megapodius freycinet (f; 117 g)	125	33	10
Megapodius freycinet (123.5 g)	130	33	11
Opisthocomus hoazin	165	34	19
Macrocephalon maleo	140	35	15
Crax rubra (m)	75	36	15
Dendragapus obscurus (f)	175	36	18

considerably larger than chickens at hatching show this characteristic embryonic behavior.

Meyer (in Meyer and Stresemann, 1928) noted the large fat deposits in late embryonic *Megapodius;* both *Talegalla* and *Leipoa* embryos (this study) also have subcutaneous fat bodies distributed similarly to those of chicken embryos but covering a wider area in embryos near hatching. These deposits in older *Talegalla* and *Leipoa* embryos are especially well developed laterally along the neck and beneath portions of the ventral feather tract.

The genus *Megapodius* (Miller, 1924; confirmed in this study) is unusual among Galliformes in having a small web

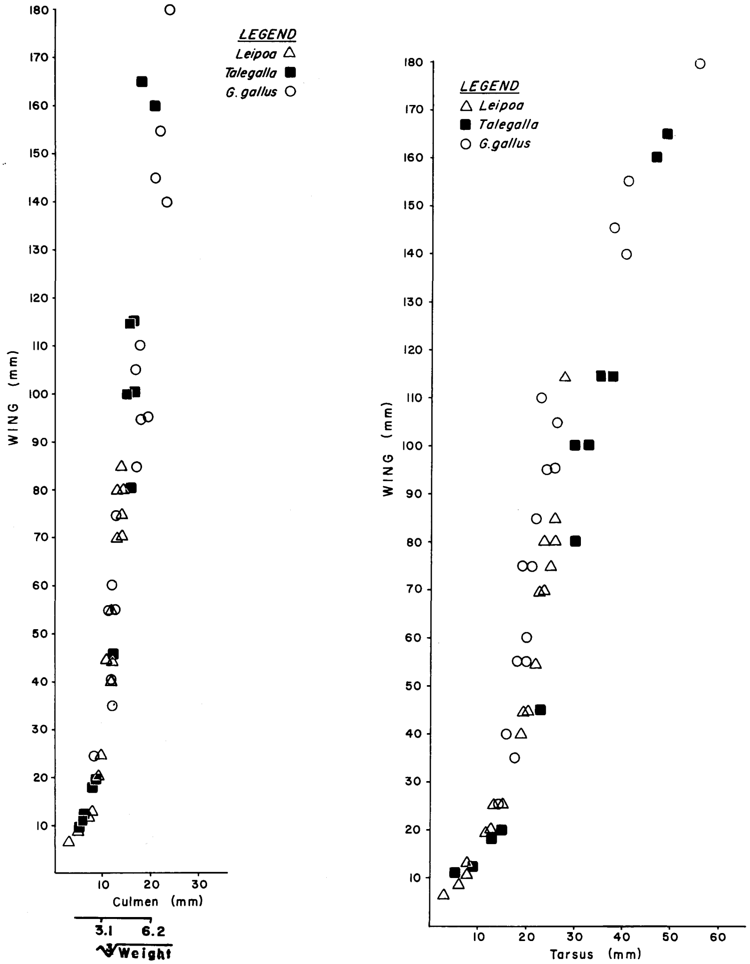

Figure 5A. (Left) Growth of the wing relative to the culmen in *Leipoa ocellata, Talegalla jobiensis* and *G. gallus.* Cube roots of weights in grams calculated by the method indicated in the text (p. 9). B. (Right) Proportional growth of the wing versus the tarsus in these three species.

between the second and third toes but, unlike forms such as *Leipoa, Talegalla* and *Gallus,* none between the third and fourth toes.

A few qualitative gross morphological changes appear at a greater absolute weight, and, for larger embryos, at a detectably greater linear size, in the megapodes (*Leipoa* and *Talegalla;* this study) than in *Phasianus* (Westerskov, 1957) or *Gallus* (structures from Hamilton, 1952, matched with weights from Romanoff, 1960). Examples of these phenomena in *Talegalla* versus phasianids (Table 6) include first appearance of feathers, egg tooth, labial groove, and coming together of the eyelids.

TABLE 6. Comparison of weights at times of certain qualitative morphological changes in *Talegalla jobiensis, Phasianus colchicus,* and domestic *G. gallus.* Weights in grams. *Talegalla* weights in parentheses were estimated from culmen lengths using the relationship reported in the text (p. 9).

Macroscopic character	*Talegalla* weight	*Phasianus* weight	*Gallus* weight
First appearance, feathers	3.5 - 4.7	0.7-1.7	0.4- 1.2
First appearance, egg tooth	4.7 - 5.0	0.7-1.7	0.4- 1.2
Formation of separate toes	3.5 - 4.7	1.4-4.8	0.7- 2.3
Formation of scales on legs	(5.5)-14.3	3.2-5.8	2.3- 7.3
Eyelids coming together	22-(40)	4.7-8.5	5.2-11.0
Hatching	110+	23	33

Sources of data: *Talegalla* from this study; *Phasianus* from Westerskov (1957); *Gallus* morphology from Hamilton (1952) combined with *Gallus* weights from Romanoff (1960: 1147).

Tarsal scutellation. My observations on the tarsal scutellation of megapodes support the findings of Ogilvie-Grant (1893). *Megapodius*, *Aepypodius*, and *Talegalla* are alike in having a single row of large scutes down most of the foresurface of the tarsus (tarsometatarsus), but *Aepypodius* has two rows distally. *Alectura* and *Leipoa* have two rows of large scutes down the fôresurface, while *Macrocephalon* has many small scutes. Tarsal scutellation is similar in juveniles and adults within a species of megapode.

Turkeys, many phasianids and some cracids have two rows of large scutes on the foresurface, while many cracids possess only one row; *Opisthocomus* has many small scutes.

