UNIVERSITY OF UTAH BIOLOGICAL SERIES

Vol. XIII December 3, 1965 No. 2

The Embryonic Development of the California Gull (*Larus californicus*)

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Published by

THE UNIVERSITY OF UTAH
SALT LAKE CITY

UNIVERSITY OF UTAH BIOLOGICAL SERIES

Editors: WILLIAM H. BEHLE, *Chairman;* GEORGE F. EDMUNDS, SEVILLE FLOWERS

Volume 13, No. 2, 26 pp., 8 pls.

Submitted by editors — July 25, 1965
Issued — December 3, 1965
Price — $2.00

UNIVERSITY OF UTAH PRESS

INTRODUCTION

The California gull (*Larus californicus*) is a summer resident in Utah nesting commonly on certain islands in Great Salt Lake as well as at man-made refuges on the east side of the lake. Many aspects of the biology of the species have been investigated (Beck, 1942; Behle, 1958; Behle and Goates, 1957; Behle and Woodbury, 1952; Greenhalgh, 1952; Johnston, 1956; Odin, 1957; Woodbury, Behle and Sugden, 1946) and it seemed that an opportunity was presented to study yet another feature, namely, the early embryonic development. This conviction was strengthened when it was noted in Romanoff's (1960) extensive work on the avian embryo that whereas there is mention of embryological studies on some species of gulls of the genus *Larus*, the California gull was not included. Furthermore, no study of the gross external anatomy of any gull seemed to have been made; rather the studies had been histological investigations of the internal anatomy. Accordingly it was decided to study initially the gross development of the species and compare the gull with the chick, which has long been the basis for laboratory study of avian development. It is hoped that subsequent studies may be forthcoming on the ontogeny of organ systems. The precise purpose of the present study then was to determine when and in what manner the external developmental changes appear in the California gull embryo and to correlate the various stages in structural development with those occurring in the embryo of the chick. In other words, the study involved the progressive external changes in body contour and size, development of limbs, beak, feathers, pigmentation and lesser structural differences peculiar to the species.

For background, the following résumé of the breeding biology of the California gull is given for the species in the Great Salt Lake region. Individuals start arriving in the region from their wintering grounds in late February and early March and soon thereafter undergo the prenesting behavior and establishment of nesting sites on suitable islands in the lake and on islands and dikes in the refuges. Eggs appear from mid- to late April depending on the season. The clutch usually numbers three. The eggs have a grey-brown ground color and are speckled and mottled with both deep and superficial blotches of brown. They vary somewhat in shape but are generally ovate, with one end broad where the air pocket is located, while the other is tapering. As determined by Behle and Goates (*op. cit.*) the average weight is 72.2 grams and the dimensions average 66.4 mm. in length and 46.3 mm. in width. Incubation begins after the second egg is laid and before the third is deposited. Hence the first and second eggs usually hatch on the same day while the third egg does so about two days later. The average incubation time for the species is 25.1 days. The young are precocial and are completely covered with down feathers when they hatch. The weight at hatching varies from 40 to 50 gm. and their length from 5¼ to 5½ in.

MATERIALS AND METHODS

Eggs and embryos were collected from colonies at the Utah State Fish and Game Department's Farmington Bay Waterfowl Management Area which is located about 12 to 15 miles north of Salt Lake City on the east side of Great Salt Lake. This was done through the courtesy of Reuben H. Dietz, refuge manager. The initial material was collected as early as 1950. The embryos were fixed in Bouin's solution and transferred to 70% ethyl alcohol. They were entirely suitable several years later when the present study commenced in the early spring of 1963. However, embryos representing the last half of the incubation period were lacking in the 1950 lot. During the nesting season of 1963, fresh eggs were collected and brought into the laboratory for incubation. The incubator was adjusted to 37.5° which was considered by Romanoff (*op. cit.*: 197) to be the optimum temperature for incubation of *Gallus gallus* eggs. Efforts

were made to control the humidity. Hamilton (1952: 75–76) noted that temperatures below or above the optimum will retard or accelerate the rate of development respectively of the chick embryos, especially during the early developmental stages, although the embryo gradually develops a homeothermic mechanism which makes it independent, within narrow limits, of the environmental temperature. Hamilton (*loc. cit.*) also states that there are certain periods in the incubation of chicken eggs when the mortality rate rises if the relative humidity in the incubator increases too far above the optimum of 60–65 per cent. Seemingly there are similar effects on California gulls' eggs for our incubation results were not entirely successful, but whether this was due to temperature, humidity, or other factors was not determined. Consequently in 1964 we planned to mark nests in the field and collect eggs at intervals of known age. It became apparent, however, that even with "fresh" eggs there had been some development. There was no ready way of determining how far gull incubation had advanced before the eggs were gathered in the field. Then in the midst of our effort to obtain unincubated eggs a program was instituted on the refuge to discourage gulls' nesting there because of their depredations on eggs and young waterfowl. As a consequence, the colonies were drastically disturbed. Somewhat in desperation, therefore, we gathered two buckets full of gull eggs at random, representing all stages of development.

The subsequent grouping of the successive stages in the development of the gull embryo was set up in a manner similar to that used by Hamilton (*op. cit.*: 78–91) for the chick, following which successive stages of development were adjusted to the longer 25-day incubation period of the gull. It was necessary to bring the embryos of the two kinds of birds into a parallel series of developmental stages so as to facilitate the comparison between them. Thus the chronological order for the gull embryos was finally determined by simply comparing them with the previously established stages of chick development (based on external morphological characters and independent of chronological age), while the time spacings of the longer incubation period of the gull were based on the closest estimations that could be made.

The initial stages in the ontogeny of the blastula were not available because of difficulties in obtaining eggs at this stage. However, after examining slightly later stages which were available, it seems very doubtful if the start of the development up to and including the blastula would show any features contrasting with those of the chick at comparable stages.

The developmental stages of the California gull are depicted in 22 figures on eight plates prepared by Mrs. Dawkins. Notes on the various stages follow from the 15–20–hour embryo through the 25–day embryo at which time the individual would normally be ready for hatching.

