Hamburger-Hamilton Staging Series (1951) [1]

By: Doty, Maria Keywords: Chicks [2] Model organisms [3]

In 1951 Viktor Hamburger [4] and Howard Hamilton created an embryonic staging series from a combination of photographs and drawings from other researchers. The Hamburger–Hamilton stages are a sequence of images depicting 46 chronological stages in chick [5] development. The images begin with a fertilized egg [6] and end with a fully developed chick [5]. The Hamburger-Hamilton staging series was produced in order to replace a previous chick [5] staging series created in 1900. The earlier attempt lacked specific details and staged the chick [5] embryo by using only morphological characteristics. As chicks were, and still remain, model organisms for experimental embryology [7], it was important to create a staging series with descriptions for determining the approximate age of a developing chick [5] embryo.

Hamburger and Hamilton based their images on a similar series by Ross Granville Harrison [8] that staged mole salamanders (*Ambystoma* [9] *mexicanum*). Harrison's series did not rely on the exact age of the embryo to determine its stage of development; instead it relied on characteristics of the developing embryo. Hamburger and Hamilton also wanted their staging series to solely depend on specific characteristics that occur at each step of the chick's development regardless of the exact age of the embryo. Chick developmental time can be difficult to exact because the egg [10] is internally fertilized and goes through a brief period of development; after the egg [10] is laid, development ceases until incubation begins. The eggs could have started incubating at different stages of development, there may have been differences in temperature during incubation, and genetics between breeds could have played a role in developmental timing.

Hamburger and Hamilton did not capture the images nor draw the illustrations themselves; instead they compiled other scientists' drawings and photographs and then added short descriptions explaining each stage in chick [5] development. The stages were determined by the number of somites [11] and each stage was at an interval of three somites [11]. Somites, or segmented blocks of mesoderm [12], bud off sequentially during vertebrate development and can therefore be used as a timing landmark. The embryos used for the photographs were from different varieties of chickens: white leghorns, barred Plymouth Rock, and Rhode Island reds. However, only white leghorn embryos were used for stages 14 through 35.

In stage 1 of chick [5] development the primitive streak [13] is not yet seen, but the embryonic shield is noticeable. In Stage 2, usually six to seven hours into incubation, the primitive streak [13] begins to appear. Stage 3, about twelve to thirteen hours into development, the primitive streak [13], but no primitive groove [14] is visible. In Stage 4, the primitive streak [13] has fully extended and the primitive groove [14], primitive pit [15], and Hensen's node are visible. Stage 5 is about nineteen to twenty-two hours into development when the notochord [16] is visible below Hensen's node. The head begins to form during that stage. In Stage 6 the head fold is present, but there are no somites [11].

The first pair of somites [11] is visible in stage 7 along with neural folds near the head. By Stage 8 there are four somite pairs and blood islands [17] appear in the bottom of the blastoderm [18]. Seven pairs of somites [11] and optic vesicles are visible in stage 9. Ten somite pairs, a hint of cranial flexure, and three primary brain vesicles are seen in stage 10. Stage 11, about forty to forty-five hours after incubation, five neuromeres, or segments of the developing brain, are visible in the hindbrain [19]. In that stage, the neuropore begins to close while the optic vesicles constrict. Stage 12, forty-five to forty-nine hours into development, sixteen somite pairs are present and the anterior neuropore has closed. The developing head starts rotating to the left and the primary optic vesicles become distinct. The heart is S–shaped and the forebrain [20] is completely covered by the headfold of the amnion [21] until the next stage. There are nineteen somite pairs in stage 13, the head is almost fully turned to the left, and the telencephalon is distinct and enlarged. At that point, the headfold of the amnion [21] completely covers the forebrain [20], midbrain [22], and the anterior portion of the hindbrain [19].

Stage 14, the last stage with a distinct number of somites [11], has twenty-two somite pairs. After that stage, the somites [11] pairs become difficult to distinguish. That stage indicates roughly fifty to fifty-three hours of incubation. The branchial arches and clefts begin to form and the amnion [21] covers somites [11] seven through ten during that stage. After fifty to fifty-five hours of incubation, stage 15 begins and the amnion [21] covers up to fourteen pairs of somites [11]. By that stage, the optic cup of the eye, the third branchial arch [23], and cleft are fully formed.

During stage 16, about fifty-one to fifty-six hours of incubation, the wing and tail bud are visible and the amnion [21] cover up to eighteen somite pairs. The limb buds are visible at stage 17, about fifty-two to 64 hours into incubation. The amnion [21] completely extends along the embryo except for somites [11] twenty-eight to thirty-six. In that stage, the nasal pits form. Sixty-five to sixty-nine hours into development, or stage 18, the allantois [24] begins to form. The leg buds appear larger than the wing buds and the amnion [21] fully closes.

In stage 19, or sixty-eight to seventy-two hours into incubation, the somites [11] extend into the tail. The eyes are unpigmented and the tail bud curves towards the head during that stage. The allantois [24] becomes vesicular by stage 20, about seventy to seventy-two hours into incubation. There is also a faint pigmentation in the eye and the second branchial arch [23] extends past the third in stage 20. The allantois [24] begins to enlarge and extend to the head and the limb buds, which are asymmetrical, become distinctly larger than the wing buds in stage 21, or about seventy-two to eight-four hours into incubation. Stage 22 describes an embryo after about eighty-four hours with distinct eye pigment and somites [11] that have fully extended into the tail. After about ninety-six hours, or stage 23, the limb buds are as long as they are wide and there is a slit in the fourth cleft.

At four and a half days, or stage 24, the limb buds are longer than they are wide and the toe plate begins to form. In Stage 25, four and a half to five days into development, the elbows and knees of the chick [5] have formed. There is a digital plate in the wings and the third and fourth clefts have begun to reduce in size. After five full days of incubation, or stage 26, the embryo has three toes and the limb continues to elongate. The third and fourth clefts have disappeared by that stage.

At stage 27, five to five and a half days of incubation, early beak formation can be seen, along with groove marks between the digits in the toes. The beak of the embryo begins growing out and the toe digits become more prominent in stage 28, or five and a half to six days into development. During stage 29, after six to six and a half days of incubation, the wing bends at the elbow and the toes begin to web. The distinct egg [10] tooth sticks out of the chick [5], the major segments of the limbs have nearly finished forming, and the feathers germinate during stage 30, after six and a half to seven days of development. In stages 31 through 39, the feather germs are progressively visible. Stages 40 through 45 include increasing beak size and toe length. After twenty-one days of development, or stage 46, the check hatches.

There is one photograph for each of the 46 stages in the Hamburger-Hamilton chick [5] development scheme. Some photographs are coupled with an illustration to clarify some morphological characteristics. Each stage has a description of developmental events that distinguish it from the stage before and the stage after. Although Hamburger and Hamilton initially created the staging series in 1951 when the chick [5] was a prominent model organism [25] for embryology [7], as of 2011 the series is still used in biology textbooks and when determining the stage of a chick [5] embryo.

Sources

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