Feathering of the oil gland. *Talegalla jobiensis* has a naked oil gland (no feathers on the tip; **Fig. 6, this study**) and thus

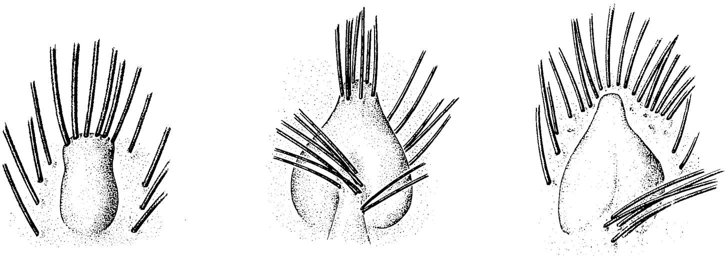

Figure 6. Oil glands of domestic *G. gallus* (19 day embryo; ca. 5.5 ×), *Magapodius laperouse* (YPM 89; juvenile; ca. 3 ×), and *Talegalla jobiensis* (No. 29, embryo; ca. 1.5 ×), from left to right. Dorsal view.

is like *Alectura* and *Leipoa* (Miller, 1924; confirmed in this study). In contrast, *Megapodius laperouse* (Fig. 6, this study) has a tufted oil gland as was reported by Miller (1924) for other species of *Megapodius* and for *Macrocephalon.* Most *Galliformes*, excluding megapodes, have tufted oil glands (Fig. 6 of this study; Miller, 1924; see also Table 7 for a summary of this character in other birds).

Eutaxy. Unlike other gallinaceous families, megapodes have variation in eutaxy (presence of the fifth secondary; Steiner, 1918; Miller, 1924). As anticipated from reports on allied species (i. e. *Alectura* and *Leipoa;* Miller, 1924), *Talegalla jobiensis* is eutaxic (this study). Both *Talegalla* and *Leipoa* are eutaxic at the first embryonic appearance of the secondaries. *Megapodius laperouse* (YPM 89) is also eutaxic, but *M. pritchardii* (Pycraft, 1900) and some (but not all) members of *M. freycinet* (Steiner, 1918; Miller, 1924) are diastataxic (lacking the fifth secondary). *Macrocephalon* is also diastataxic (Miller, 1924). In contrast, all other Galliformes, including chickens, are eutaxic (Miller, 1924; see also Table 7 for a summary of diastataxy and eutaxy in other birds).

Carotid arteries. In agreement with the data reviewed by Glenny (1955) for *Megapodius freycinet*, *M. pritchardii*, *Macrocephalon*, and *Alectura*, the megapodes dissected in this study (e. g. *Leipoa* No. 17, *Talegalla* No. 29, *Megapodius laperouse* YPM 89) had a left dorsal carotid artery but none on the right side; in contrast, chicken embryos possessed both right and left dorsal carotids. Glenny (1955) has reported that all Galliformes except megapodes are bicarotid (see Table 7 for a summary of this feature in other birds).

Early plumages. Studer (1878) and Pycraft (1900) believed that megapodes molt natal downs before hatching, but Portmann (1955) and Becker (1959) have contended

TABLE 7. Status of dorsal carotid arteries, disastataxy versus eutaxy, and oil gland feathering in nongallinaceous birds. Symbols: 2, bicarotid; 1, unicarotid; E, eutaxy; D, diastataxy; T, tufted oil gland; N, naked oil gland; O, no oil gland.

Taxonomic group	Carotid arteries	Fifth secondary	Oil gland
Tinamidae	2	E	T
"Ratites"	1,2	D,E	O, ?
Gaviidae	2	D	T
Podicipediformes	1	D	T
Procellariiformes	2 (1)	D	T
Spheniscidae	2	D	T
Pelecaniformes	1, 2	D, E	T
Ciconiiformes	1, 2	D	T, N
Anhimidae	2	D	T
Anatidae	2	D	T
Falconiformes	2	D	T, N
Gruiformes	1, 2	D, E	T, N, O
Charadriiformes	2 (1)	D, E	T
Columbiformes	2	D, E	N, O
Psittaciformes	1, 2	D	T, O
Musophagidae	2	E	T
Cuculidae	2	E	N
Strigiformes	2	D	T, N
Caprimulgiformes	1, 2	D	N, O
Apodiformes	1, 2	D, E	N
Coliiformes	1	E	N
Trogoniformes	1	E	N
Coraciiformes	1, 2	D, E	T, N
Piciformes	1, 2	E	T, N, O
Passeriformes	1	E	N

Sources of data: arteries, Glenny, 1955; eutaxy and diastataxy, Steiner, 1956; oil gland, Beddard, 1898, and Miller, 1924.

that megapodes lack natal downs and that their first feathers represent the phylogenetic precursors of natal downs. In contrast, Friedmann (1931) stated that megapodes at hatching bear juvenal feathers in opposition to several authors (e. g. Ogilvie-Grant, 1893), who referred to the downy young. In order to determine which, if any, of these conflicting views is correct, it was necessary to analyze many features of pterylosis, feather growth, and molt.

In the embryonic early growth of the megapode feathers, those of the tail are longest. For example, on one *Leipoa* (No. 5) the caudal sheaths (10 mm long) were 5 mm longer than the next longest ones on the cervical region and femoral tract. Similarly, a *Talegalla* embryo (No. 24) with tail feathers of 10 mm had the next longest sheaths (3 mm) on the cervical region. Precocious embryonic early growth of caudal natal downs occurs in chickens (Hamilton, 1952) and Coturnix Quail (Padgett and Ivey, 1960) and is apparently a gallinaceous trait.

Although a row of 9 or 10 relatively large papillae initially were formed on the posterior surface of the manus (e. g. on Nos. 3, 22, 23), of these only primaries 1 through 8 were large on older embryos and newly hatched *Talegalla* and *Leipoa* (see also Pycraft, 1900, for *Megapodius*). Such embryonic repression of the juvenal outer primaries (9 and 10) is characteristic for many Galliformes.

Embryonic megapodes do not molt, contrary to the report of Studer (1878), who was misled partly by the ease with which immature sheaths are dislodged from the skin. Indeed, feather maturation, manifested by hardening, does not occur on the body in *Talegalla* and *Leipoa* until the last quarter of incubation as determined by dissection of sheaths from eight tracts. At hatching, as in other Galliformes, the feathers on the body are fully grown or nearly so, but the vanes of the remiges continue growing.