DESCRIPTION OF THE GULL DEVELOPMENT

Fifteen to Twenty-Hour Embryo

Plate I, Fig. 1

Comparable to Stage 4 or 18–19 hours in the chick.*

One specimen was examined that approximated this stage. The *area pellucida* is roughly oval; tissue shrinkage caused by fixation has probably destroyed the symmetry. The *primitive streak* extends for almost the entire length of the *area pellucida.* The *primitive groove* and the *primitive pit* are evident, and *Hensen's node* is present as a small nodule of cells. Around this interior region, the *neural plate* appears to be thickening.

Eighteen to Twenty-two-Hour Embryo

Plate I, Fig. 2

Comparable to Stage 5 or 19–22 hours in the chick.

One specimen was examined showing the swelling and condensation of tissue in the *head* region, just anterior to *Hensen's node.* The *area pellucida* appears rough and opaque from fixation. The *neural groove* is the most outstanding structure.

Twenty-two to Twenty-six-Hour Embryo

Specimens comparable to Stages 6 and 7 of Hamilton's sequence were not obtained. These are still within the first day and a half of incubation, leading up to and demonstrating the formation of the first *somite.*

Twenty-six to Twenty-eight-Hour Embryo

Plate I, Fig. 3

Comparable to Stage 8 or 26–29 hours in the chick.

In the one specimen examined three *somites* are clearly defined with evidence of the fourth one in early formation. Anteriorly, the *neural fold* is marked, yet not quite meeting in the mid-dorsal region. The *head fold* had raised the anterior portion of the embryo, but had not yet reached the level of the *mid-brain* region. The *neural groove* is evident for most of the length, except in the region just anterior to the diminishing *primitive streak.* The length of the specimen, including the *primitive streak,* is 3.1 mm. The *area pellucida* was intact and pear-shaped, with the wider portion at the anterior end of the embryo.

Twenty-eight to Thirty-Hour Embryo

Plate I, Fig. 4

Comparable to Stage 9 or 29–33 hours in the chick.

Two specimens closely approaching early Stage 9 of Hamilton were observed. In these, the *neural groove* extends most of the length of the embryo, widening in the midsection and coming together as a point posteriorly. The *primitive streak* is evident posteriorly to this. The *primary optic* vesicles are now present as a slight bowing at the sides of the fore-brain. There is still a fissure between the two joining halves of the *fore-brain.* The *heart* primordia appears as a dense mass on the ventral side of the embryo. The total length of the specimens averages 2.8 mm., not including the primitive streak. Six *somites* and evidence of the seventh one appear at this stage.

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*Hamilton, 1952: 78–91.

THIRTY TO THIRTY-FIVE-HOUR EMBRYO

Plate II, Fig. 1

Comparable to Stage 10 or 33–38 hours in the chick.

Two specimens at this stage show a slight constriction of the optic vesicles. The three primary brain regions are distinguishable: *prosencephalon (fore-brain)*, *mesencephalon (mid-brain)*, and *rhombencephalon (hind-brain)* and, according to Hamilton, the first four *somites* are considered cephalic, thus marking the end of cranial and the beginning of spinal sections. The *omphalo-mesenteric veins* have thickened. One specimen showed the first evidence of *cranial flexure*, with the *head* bending ventrad. The average total length of the specimens was 3.8 mm., and there were ten and one-half to eleven *somites*.

THIRTY-FIVE TO FORTY-HOUR EMBRYO

Comparable to Stage 11 or 40–45 hours in the chick.

One specimen at about this stage shows an evident *cranial flexure*. The *neural groove* is almost completely closed, and the *primitive streak* is disappearing. The *optic vesicles* show a more noticeable bulge. The embryo now shows twelve *somites* clearly and the total body length measures 4.3 mm. At this stage, the total body length is now losing diagnostic value because of the varying degree of cranial flexure.

FORTY TO FORTY-FIVE-HOUR EMBRYO

Plate II, Fig. 2

Comparable to Stage 12 or 45–49 hours in the chick.

Five specimens were studied showing varying degrees of development at this stage. The *cranial flexure* begins to turn laterally which will eventually cause the embryo to lie on its left side. The *primitive streak* is gone and the *primitive groove* remains only as a *primitive tube opening*. There is now a very clear demarcation of the *telencephalon*, foremost portion of the *prosencephalon*. The *auditory pit* is a deep, wide opening. The *optic stalk* begins to appear as a slight constriction proximal to the *optic vesicle*. The fold of the *amnion* is beginning to cover the *fore-brain* region. The somites are now difficult to count because of the increasing density of the embryo; also, the Bouin's fixative renders these thicker specimens opaque. The average body length was 4.4 mm. and the *somites* numbered from thirteen and one-half to fifteen. The length of the embryos in these stages varies greatly, due to a slight difference in degree of flexure. Even though the somite count might more closely approximate Stage 11, there are numerous other features exhibited in the specimens which are not scheduled to appear in the previous stage of the chick.

FORTY-FIVE TO FORTY-EIGHT-HOUR EMBRYO

Plate II, Fig. 3

Comparable to Stage 13 or 48–52 hours in the chick.

Two specimens showed very broad *cranial* and *cervical flexures*. In one embryo the *head* is partly turned on the left side, while in the other one there is a bit more rotation and flexure. The *telencephalon* has enlarged. Only the right *auditory vesicle* shows since the head is turning on its left side. The specimens averaged a total body length of 5.1 mm.

Forty-eight to Fifty-two-Hour Embryo

Plate II, Fig. 4

Comparable to Stage 14 or 50–53 hours in the chick.

Four specimens, ranging from early to full development of this stage, show the *telencephalon* and *mesencephalon* considerably enlarged, while the *cranial flexure* is more marked, with an obtuse to right angle forming between the axis of *fore-brain* and *hind-brain*. Early evidence of the *lens placode* appears as a large circular bulge in the region of the *optic vesicle*. The first *visceral arch* and *cleft* show as a slight bulge and line near the *auditory cup*. *Trunk flexure* and *rotation* are evident. *Tail flexure* is appearing as a slight ventrad turning. The fold of the *amnion* has passed the entire head region and is just past the posterior margin of the *heart*.

Fifty to Fifty-four-Hour Embryo

Comparable to Stage 15 or 50–55 hours in the chick.