Feather sheaths at hatching are longer on *Talegalla* and *Leipoa* than on chickens. To illustrate this condition, the mean lengths (M) and coefficients of variation (CV) were calculated for six sheaths from each of three embryos near hatching. The six sheaths were taken from corresponding positions on six

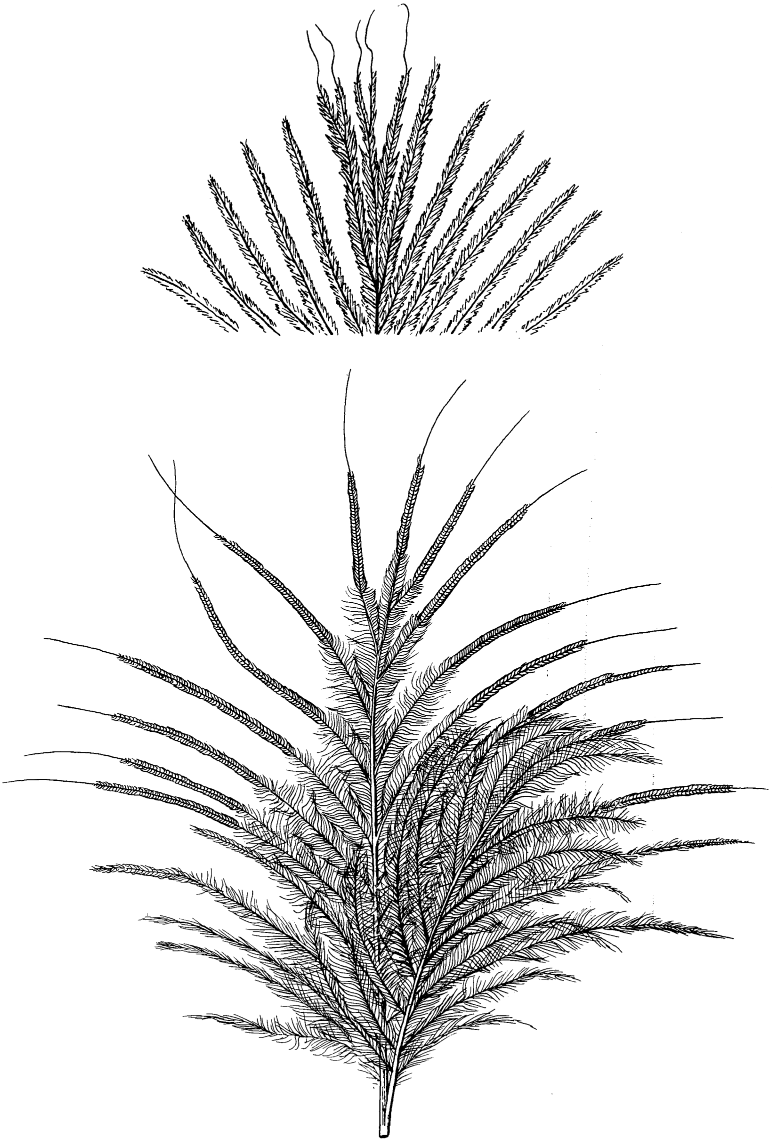

Figure 7. Comparison of the tip of secondary No. 9 of the right wing (top; ca. 4×) with a natal down from the body (bottom; ca. 3×). *Leipoa ocellata* No. 19; 60-73 days of incubation.

tracts on the body of each of the embryos. The values were: *Gallus* (19 day) M 13.8 mm (CV 37.6); *Leipoa* (No. 19) M 28.6 (CV 39.9); and *Talegalla* (No. 30) M 36.5 mm (CV 38.8). In view of the great variation in lengths of sheaths within a tract, these values are useful only to indicate the great difference between megapodes and chickens.

Sheaths on the body of *Talegalla* and *Leipoa* embryos appeared conventional, having opaque and unshriveled tips, but sheaths of remiges, alula quills, and certain alar upper coverts of the older *Talegalla* and *Leipoa* embryos had unusual translucent and shriveled tips as noted by Pycraft (1900) for remiges of embryonic *Megapodius*. Pycraft (1900) figured a constriction of the sheath of the *Megapodius* remex in the region of transition from opaque to translucent portions. This constriction does not occur in *Leipoa* and *Talegalla* (this study); due to lack of a suitable specimen of *Megapodius*, it was not possible to check Pycraft's report of a constriction in that genus.

Within the translucent tips of the sheaths of remiges on older *Talegalla* and *Leipoa* embryos are weak filaments which are distal portions of the central barbs of the tip of the remex (Fig. 7). These distal filaments are easily dislodged in removing remiges from the sheaths so that some or all filaments are missing from the expanded remiges of embryos (as in Fig. 7) and juveniles. Unlike the correspondingly placed natal downs on the tips of juvenal remiges of phasianids or cracids, these filaments on the tips of remiges of embryonic megapodes are weakly developed and lack barbules.

On juveniles of six megapode genera (this study), the feathers at hatching have 1) barbule-free distal ends of central barbs of body feathers (Fig. 7); 2) a central rhachis; 3) a large aftershaft on the body feathers (Fig. 7); 4) a well-formed vane in the remiges; these features in common demonstrate that megapodes had common ancestors possessing such features at hatching. In contrast, the feathers of chickens at hatching have 1) barbule-free distal ends of central barbs; 2) a distinct rhachis only in the short and growing juvenal remiges; 3) no aftershaft; 4) a well formed vane only in the growing remiges.

Hall (1901), Blasyzk (1935), and Frith (1962) have reported for juvenile *Leipoa* and *Alectura* that the feathers on the body at hatching are later carried out on the tips of the growing second feathers. The finding of these connections (this study) on *Leipoa ocellata* (Fig. 8), *Alectura lathami*, *Talegalla jobiensis*, and *Megapodius freycinet*, demonstrates that this is another general feature of megapodes. As the first feathers are easily dislodged from the tips of the second ones, the rarity of observations of these junctions on preserved specimens is to be expected. These connections resemble those between natal downs and juvenal feathers in other Galliformes.

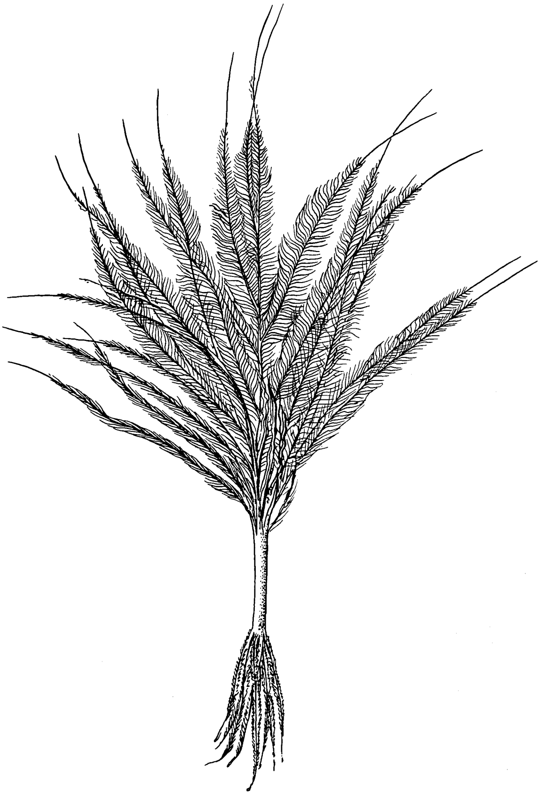

Figure 8. A natal down attached to the tip of a juvenal rectrix from juvenile *Leipoa ocellata*. (YPM 1195) ca. 3×.

However, since similar connections occur between other generations of feathers in Galliformes (Watson, 1963), these attachments, considered alone, do not demonstrate conclusively that the first feathers on the body of megapodes are natal downs.

Nevertheless, the homology of megapode feathers on the body at hatching with the natal downs of other Galliformes is shown by the following features in common: 1) the precocious early growth of embryonic tail feathers; 2) the plumulaceous structure of the feathers on the body at hatching relative to the more pennaceous structure of later generations of feathers and of the first remiges; 3) attachment of the first feathers to the tips of growing feathers of the second generation; 4) barbule-free distal ends of central barbs; 5) start of the first body molt within two weeks posthatching (data on *Leipoa* timing from Hall, 1901, and Frith, cited in Nice, 1962).

The following group of characters demonstrates that the megapode first remiges are juvenal like those of other Galliformes: 1) only eight primaries at hatching but ten on older juveniles and adults; 2) similar lengths of growing primaries Nos. 1(first basic = postjuvenal) and 10 (juvenal) on juvenile *Megapodius* (YPM 89) as in certain juvenile phasianids (cf. Heinroths, 1928) ; 3) remiges more pennaceous than other feathers at hatching; 4) similar location of the distal filaments on the embryonic remiges of megapodes and of the corresponding natal downs on other Galliformes; 5) time of initial loss of a first remex (two weeks posthatching in *Leipoa;* Hall, 1901); synchrony of molt of natal downs on the body and juvenal remiges is characteristic for Galliformes.

The lengths of rhachises in the natal downs of Galliformes can be partly correlated with the size of the newly hatched birds. For example, the young of small phasianids, e. g. *Coturnix*, lack rhachises in their natal downs, while turkeys (*Meleagris;* Pycraft, 1900, and confirmed in this study; and *Agriocharis;* this study) and tragopan pheasants (this study), both of which are larger at hatching than are the small phasianids, have short rhachises in their natal downs. Megapodes, still larger at hatching, have longer rhachises (Fig.7). Certain cracids, e. g. *Crax*, are exceptional in being large at hatching (over 100 grams; Heinroth, 1931), while lacking or having only short rhachises in their natal downs (this study).

As might be expected from the data thus far presented, many phasianids molt the last of their natal downs at a body size smaller than that of juvenile megapodes at the time of loss of the last natal downs. For example, *Phasianus colchicus* at 160 grams has lost nearly all the natal downs (Westerskov, 1957), while *Talegalla* (e. g. B of Table 3) at this weight retains many natal downs on the breast, back and head.

Thus the hatching plumages of megapodes and other Galliformes are homologous but differ structurally.

Structures associated with hatching. Several authors (e. g. Frith, 1959) have reported megapodes at hatching kicking their way out of the shell, and some observers (e. g. Elvery in Campbell, 1901) have emphasized the difference from hatching in chickens. A relatively detailed description of megapodes at hatching is that of Bergmann (1961), who observed that, in *Talegalla cuvieri*, at the time of breaking open of the shell, the only parts of the body to break through the shell membrane were the legs and feet. Thus *Talegalla* is unlike both chickens (Hamilton, 1952) and Coturnix Quail (Clark, 1960) which use the egg tooth of the beak conspicuously in breaking open the shell.

Although Friedmann (1931) could not find an egg tooth on one *Megapodius pritchardii* embryo, and Bergmann (1961) could not find an egg tooth on *Talegalla cuvieri* at hatching, I (1960, 1961) have found egg teeth on both *Talegalla jobiensis* and *Leipoa ocellata* embryos (latter observation made independently by Frith, 1962). Frith has kindly shown me one specimen of prematurely hatched *Leipoa* bearing an egg tooth, which, together with my finding that many other specimens of newly hatched megapodes lack egg teeth, suggests that egg teeth are usually lost about the time of hatching in megapodes. The egg teeth of chickens near hatching are approximately two times larger in linear dimensions than the fully grown egg tooth of *Leipoa* (Fig. 9) or *Talegalla*. Especially when considered relative to body size at hatching, the megapode egg tooth is quite small. I (1961) have reviewed the occurrence of egg teeth in birds as a whole; egg teeth probably occur on most, if not all, birds. Megapodes are the only birds for which egg teeth are thought to be nonfunctional at hatching.