In three specimens the *cranial flexure* begins to turn the *head* caudad. The axis of the *fore-brain* and *hind-brain* forms a right angle. The *cervical flexure* assumes a broad curve. The *optic cup* has formed and a large concentric circular bulge is shown in the *iris* region. *Visceral arch 1* and *cleft 1* are evident, and the region where *arch 2* will develop is raised. Up to and including this stage, the development of the arches lags slightly behind that of the chick; now that they are clearly demarcated, the subsequent stages show just the opposite condition. The *body rotation* extends approximately half the total length of the embryo. The prospective *limb areas* are still flat. The fold of the *amnion* now extends more than half the total body length. Posteriorly, the *neural groove* is still noticeable.

Fifty-four to Sixty-Hour Embryo

Comparable to Stage 16 or *ca.* 51–56 hours in the chick.

In four specimens at this stage the *fore-brain* has lengthened and there is a deepening constriction between *mid-brain* and *hind-brain*. There is a noticeable pit in the central *pupillary area* of the *eye*, giving it the appearance of two concentric circles. *Visceral arches 1, 2,* and *3* are noticeable and *clefts 1* and *2* are distinct. Arch 2 is the largest and thickest. There is the slightest indication of a thickening ridge in the area of the *lateral body fold* where the wing bud will develop. In the leg area there is very little thickening in the lateral body fold. The fold of the *amnion* now extends two-thirds to three-fourths of the total body length. The *tail bud* is lifting.

Sixty to Sixty-five-Hour Embryo

Plate III, Fig. 1

Comparable to Stage 17 or *ca.* 52–64 hours in the chick.

Nine specimens at this stage show a more accentuated *cervical flexure* which forms an acute angle. The *nasal pits* are evident as slits in the earlier specimens and as rounded depressions in the full-stage specimens. *Visceral arch 2* has elongated considerably, *cleft 3* is now clear, and in the full-stage specimens *visceral arch 4* is just appearing. In the present specimens the formation of the visceral arch and cleft seems a bit more precocious than that exhibited by the chick at this stage and subsequent stages according to Hamilton's descriptions. The *optic cup* appears as a decided bulge, and the *lens* is now set in. The

trunk flexure has reached the level of the wing buds, and the extreme posterior portion of the body is still in the horizontal plane. In two of the earliest specimens, the thickening wing buds show no raised body folds, but in the full-stage embryos both *wing buds* and *leg buds* appear as decided bulges. Posteriorly, the *tail bud* is bent ventrad, and the *amnionic fold* is nearly closed dorsally.

Sixty-five to Seventy-Hour Embryo

Comparable to Stage 18 or *ca.* 3 days in the chick.

In ten specimens *visceral arch 4* is clearly evident and *cleft 4* shows as a small opening. The *nasal pits* are now enlarged openings. The *epiphysis* is now marked as a small protrusion. The *wing* and *leg buds* are enlarging, with the former showing a bit more progress with a slight folding over the body surface. The embryo has now turned onto its left side down to the level of the leg buds, with the *tail bud* still facing predominantly ventrad.

Three to Three-and-One-Half-Day Embryo

Comparable to Stage 19 or *ca.* 3 to 3½ days in the chick.

In fourteen specimens the flexure of the entire embryo is more acute than in the previous stage. The *cranial* and *cervical flexures* form a sharp angle. *Visceral arches* and *clefts 1* through *4* are all clearly marked. *Visceral arch 2* is the most conspicuous as it projects over the surface. The *maxillary process* is now evident and is elongating in the later specimens. The *epiphysis* still shows as a distinct knob. The limb buds have increased in size, with the *wing bud* showing a bit more bulk. This is one growth aspect in the gull embryo that differs from the chick. Hamilton states that the leg bud appears slightly larger at this and subsequent stages in the chick embryo. A possible explanation of the precocious enlargement of the wing bud in the gull lies in the fact that a sedentary bird is being compared with one that has strongly developed wings. In most cases, *body rotation* is almost complete. The *allantois* now appears as a small sac.

Three-and-One-Half-Day Embryo

Plate III, Fig. 2

Comparable to Stage 20 or *ca.* 3 to 3½ days in the chick.

Seven specimens of this stage showed conspicuous *nasal pits*. The *maxillary process* is equal to or slightly longer than the *mandibular process*. The *wing bud* and *leg bud* are about equal in bulk although the former appears longer. The embryo is now completely turned on its left side. The *trunk* forms a very broad curve, and the *tail bud* is curled anteriorly. The *allantois sac* is now equal to the mesencephalon in size. Hamilton states that eye pigment is faintly visible in the chick at this stage, but it was undetected in the gull.

Three-and-One-Half to Four-Day Embryo

Comparable to Stage 21 or *ca.* 3½ days in the chick.

In four specimens the *mesencephalon* is more noticeably bulged and the *isthmus* between it and the *metencephalon* is more pronounced. Unlike the chick at this stage, the eye pigmentation is still not evident, but the other structures are clearly outlined. The *maxillary process* is longer than the *mandible*. *Visceral arch 2* is enlarging posteriorly over *arches 3* and *4*. The *wing bud* still appears slightly larger than the *leg bud*; in general they appear about

as long as they are wide. The *allantois* has enlarged and become vesicular; hereafter it has been destroyed with the fixation of the specimen. At this stage the average length of the body was 7.0 mm., and the average length of the head 3.7 mm. The latter measurement proved to be more significant because of the different degrees of body flexure. The head was measured from the bulging mesencephalon to the foremost portion of the enlarging telencephalon.

Four-Day Embryo

Plate III, Fig. 3

Comparable to Stage 22 or *ca.* 3½ to 4 days in the chick.

In five specimens of this stage the *visceral arch 2* is beginning to form a "collar" as it continues to overlap *arches 3* and *4*. The *heart*, as in the previous stages, causes a large irregularly-shaped protrusion from the ventral body wall. The *limb buds* are slightly longer than those in the previous stage, about equal in size, and now point caudad. The average body length was 7.1 mm. and the head length 4.1 mm. Hereafter, the total body length will be omitted as it becomes too variable within the same stage.

Four to Four-and-One-half-Day Embryo

Comparable to Stage 23 or *ca.* 4 days in the chick.

In four specimens the *visceral arches 3* and *4* are obscured by the formation of the *collar*. The *maxillary process* is half again as long as the *mandibular process*. The *eye pigment* becomes barely perceptible in the advanced embryos. It could not be determined whether the formation of pigment appears later in the gull than in the chick, or whether its absence at this stage might be due to bleaching by the Bouin's fixative. The Gilson's fixative that was used on later stages permitted a clear display of eye coloring, and in the earliest specimens that were prepared with this fixative, the pigment was not distinctly outlined until Stage 25. From the present evidence, it appears that pigment does form later in the gull. Both *wing* and *leg* buds are distinctly longer than wide, and both point caudad. At this stage, the length of the limbs, from the proximal to distal ends, and the width were measured. Plate IV Fig. 3 shows these features. The average length of the wings was 1.7 mm. and the average width 1.3 mm. The average length of the legs was 1.7 mm. and the average width 1.4 mm. The average head length was 4.5 mm.

Five-Day Embryo

Comparable to Stage 24 or *ca.* 4½ days in the chick.

In seven specimens at this stage *visceral arch 3* becomes totally obscured by the folding of the *collar*, and *cleft 4* shows as a deep pit. The *maxillary process* has elongated almost to the anterior margin of the eye. *Eye pigmentation* becomes faintly evident. There is a slight dilation of the distal portion of the *wing*, and a slight protrusion suggests the point where the *elbow joint* will form. The average wing length is 2.0 mm. and the width 1.3 mm. The average leg length is 1.7 mm. and the average leg width is 1.3 mm. The average head length is 5.0 mm. In this stage the gull shows another difference from the chick. According to Hamilton, the leg bud shows the first evidence of the toe plate, a feature not shown by the gull at this time.

Five to Five-and-One-half-Day Embryo

Plate III, Fig. 4

Comparable to Stage 25 or *ca.* 4½ to 5 days in the chick.

Nine specimens showed the closing of *visceral cleft 1* had left a slit. According to Hamilton this condition first appears in Stage 27 in the chick. The *collar* is lifting and enlarging but has not yet completely covered *arch 4*. The *eye pigment* is still quite faint, but it is spreading outwardly from the inner *iris* area. This condition certainly seems more retarded in the gull than in the chick. Both limb tips are broadening into the *digital* and the *tarsal plates*, and the *elbow* and *knee* joint areas are prominent. The average wing length is 2.5 mm. and the width 1.3 mm. The average leg length is 2.3 mm. and the width 1.4 mm. The average head length is 5.4 mm.

Six-Day Embryo

Comparable to Stage 26 or *ca.* 5 days in the chick.

Seventeen specimens at this stage showed that the *collar* formed from *visceral arch 2* had obscured *arch 4*. The *pigmentation* in the *eye* is now marked. The *wing* continues to appear longer than the *leg*. There is a faint demarcation on the *tarsal plate* where the *third toe* is enlarging. No digits are clearly evident, but the *elbow* is more noticeably bent than the *knee* joint. The more advanced embryos show both knee and elbow joints distinctly bent. With the bending of the limbs, the length can no longer be accurately measured. The changes now beginning to take place in the shape of the limbs are good diagnostic features. The protuberance caused by the *heart* is smoothing down.

Six-and-One-half to Seven-Day Embryo

Comparable to Stage 27 or *ca.* 5 to 5½ days in the chick.

In fourteen specimens, the *mesencephalon* is still a distinct bulge. *Visceral cleft 1* shows a series of prominences with a slit for the *external auditory meatus*. The *collar* has become smaller and the *beak* is just barely recognizable. *Eye pigment* is very marked. The *leg* is thicker but not longer than the *wing*. The *digital plate* has become angular in the region of the *first digit*. The chick shows more detail at this stage, with grooves indicated between the three digits. The fanning of the tarsal plate in the gull now shows slight demarcations where the *three toes* are forming.

Seven to Seven-and-One-half-Day Embryo

Plate IV, Fig. 1

Comparable to Stage 28 or *ca.* 5½ to 6 days in the chick.

In twenty-two specimens the *telencephalon* has become smoother so that it does not dominate the facial profile. This makes the *beak* more noticeable. The *lens* area stands out distinctly as it is surrounded by the large, darkening *iris*. The *mandible* is thickening and continues to lengthen. Several of the prominences are still noticeable on *visceral cleft 1*, but they are smoothing, so that only the *auditory pit* is clearly defined. The *collar* is flattening and the distance between it and the mandible is gradually increasing. On the *wing* the *second digit* is noticeably the longest, and the *elbow* is sharply bent. The *third toe* shows a *webbing* effect on each side. Posteriorly, the *tail* is curled cephalad and is thin and tapered.

Seven-and-One-Half to Eight-Day Embryo

Comparable to Stage 29 or *ca.* 6 to 6½ days in the chick.

In nineteen specimens the *nictitating membrane* is in view as a small crescent in the anterior corner of the *eye*. Hamilton notes that this structure does not differentiate until the seventh day for the chick. *Visceral cleft 1* is closed except for the *auditory slit*, and now the lengthening *mandible* is broadly fused with *arch 2*. The *collar* is still evident, but the rest of the *neck* is smooth and elongated to make it appear as a distinct structure. The *beak* has lengthened. The *thigh* and *upper wing* areas are thickening. Three *digits* are now distinct and the second is the longest. The second, third, and fourth *toes* show as definite ridges with *webbing* in between. Hamilton mentions the transitory appearance of the rudimentary fifth toe in the chick; this was not detected in the gull.

Eight-Day Embryo

Plate IV, Fig. 2

Comparable to Stage 30 or *ca.* 6½ to 7 days in the chick.

In nine specimens *scleral papillae* have appeared on the surface of the *iris* and they range in number from one to three. Hamilton states that there are never more than two papillae present in the chick at this stage. Four gull embryos showed three papillae and were classed as late examples of this stage because the gull normally has two more papillae than the chick. The *collar* is greatly flattened and inconspicuous. The profile of the embryo becomes more "birdlike," since the *mesencephalon* no longer looks inflated and the neck is lengthening. Three limb regions are demarcated on both the *wing* and the *leg*. Hamilton's description of the chick at this stage includes the appearance of the egg tooth and feather germs; these two characters are not evident until later in the gull.