In *Talegalla* and *Leipoa* the Musculus complexus or "hatching muscle" is located dorsally on the neck immediately under the skin (and under fat deposits in larger embryos), attached anteriorly to the parietal of the skull, and posteriorly connected to the third, fourth, and fifth cervical vertebrae and the muscular complex overlying these vertebrae. The two complexus muscles were separated in the dorsal midline in the 20 examined anatomical specimens of megapodes: in *Leipoa* by minimal distances of 1.5 (No. 4) to 3 mm (No. 19) and in *Talegalla* by 2.5 (No. 26) to 5 mm (No. 30). In contrast, in chicken embryos near hatching, the two complexus muscles met in the dorsal midline (Fig. 10). The anterior insertions meet in the dorsal midline long before hatching and after hatching move laterally, separating in the dorsal midline (Fisher, 1958; this study). The M. complexus of megapodes and chickens also differed in the apparent lack of a temporary enlargement about the time of hatching in megapodes. In chickens near hatching this muscle appears swollen, protruding above the level of adjacent cervical muscles and reaching a thickness of at least 2.5 mm, whereas in megapodes no swelling was observed and maximal thickness was always less than 1 mm. Similarly, although maximal width of the complexus muscle in each of four chickens near hatching was 7 mm, in none of the megapodes did this width exceed 5-7 mm, which was reached only in the largest specimens (e. g. Nos. 19, 30).

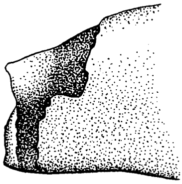

Figure 9. Egg tooth of an embryonic *Leipoa ocellata*. (No. 9) Overlying periderm removed. Ca. 7 ×.

Length measurements of the M. complexus were unreliable due to the lack of a clear posterior boundary of the muscle. When measurements of width and midline separation were analyzed relative to body size by plotting on arithmetic and double logarithmic graphs, no indications of prehatching variations other than growth and individual variations were detected for the megapodes, but the precision of these measurements (about ± 0.5 mm) is not very great relative to the dimensions measured. These observations do not eliminate the possibility of a transient enlargement of the M. complexus at hatching in megapodes, but they provide no support for such a view. The separation in the dorsal midline and apparent lack of special enlargement of the complexus muscle at hatching in megapodes are very likely correlated with the larger size of megapodes at hatching.

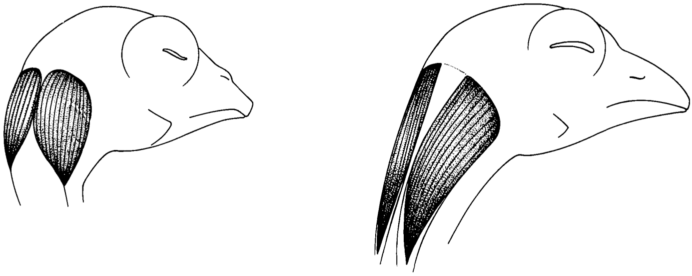

Figure 10. The Musculus complexus of domestic *G. gallus* (19 day embryo; ca. 1.2×) and of *Talegalla jobiensis* (No. 30; ca. 1.4×). *Talegalla* on the right.

The small egg tooth and unusual features of development of the M. complexus of megapodes appear to be associated with the different methods of hatching in megapodes and phasianids.

DISCUSSION AND CONCLUSIONS

Gallinaceous growth and maturation. The embryonic megapodes *Leipoa* after the first 20 days were relatively immature compared with chickens of similar age. Although slow early embryonic development is a reptile-like character, not too much phylogenetic significance can be attributed to this condition in *Leipoa,* since the slow developmental rate is associated with the methods of incubation including relatively low incubating temperatures. It is possibly phylogenetically significant that *Leipoa* can hatch successfully (Frith, 1959) at incubating temperatures so low (below 95°F) as to be lethal for chicken embryos (Romanoff, 1960) ; however, data on the normal range of egg temperatures of wild birds in general (Huggins, 1941) indicate that megapodes are perhaps not unusual among birds with respect to tolerated incubating temperatures.

Interpretation of the chronology of embryonic megapodes is complicated by great individual variation. For example, normal prehatching periods in *Leipoa* from different mounds range from 50 to 90 days in association with intermound variations from 96° down to 80°F in incubating temperatures (Frith, 1959). Since incubating temperatures of the megapode *Talegalla jobiensis* (Ripley, 1964) are within the range for *Leipoa* (Frith, 1959), it is possible, though unproven, that *Talegalla* has an embryonic chronology similar to that of *Leipoa.* Analysis of differences in embryonic chronology between megapodes and phasianids is further complicated by the great interspecific variation among phasianids incubated at 100°F. For example, *Colinus* weighing 6 grams (egg weight, 9 g) and *Phasianus* weighing 18 grams (egg weight, 32 g) are both hatched in 24 days, while chickens of 31 grams (egg weight, 60 g) are hatched in only 21 days (Romanoff, 1960: 1143). Data are not available for a quantitative comparison of the effects of varied incubation temperatures on the development of chickens versus megapodes.

Both the phasianid *Phasianus colchicus* (Westerskov, 1957) with an adult (male) weight of 1400 grams and the megapode *Alectura lathami* (Coles, 1937) with a slightly higher adult weight (Heinroth, 1922) reach full size about 25-30 weeks after laying of the egg, indicating that the posthatching growth of *Alectura* is neither unusually fast nor slow compared with that of phasianids.

The data of this study show that *Leipoa* and *Talegalla* before hatching undergo proportional and relative growth analogous to that occurring up to several weeks posthatching in other Galliformes. The similarity of relative growth in young Galliformes is in agreement with the morphological homogeneity of adults (cf. data of Verheyen, 1956). The relative growth appears, in this case, to be phylogenetically generally more conservative than chronological growth. The differences in relative growth of radius and humerus between megapodes and phasianids do not indicate that either group is more primitive than the other.

The noted interspecific variations in the size of embryos at the first macroscopic appearance of certain structures may represent interspecific differences in the growth of anlage of these structures, for, as Schmalhausen (1926) and others have pointed out, relative growth itself can produce qualitative changes in form.

Although the weight of a bird at hatching is relatively directly correlated with the weight of the egg (Heinroth, 1922), the ratio of the size of the egg relative to that of adults often shows considerable intergeneric variation (Heinroth, 1922). Megapodes and certain small phasianids (e. g. *Coturnix*) have eggs generally in the range from 8 to 18 per cent of adult body weight in contrast to other phasianids and turkeys with eggs weighing less than 5 per cent of adult body weight (Heinroth, 1922).