Eight-and-One-Half-Day Embryo

Comparable to Stage 31 or *ca.* 7 to 7½ days in the chick.

At this stage four specimens showed four to six *scleral papillae* on the *iris*. The *mandible* and *maxilla* are unequal in length, with a gap between the *beak* and the mandible. The *collar* is gone, so the elongating *neck* appears smooth. According to Hamilton's description of the chick, the collar may still be inconspicuous or absent at this stage. On the *wing*, the *first digit* is just beginning to stand out separately. Along the outside of the *tail*, there is a continuous ridge which will differentiate into feather papillae in the next stage.

Nine-Day Embryo

Plate V, Fig. 1

Comparable to Stage 32 or *ca.* 7½ days in the chick.

One of the two embryos exhibited eight *scleral papillae*, which is comparable to the number found in the chick. The other specimen had eleven papillae and represented late-stage development. The *mandible* and *maxilla* (beak) continue to elongate and taper at the tip. The *auditory pit* is still a clear opening. The *webbing* between the *digits* (first, second, and third) and the *toes* (first, second, third, and fourth) is becoming thinner. *Feather primordia* are beginning to appear as tiny papillae along special *tracts* (pterylae). One or two rows are seen along the edge of the *tail*, forming the *caudal tract*. Two

other rows are faintly visible on each side of the mid-dorsal area, between the limb regions; these constitute the *spinal tract*. The appearance of the feather germs in the gull definitely lags behind the chick in regard to this feature. Hamilton first mentions the appearance of feather germs in the chick at Stage 30, at which time they appear as two to three rows on each side of the dorsal region and at Stage 31 the femoral tract and the caudal tract appear. In the gull, feather papillae appear first along the caudal tract.

Ten-Day Embryo

Comparable to Stage 33 or *ca.* 7½ to 8 days in the chick.

In three specimens a scleral ring of twelve to thirteen *scleral papillae* now forms on the *eye*. The *nictitating membrane* enlarges at this stage. The *mesencephalon* bulge has greatly diminished and the lengthening *neck* has straightened, while the *mandible* and *maxilla* meet at the tip. There is a right-angle flexure of the *wing*. The *feather tracts* showed the following arrangement: three rows on each side of the *spinal tract*; two rows on the *caudal tract* with the outermost row the more advanced; and several very faint rows just visible on the *femoral tract*. Hamilton mentions the webbing on the radial margin of the wing as being noticeable now in the chick. It has not yet differentiated in the gull.

Ten-and-One-Half to Eleven-Day Embryo

Plate V, Fig. 2

Comparable to Stage 34 or *ca.* 8½ to 9 days in the chick.

In seven specimens fifteen to sixteen *scleral papillae* develop on the *eye*, which is the full number in the gull. Hamilton states that the full number attained in the chick is fourteen. At the tip of the beak, the maxilla slightly overlaps the mandible. For the first time there is evidence of the *egg tooth* on the maxilla. Hamilton mentions this structure appearing in Stage 30 in the chick, but it has not been noticed until this stage in the gull. The *feather tracts* show the following changes: numerous rows extending most of the length of the *spinal tract*; numerous rows on the *femoral tract*; several faint rows on the *humeral tract*; and (on one specimen) one row of feather papillae just perceptible on the upper eyeball region, the *capital tract*.

Eleven-and-One-Half to Twelve-Day Embryo

Comparable to Stage 35 or *ca.* 8½ to 9 days in the chick.

The *beak* continues to lengthen with the ten specimens studied for this stage. Beginning with this stage and continuing until the time of hatching, the beak was measured from the proximal border of the nostril to the tip, and the average length for the gull embryo at this stage was 1.9 mm. The *nictitating membrane* touches the outer rim of the *scleral papillae*. The *eyelids* are developing over the eyeball so that the lower papillae are covered. The feather tracts show the following advances: the *capital tract* now has from three to four rows of feather papillae above the eye; and two broken rows of papillae are just barely noticeable on both sides of the *ventral tract*, starting together from the sternal region and separating laterally around the *umbilical cord*. The *digits* and *toes* show marked elongation over previous stages. Unlike the changes in the chick, the *webbing* between the toes has not diminished. This can be understood, since the adult gulls retain this condition.

Twelve-and-One-Half to Thirteen-Day Embryo

Plate VI, Fig. 1

Comparable to Stage 36 or *ca.* 10 days in the chick.

In eleven specimens the *egg tooth* begins to whiten, showing the onset of cornification. The average distance from the *nostril* to the *beak* tip is 2.5 mm. The *maxilla* is now conspicuously hooked over the *mandible* and the beak has a decided gull-like appearance. The primordia of *claws* have just begun to appear on the *toes*. The feather tracts show the following changes: the *capital tract* consists of continuous rows from above the eye to the midline; the *alar tract* now appears with rows of feather papillae in the *web* of the *wing* and along the ulnar edge of the fore-wing (flight feathers); scattered feather papillae are now evident in the fibular-tibia region of the *crural tract*; the *ventral tract* has separated into four rows with two rows on each side of the midline. Hamilton does not mention this detail in the chick, so it may be a difference in the plumage pattern between these two species. One other feature that has shown itself at this stage in the gull, and was not mentioned by Hamilton in the chick descriptions, is the appearance of *black pigmentation* in the *feathers*. These first show as small scattered patches of color on the lower *spinal tract*.

Thirteen-and-One-Half to Fourteen-Day Embryo

Comparable to Stage 37 or *ca.* 11 days in the chick.

In seven specimens the beak measurement averaged 3.1 mm. Along the edges of the *beak* the *labial groove* is forming. The *eyelids* have now completely covered all the scleral papillae. On the *foot*, the *planter pads* have just become evident. The *feather tracts* have filled in considerably by now, and the dorsal patches of *pigment* are increasing. The last area to develop feather primordia is the region starting under and around the beak and extending laterally to encircle the *auditory opennig*.

Fifteen-Day Embryo

Plate VI, Fig. 2

Comparable to Stage 38 or *ca.* 12 days in the chick.

Five specimens were examined. Since the previous stage, the *beak* has thickened at the base and the average length is 3.5 mm. Now the *labial groove* is marked. The *auditory opening* is completely surrounded by a fine *feather tract*, and it has started to constrict. More feathers have gained *pigmentation* so that patches are scattered on the entire *back*, the upper *thigh*, the back of the *neck*, and the top of the *head*. *Scalation* has appeared on the superior surface of the tarsometatarsus; the inferior surface is smooth. The development of this character in the chick was first mentioned by Hamilton in the previous stage. Beginning with this stage and continuing through the remainder of the incubation period, the *third toe* was measured from the tip to its union with the tarsometatarsus. At this stage the average is 8.6 mm.

Sixteen-Day Embryo

Comparable to Stage 39 or *ca.* 13 days in the chick.

In one specimen the *eye* opening has become greatly reduced; the lower *lid* now covers the entire lower half of the *cornea* and only the upper anterior quadrant of the cornea is visible. The deepening *auditory opening* is reduced

and slightly sunken. The *beak* is 3.8 mm. long, and continues to thicken noticeably at the base, while the entire distal portion is heavily cornified. The *feathers* all over the body have tapered and lengthened (e.g., those from the mid-dorsal area are 4.8–5.0 mm. long). The regions of the body that are not covered with feather tracts (*apteria*) show minute papillary structures. The *scalation* on the superior surface of the *tarsometatarsus*, shown now as faint ridges across the surface, has not advanced much since the previous stage. The length of the *third toe* is 8.8 mm. and the *plantar pads* have begun to thicken.

Seventeen-Day Embryo

Plate VII, Fig. 1

Comparable to Stage 40 or *ca.* 14 days in the chick.

From this stage until hatching, Hamilton has based the age of the embryo on measurements of the beak tip and the length of the third toe, since other external features have lost their diagnostic value. He considers the length of the beak tip to be the more accurate and less variable. In the present account of the gull any other features that may help in identifying the age of the gull embryo will be cited.

In three specimens the *eyelids* have formed a narrow slit across the *eye*. There is dark *pigmentation* in the *labial groove areas* and in the upper midline section of the *beak*. The distance from the nostril to the beak tip averages 4.4 mm. The *egg tooth* has formed a large raised point. *Scalation* has become distinct on the superior and inferior surfaces of the *tarsometatarsus* and the *foot*, and the claws seem completely cornified. The plantar surface of the *toes* is covered with well-developed *pads*. The average length of the *third toe* is 9.8 mm.

Eighteen-Day Embryo

Comparable to Stage 41 or *ca.* 15 days in the chick.

In four specimens the dark *pigmentation* has spread on the *beak*. The tip of the *mandible* has become bulb-shaped on the bottom. The average length of the beak tip is 5.3 mm., and the *labial groove* is diminishing so that it is evident only on the proximal half of the beak edges. The canal of the *auditory opening* is hardly discernible, due to the growing *feathers*. The *foot* and *tarsometatarsus* show heavy raised *scalation* over their entire surface. The length of the *third toe* averaged 10.4 mm.

Nineteen to Twenty-Day Embryo

Plate VII, Fig. 2

Comparable to Stage 42 or *ca.* 16 days in the chick.

Three specimens showed considerable increase in bulk-size over the previous stage. The *beak* has become greatly thickened throughout, with an average tip length of 5.8 mm. The *claws* of the *toes* are noticeably longer; the proximal portion (of the third toe in particular) shows striking *pigmentation*. The average length of the *third toe* is 12.1 mm.

Twenty to Twenty-One-Day Embryo

Comparable to Stage 43 or *ca.* 17 days in the chick.

In three specimens the *beak* tip is 6.6 mm. long and black *pigmentation* in the beak continues to spread. The *tarsometatarsus* has thickened noticeably since the previous stage. The average length of the *third toe* is 12.9 mm.

With some of the specimens for these final incubation stages there is a gradual gradation from one stage to the next where measurements are concerned. Where this has occurred, the embryo has been placed with other specimens of comparable gross size.

Twenty-two-Day Embryo

Comparable to Stage 44 or *ca.* 18 days in the chick.

In one specimen the *beak* is 7.8 mm. long, and the tip has a swollen appearance. There is evidence that the *peridermal covering* of the beak is becoming loosened. Spots of black *pigment* appear in the *scalation* of the *legs*. The *claws* are curved and darker. The length of the *third toe* including the claw is 14.7 mm.

Twenty-three to Twenty-four-Day Embryo

Comparable to Stage 45 or *ca.* 20 days in the chick.

During examination of two eggs of this group a faint squawk was heard from within one of them indicating that the air space had been punctured and that the gull would probably hatch during the day. Both young birds were removed from the shell. The translucent *peridermal covering* on the distal portion of the *beak* is shed very easily. Before this became moved out of place, the average beak tip length was 8.8 mm. The *yolk sac* has shrunken in size and is now about the size of the *head*. The length of the *third toe* averaged 18.5 mm.

Twenty-five-Day Embryo

Plate VIII

Comparable to Stage 46 or *ca.* 20 to 21 days in the chick.

One specimen emerged from the shell but died shortly afterwards, and this established the newly-hatched stage. A portion of the *yolk sac*, about half the size of the *head*, had not yet been absorbed. The length of the *beak* tip was 8.6 mm. which was smaller than that of the previous stage and partly due to the absence of the peridermal covering which was lost in hatching. The length of the *third toe* was 17.0 mm.

SUMMARY AND CONCLUSIONS

The principal points of comparison between the developing embryos of the gull and chick are summarized as follows:

1. The length of the incubation period for the California gull is approximately twenty-five days, whereas the chick incubation period is established at twenty to twenty-one days.

2. The first external morphological difference noted between the gull and the chick is in the clarification of the visceral arches. The concise demarcation of the arches appears later in the gull, but their differentiation progresses more rapidly, so that the last remnants disappear before those in the chick.

3. The initial development of the limb buds in the gull is slightly retarded when compared with those in the chick. Subsequent changes show that the wing differentiates more rapidly for the gull, while the leg differentiates more rapidly for the chick.

4. Eye pigmentation in the gull does not become apparent until a much later stage than in the chick.

5. In the gull, the nictitating membrane becomes a noticeable crescent-shaped fold at an earlier stage than that noted for the chick.