The precocity of megapodes at hatching is associated with 1) the large absolute egg size and correspondingly large size of young at hatching together with 2) an embryonic relative growth of the wing analogous to that occurring up to several weeks posthatching in phasianids. No birds other than megapodes have large eggs plus extensive embryonic growth of the wings.

Megapodes and reptiles. Portmann (1938) listed the following as primitive (reptile-like) traits of megapodes: lack of natal downs, possible lack of an egg tooth at hatching, absence of parental care for young, eggs incubated in sand by solar heat, long incubation period, large clutch size, slow growth to adult size, and precocity of young at hatching. However, as shown by my study, megapodes do have natal downs, and at least some species have egg teeth. Furthermore, there is no good evidence for an especially slow posthatching growth of megapodes.

Moreover, the many adaptive interrelationships (coadaptations) of the reptile-like characters of megapodes should be considered. For example, the long incubation period is correlated with the methods of incubation and the large size and precocity of young at hatching. The precocity of young is also correlated with the lack of parental care which in turn is associated with the incubating methods and clutch size. The reptile-like traits of megapodes all belong to one, or perhaps two, group(s) of coadapted characters. Considered in this way, the evidence for special affinities of megapodes and reptiles is unconvincing, since the points of similarity are all related to common reproductive adaptations.

The case for special reptilian affinities of megapodes would be greatly strengthened if there were reptile-like characters relatively independent of the central adaptation in megapodes; however, no such characters have yet been found. As one example, there is reported to be a significant difference in the caloric values of reptilian and avian egg yolks (Slobodkin, 1962), yet samples of yolk collected during this study from relatively fresh eggs of *Leipoa* and *Gallus* had values agreeing with those of other avian species (Slobodkin, 1962).

Furthermore, advocates of the primitiveness of the megapodes among birds as a whole have generally failed to analyze the possibility of convergent evolution. In short, evidence for the primitiveness of megapodes among birds as a whole is unacceptable.

Evolution of the megapode family. Megapodes are basically similar in morphological development to phasianids. Differences in the structure of natal downs, in absolute and relative sizes of eggs, in sizes of subcutaneous fat bodies, in development of the hatching apparatus, etc., are all directly or indirectly correlated with the sizes of the young at hatching.

Huxley (1868) emphasized that, in contrast to other Galliformes, megapodes and cracids are alike in depth of the sternal notches and in position of the hallux. From this anatomical basis, he postulated that these forms, isolated respectively in the Australian and Neotropical regions, are remnants of an ancestral gallinaceous stock which has been replaced through most of the Old World and Nearctic region by more modern Galliformes.

However, the differences at hatching in feather structure between cracids and megapodes support the generalization that megapodes and cracids are not especially closely related in evolution, contrary to some current classifications (e. g. Peters, 1934).

The contemporary megapodes are characterized by 1) rhachidial natal downs on the body, 2) long juvenal remiges and large body size at hatching, 3) a relatively high ratio of egg to adult weights compared with other Galliformes, and 4) the unicarotid condition; it is likely that these distinctive traits were present in a population ancestral to all living megapodes. Megapodes are apparently unique among birds in having such long and weak natal downs preceding the embryonic juvenal remiges. These weak natal downs are clearly vestiges rather than preadaptations and indicate the evolution of megapodes from unknown gallinaceous ancestors possessing a natal plumage and less precocious chicks resembling those of extant phasianids.

This phylogenetic interpretation is also supported by the finding of a vestigial egg tooth and the apparent lack of special enlargement of the complexus muscle at hatching; these features strongly indicate an evolutionary origin of megapodes from forms less precocious at hatching. One aspect of the evolution of megapodes has been the transition from the use of the egg tooth in hatching to kicking open the shell.

The variation in the number of carotid arteries in birds as a whole (Table 7) appears to be due to much convergent evolution. The most readily conceived sequence is a loss of one carotid artery (Glenny, 1955), but a possible evolutionary increase cannot be excluded. The occurrence of only one carotid in megapodes in contrast to two in all other known Galliformes suggests that megapodes are specialized in this respect.

My conclusions, based on morphology, are compatible with the concept of Mainardi and Taibel (1962: Fig. 4), based largely on erythrocyte antigens, that megapodes, cracids, and phasianids have evolved as three separate lines from unknown gallinaceous ancestors.

It is pertinent that there are living forms intermediate in structure of feathers at hatching and in precocity of young between megapodes and phasianids such as *Phasianus* or *Gallus*. For example, the phasianid genus *Tragopan* has natal downs with short rhachises (this study), relatively long juvenal remiges at hatching (Beebe, 1918), and initial flight on the third day posthatching (Nice, 1962; after the Heinroths). Although *Tragopan* probably does not represent the phylogenetic ancestors of megapodes, certain aspects of its structure and behavior of young aid in visualizing the evolutionary origin of the megapodes.

Evolution within the megapodes. *Megapodius* and *Macrocephalon* lay their eggs in holes (*Megapodius* also uses mounds) and are known to lay their eggs communally, while the four other genera use mounds exclusively as far as known. (In accord with the study of Ripley (1964) the form *Eulipoa wallacei* is here included in the genus *Megapodius*.)

The specialized *Macrocephalon* is somewhat intermediate in adult proportions of wing, tarsus, and tail between other large megapodes (4 genera) and the smaller *Megapodius* (data in Ogilvie-Grant, 1893). The relatively uniform color of *Megapodius* and its relative simplicity of nesting habits have led some authors (e. g. Becker, 1959) to consider *Megapodius* primitive among the megapodes. The uniform color pattern of *Megapodius* resembles that of *Aepypodius* or *Talegalla* and may indeed be a primitive trait among living megapodes. But simplicity of nesting site (e. g. the incubation of eggs in holes in the ground) does not necessarily imply primitiveness as illustrated by the specialized brood-parasitic avian species which also build no nests.