6. The transitory appearance of the rudimentary fifth toe was noted for the chick, but was not detected on the gull.

7. In the gull sixteen scleral papillae form on the surface of the iris, as compared with fourteen in the chick.

8. The egg tooth appears at a much earlier stage in the chick than in the gull.

9. The feather tracts appear later in the gull than in the chick and follow a different sequence of distribution. The spinal tract appears earlier in the chick, while the caudal tract appears earlier in the gull. In the gull, two changes were noted that are not mentioned diagnostically by Hamilton for the chick. One is the separation of the ventral feather tract into four longitudinal bands. The other feature is the appearance of pigment in the feather papillae.

10. The webbing between the toes of the gull does not diminish rapidly as it does in the chick but progresses steadily throughout the incubation period.

11. It is of interest to note that a labial groove does form on the beak of the gull as in the chick, and that according to Romanoff (1960: 1028) it is not observed in all avian species.

12. Dark pigmentation on the beak appears at about the seventeenth day of incubation in the gull and was not noted for the chick.

13. During the nineteenth and twentieth days dark pigmentation appears on the claws of the gull; this feature is not mentioned for the chick.

14. By the twenty-second day of gull incubation dark spots of pigment appear in the leg scalation.

15. The newly hatched gulls still possess a portion of unabsorbed yolk sac which is absorbed by the following day.

In general, the majority of the differences found between the chick and the gull indicate that the gull embryo lags slightly behind the chick in developmental change. This is readily understandable since the incubation period for the gull is spread out over a longer period of time.

Incubating the eggs of the California gull in the laboratory was of little help in establishing set times in the embryonic ontogeny. There was no conclusive way of knowing the age of the eggs when they were placed under incubation, and those eggs that were suspected of being of similar age showed considerable variation in stages of development when opened.

More accurate knowledge of the environmental requirements for the developing gull embryo is needed. This is especially true for the earliest stages when temperature and humidity factors are most critical. The specimens that were successfully incubated were undoubtedly in the later stages of development when they were placed in the incubator, at which time the adverse environmental conditions were not severe enough to be lethal.

This embryological study was based on a comparison between examples from two different avian orders, the California gull (*Larus californicus*) of the Order Charadriiformes and the domestic chick (*Gallus gallus*) of the Order Galliformes, yet both birds are similar during their early ontogeny in that they have relatively long incubation periods and the young are precocial when they hatch. There are striking differences apparent even to the most casual observer, but the significance of most of these differences does not become apparent until the progression of morphological changes is observed and compared, step by step, throughout the total incubation period.

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PLATE I

Fig. 1, x 12
15–20 Hours

Fig. 2, x 12
18–22 Hours

Fig. 3, x 12
26–28 Hours

Fig. 4, x 12
28–30 Hours

PLATE II

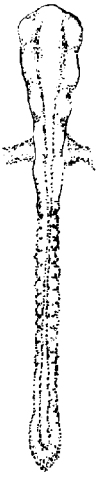


Fig. 1, x 12
30–35 Hours

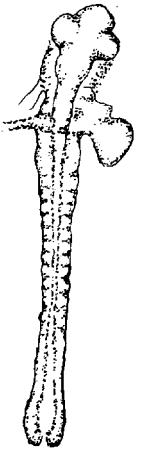


Fig. 2, x 12
40–45 Hours

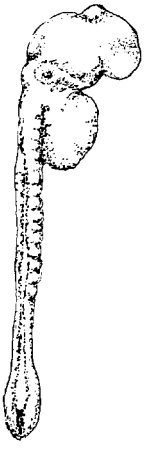


Fig. 3, x 12
45–48 Hours

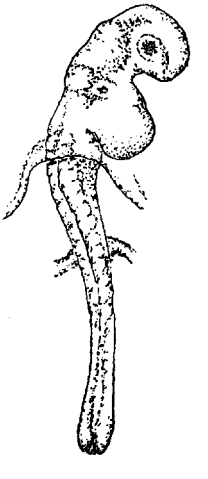


Fig. 4, x 12
48–52 Hours

PLATE III

Fig. 1, x 6
60–65 Hours

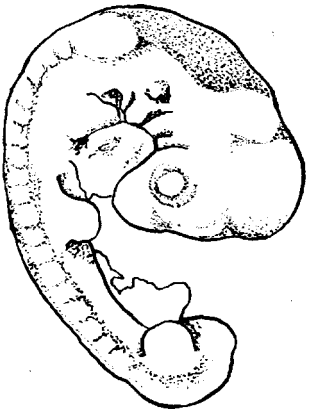


Fig. 2, x 8
3–3½ Days

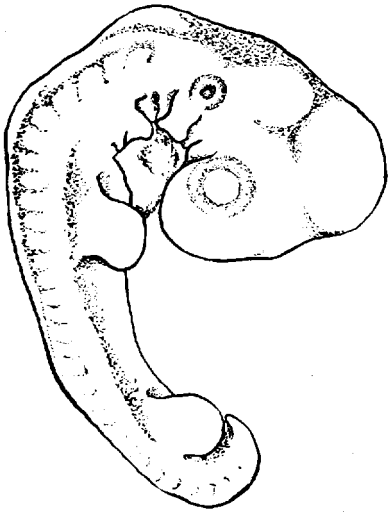


Fig. 3, x 8
4 Days

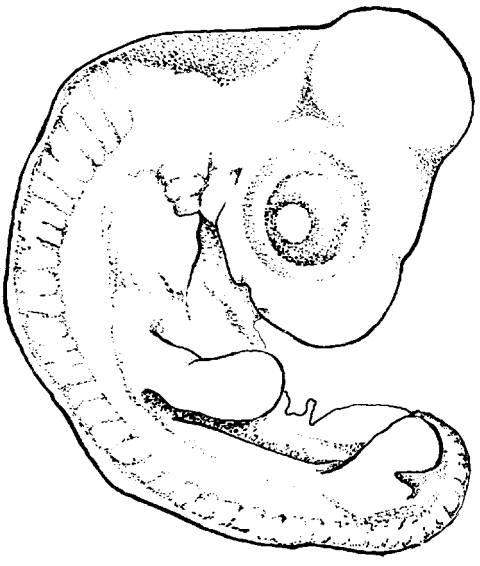


Fig. 4, x 8
5–5½ Days

PLATE IV

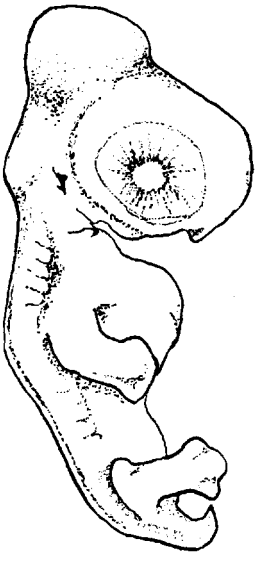


Fig. 1, x 4
7–7½ Days

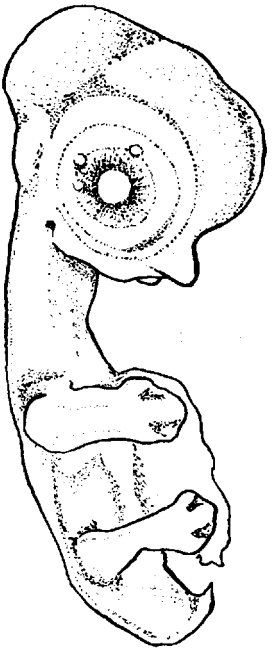
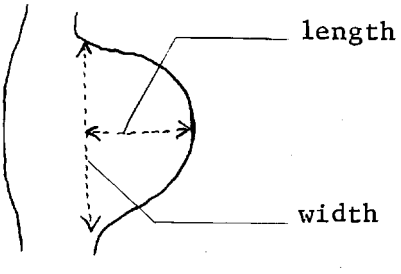


Fig. 2, x 4
8 Days



Early Limb Bud

Fig. 3

PLATE V

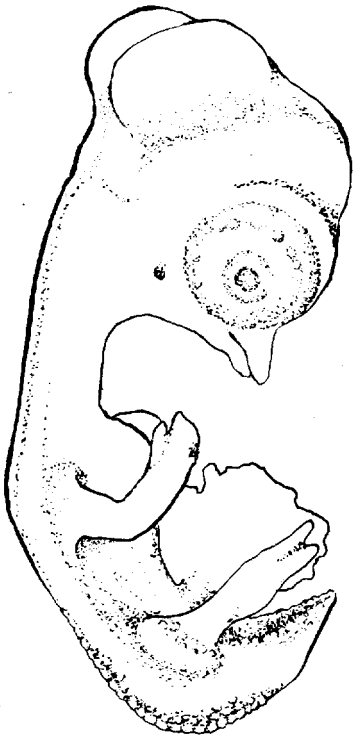
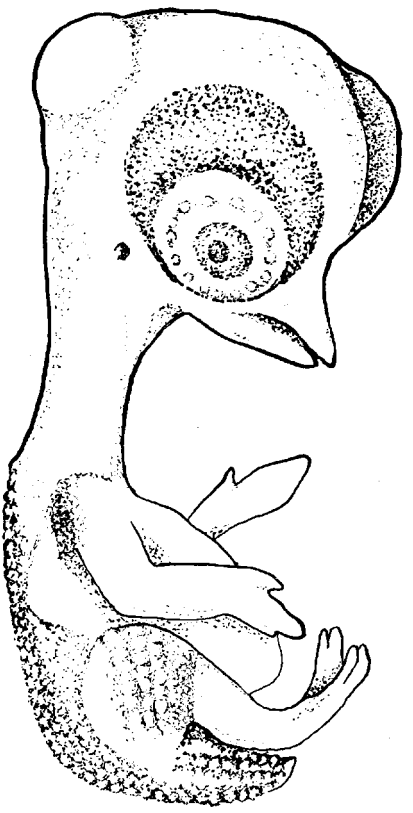


Fig. 1, x 4
9 Days



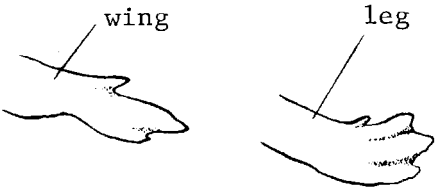


Fig. 2, x 4
10½–11 Days

PLATE VI

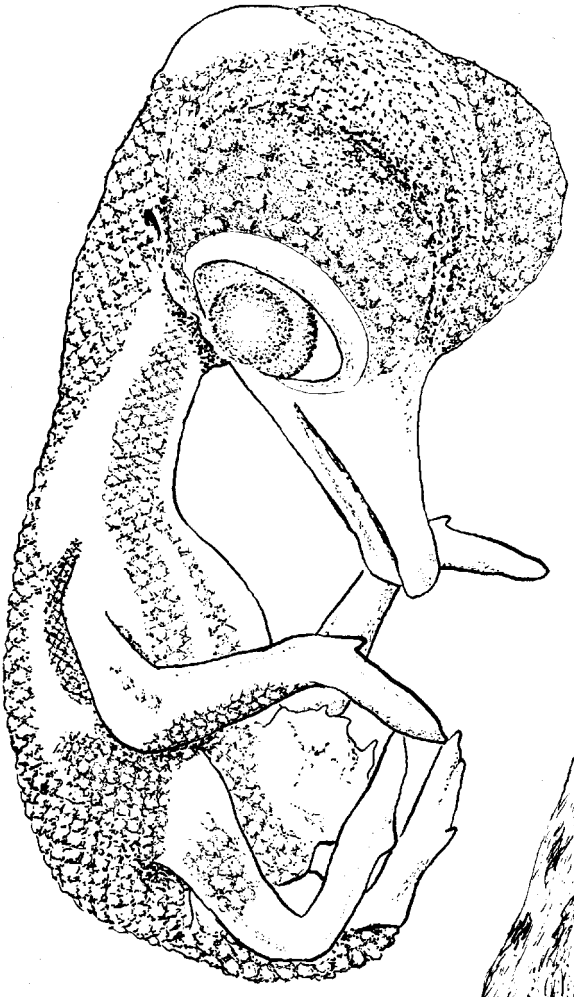


Fig. 1, x 4
13 Days

Fig. 2, x 2
15 Days

Fig. 1, x 2
17 Days

Fig. 2, x 2
20 Days

PLATE VIII

Newly Hatched Gull, x 2
25 Days