Since one trait of the megapodes is the relatively high ratio of egg weight to adult weight, and since megapodes have evolved from apparently more conventional gallinaceous ancestors, it is likely that, during megapode evolution, sizes of eggs increased relative to adult size. Although megapode evolution has very likely also involved an increase in the absolute size of eggs and chicks at hatching, the absolute sizes of newly hatched young do not necessarily indicate the relative primitiveness of the contemporary megapodes. Indeed, if, as seems likely, the evolution of megapodes has involved an increase in the absolute size of eggs and hence of young at hatching, then a large ancestral adult would have been better preadapted, in terms of size, than a small ancestral adult for the evolution of larger absolute sizes of eggs.

More critical features suggesting the direction of evolution within the megapodes are the proportions at hatching. In this respect *Megapodius* is more remote than *Talegalla* or *Leipoa* from the conditions in non-megapode Galliformes. In view of the relatively shorter bill and longer wing at hatching and the unusual webbing of the toes in *Megapodius*, the simplest hypothesis is that *Megapodius* has secondarily evolved from a form like *Talegalla* or *Aepypodius.* Thus *Megapodius*, perhaps most reptile-like of the megapodes in certain respects, is structurally specialized.

The small size (and relatively short culmen) of adult *Megapodius* appear to be adaptive in reducing potential ecological competition where *Megapodius* and other megapode genera occur sympatrically (Ripley, 1960). From the present study it is apparent that a shorter culmen and smaller body size at hatching also characterize *Megapodius* when compared with other megapodes.

Megapodius and *Macrocephalon* have possibly primitive characters in the occurrence of diastataxy (variable in *Megapodius*) and the tufted oil gland. Distribution of these characters in birds as a whole (Table 7) indicates that there is no necessary correlation in the presence of these features and that they have been subject to considerable convergent evolution. Despite the contention of Steiner (1918, 1956) that diastataxy is primitive because it occurs in "primitive" birds, there is no convincing evidence against the possibility that diastataxy might evolve from eutaxy (see Humphrey and Clark, 1961, for a review of the various hypotheses on the origin of diastataxy). Similarly, there is no reason to assume that a tufted oil gland is necessarily primitive.

In view of the intraspecific constancy of tarsal scutellation and its intergeneric variation in the megapodes, it appears useful in dividing the megapodes into subgroups; however, in view of the range of variation within the megapode family, it would probably be unwise to emphasize this feature in attempting to determine the affinity of megapodes with other gallinaceous families.

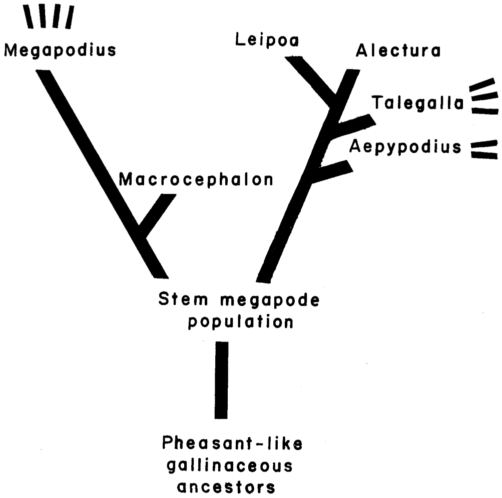

Figure 11. Provisional phylogeny of the family Megapodiidae. The smaller branches leading from the genera represent speciation.

From these considerations, the first phylogeny to cover intergeneric relationships within the megapodes has been developed (Fig. 11). The ancestral stem population (Fig. 11) would have possessed large adult and chick sizes, like *Talegalla*, rhachidial natal downs, a relatively long culmen at hatching, and egg laying in mounds. If this phylogeny is correct, then current classifications (e. g. Peters, 1934) are misleading in placing *Megapodius* first in the sequence of megapode genera.

In examining megapode development, I have found no characters indicating that megapodes are especially primitive birds; indeed, the evidence demonstrates the specialized nature of megapode ontogeny which has probably evolved from a phasianid-like condition.

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SUMMARY

Many differences found in development between megapodes and phasianids are associated with megapodes having before hatching proportional and relative growth equivalent to that occurring up to several weeks posthatching in phasianids.

Contrary to published reports, megapodes at hatching bear juvenal remiges and natal downs on the body and are thus like other Galliformes, although there are structural differences in the natal downs. Vestigial natal downs preceding the embryonic juvenal remiges indicate that megapodes evolved from forms with more conventional gallinaceous feathering at hatching and less precocious young.

This interpretation of megapodes as evolutionarily specialized is also upheld by their vestigial egg teeth and apparent lack of a special enlargement of the complexus muscle which aids in the hatching of other Galliformes.

Compared with other megapode genera and other Galliformes, young juvenile *Megapodius* have a long wing and unusually short bill. It is therefore concluded, contrary to published

reports, that, despite its apparent simplicity in color pattern and egg laying habits, *Megapodius* is specialized among megapodes.

A phylogeny of the megapode genera is proposed on the basis of proportions at hatching, tarsal scutellation, foot webbing, eutaxy, oil gland feathering, and other characters.

REFERENCES CITED

Amadon, D., 1943. Bird weights as an aid in taxonomy. Wilson Bull. **55**: 164-177.

Becker, R., 1959. Die Strukturanalyse der Gefiederfolgen von *Megapodius freyc. reinw.* und ihre Beziehung zu der Nestlingdune der Hühnervögel. Rev. suisse Zool. **66**: 411-527.

Beddard, F. E., 1898. The structure and classification of birds. Longmans, Green, London. p. xx + 1-548.

Beebe, W., 1918. A monograph of the pheasants. Vol. 1. Witherby, London. p. xlix + 1-198.

Bergmann, S., 1961. My father is a cannibal. Hale, London. 192 p.

Blaszyk, P., 1935. Untersuchungen über die Stammesgeschichte der Vogelschuppen und Federn . . . . Morph. Jahrb. **75**: 483-521.

Campbell, A. J., 1901. Nests and eggs of Australian birds. Pt. 2: 525-1102. Sheffield, England.

Clark, G. A., Jr., 1960. Notes on the embryology and evolution of the megapodes (Aves: Galliformes). Yale Peabody Mus. *Postilla* no. **45**: 1-7.

Clark, G. A., Jr., 1961. Occurrence and timing of egg teeth in birds. Wilson Bull. **73**: 268-278.

Coles, C., 1937. Some observations on the habits of the Brush Turkey (*Alectura lathami*). Proc. Zool. Soc. Lond. 107A: 261-273.

Fant, R. J., 1957. Criteria for aging pheasant embryos. J. Wildl. Mgt. **21**: 324-328.

Fisher, H. I., 1958. The "hatching muscle" in the chick. Auk **75**: 391-399.

Friedmann, H., 1931. Observations on the growth rate of the foot in the mound birds of the genus Megapodius. Proc. U. S. Nat. Mus. **80** (Art. 1): 1-4.

Frith, H. J., 1959. Breeding of the Mallee Fowl, *Leipoa ocellata* Gould (Megapodiidae). CSIRO Wildl. Res. **4**: 31-60.

Frith, H. J., 1962. The Mallee-fowl. Angus & Robertson, Sydney. p. xii + 1-136.

Glenny, F. H., 1955. Modifications of pattern in the aortic arch system of birds and their phylogenetic significance. Proc. U. S. Nat. Mus. **104**: 525-621.

Hall, R., 1901. Descriptions of the young of some Australian birds. Vict. Nat. **18**: 19-25.

Hamilton, H. L., 1952. Lillie's development of the chick. 3rd ed. Holt, New York. p. xv + 1-624.

Heinroth, O., 1922. Die Beziehungen zwischen Vogelgewicht, Eigewicht, Gelegegewicht und Brutdauer. J. f. Orn. **70**: 172-285.

Heinroth, O., 1931. Beobachtungen bei der Aufzucht eines Knopfschnable-Hokko's (*Crax globicera*) und eines Mitu's (*Mitua mitu*). J. f. Orn. **79**: 278-283.

Heinroth, O. and M. Heinroth, 1928. Die Vögel Mitteleuropas. Bd. 3. Bermühler, Berlin. p. x + 1-286.

Huggins, R. A., 1941. Egg temperatures of wild birds under natural conditions. Ecology **22**: 148-157.

Humphrey, P. S., and G. A. Clark, Jr., 1961. Pterylosis of the Mallard duck. Condor **63**: 365-385.

Huxley, T. H., 1868. On the classification and distribution of the Alectoromorphae and Heteromorphae. Proc. Zool. Soc. Lond., 294-319.

Lyon, D. L., 1962. Comparative growth and plumage development in *Coturnix* and Bobwhite. Wilson Bull. **74**: 5-27.

Mainardi, D., and A. M. Taibel, 1962. Studio immunogenetico sulle parentele filogenetiche nell'ordine dei Galliformi. Inst. Lombardo, Rend. Sc., B **96**: 131-140.

Meyer, O., and E. Stresemann, 1928. Zur Kenntnis der Entwicklung von *Megapodius* und *Oxyura* im Ei. Orn. Monatsber. **36**: 65-71.

Miller, W. DeW., 1924. Further notes on ptilosis. Bull. Am. Mus. Nat. Hist. **50**: 305-331.

Nice, M. M., 1962. Development of behavior in precocial birds. Trans. Linn. Soc. N. Y. **8**: xii + 1-211.

Ogilvie-Grant, W. R., 1893. Catalogue of the game birds . . . of the British Museum. p. 445-472.

Padgett, C. S., and W. D. Ivey, 1960. The normal embryology of the Coturnix Quail. Anat. Record **137**: 1-11.

Peters, J. L., 1934. Check-list of the birds of world. Vol. 2. Harvard Univ. Press, Cambridge, Mass. p. xvii + 1-401.

Portmann, A., 1938. Beiträge zur Kenntnis der postembryonalen Entwicklung der Vögel. Rev. suisse Zool. **45**: 273-348.

Portmann, A., 1950. Le développement postembryonaire. p. 521-535; *in*: Grassé, P.-P. (ed.) Traité de Zoologie, Tome **XV**, Oiseaux.

Portmann, A., 1955. Die postembryonale Entwicklung der Vögel als Evolutionsproblem. Acta XI Congr. Internat. Orn., Basel **1954**: 138-151.

Pycraft, W. P., 1900. A contribution towards our knowledge of the pterylography of the megapodii. p. 483-492; *in*: A. Willey (ed.) Zoological results . . . New Britain . . . Part IV. Cambridge at Univ. Press.

Pycraft, W. P., 1910. A history of birds. Methuen, London. p. xxxi + 1-458.

Ripley, S. D., 1960. Distribution and niche differentiation in species of megapodes in the Moluccas and Western Papuan area. Proc. 12th Internatl. Orn. Congr., Helsinki **1958**: 631-640.

Ripley, S. D., 1964. A systematic and ecological study of birds of New Guinea. Yale Peabody Mus. Bull. no. **19**: 87 p.

Romanoff, A. L., 1960. The avian embryo. Macmillan, New York. p. xvi + 1-1305.

Schmalhausen, I., 1926. Studien über Wachstum und Differenzierung. III. Die embryonale Wachstumskurve des Hühnchens. Roux' Archiv **108**: 322-387.

Simpson, G. G., A. Roe, and R. C. Lewontin, 1960. Quantitative zoology. Rev. ed. Harcourt, Brace, New York. p. vii + 1-440.

Slobodkin, L. B., 1962. Energy in animal ecology. p. 69-101; *in*: J. B. Cragg (ed.) Advances in ecological research. Vol. 1.

Steiner, H., 1918. Das Problem der Diastataxie des Vogelflügels. Jena. Z., N. F. **48**: 221-496.

Steiner, H., 1956. Die taxonomische und phylogenetische Bedeutung der Diastataxie des Vogelflügels. J. f. Orn. **97**: 1-20.

Studer, T., 1878. Beiträge zur Entwicklungsgeschichte der Feder. Z. f. wiss. Zool. **31**: 421-436.

Verheyen, R., 1956. Contribution à l'anatomie et à la systematique des Galliformes. Inst. Roy. Sci. Nat. Belgique 32 (**42**): 1-24.

Watson, G. E., 1963. Feather replacement in birds. Science **139**: 50-51.

Westerskov, K., 1957. Growth and moult of pheasant chicks. New Zealand Dept. Int. Aff. Wildl. Publ. **47**: 1-64.