

Post-laying Stages of Embryonic Development for Crocodylians

Mark W. J. Ferguson¹

IN embryological, ecological and farming studies of crocodylians, it is important to have a staging system for embryos and to be able to relate those stages to a time scale under specified incubation conditions (particularly temperature and humidity). The shortcomings of a classification based on chronological age alone are obvious. The exact time of egg laying is frequently unknown and variation in development rate may occur between embryos of the same age, even within the same clutch. Many factors may be responsible for reducing the correlation between chronological and structural age: variation in the temperature of egg incubation; variation in the humidity and gaseous environments of incubation; genetic differences in the rate of development within and between species; variation in the size of individual eggs; and, variation in the thickness of eggshells and eggshell membranes.

The two major objectives of a crocodylian staging system are:

1. For embryologists, or others conducting experiments on crocodylian embryos, to have a series of obvious morphological characters which define particular uniform developmental states (stages) regardless of the previous incubation history of the embryos. Thus, experimental treatments (for example drug injections) or developmental descriptions can be standardized and many of the sources of variation discussed above can be controlled. If a staging system is related to chronological age under specified incubation conditions, this will enable investigators to efficiently incubate embryos to the time required for particular stages to be reached.
2. If the staging system can be related to real age by accounting for variation in incubation temperature, then by staging an embryo from an unknown nest, and measuring nest temperature, it should be possible for the ecologist and crocodile farmer to estimate approximately the time of egg-laying, the duration of incubation which has elapsed and the expected hatching date.

Staging systems are available for turtles [see reviews by Miller (1985) and Ewert (1985)], lizards and snakes [see review by Hubert (1985)] and chickens (Hamburger and Hamilton 1952). This chapter presents the staging system that I have described previously for crocodylians (Ferguson 1985) in a near identical format, and discusses various aspects of staging and aging crocodylian embryos.

THE LITERATURE

Clarke (1891), Voeltzkow (1899) and Reese (1908, 1915) described the appearance of some crocodylian embryos in both surface view and histological sections, but none of these accounts forms a complete series and they are poorly related to chronological age, incubation temperature and humidity. Random isolated accounts of embryos of unknown age and developmental history have been provided by some field biologists (Deraniyagala 1934, 1936, 1939; Pooley 1962; Magnusson and Taylor 1980), but these are of very little value as staging guides or systems. Webb *et al.* (1983a,b) have provided useful preliminary details for estimating the ages of *C. porosus* and *C. johnstoni* embryos in wild nests, including some data on the effects of varying incubation temperatures, but they do not provide detailed descriptions of any embryological stages.

STAGE OF DEVELOPMENT AT LAYING

There is some controversy in the literature concerning the stage of embryonic development at the time of egg-laying. Some field workers (McIlhenny 1934, 1935; Pooley 1962) state that crocodylian embryonic development begins with egg-laying and that freshly laid eggs show no signs of pre-laying development. However, these observations are incorrect, for an embryo is present, although it is minute, transparent and has few macroscopic signs of blood vessel development. It is unlikely that the above authors could either find or see such embryos without the aid of a dissecting microscope, a point

¹Department of Basic Dental Sciences, University of Manchester, Turner Dental School, Higher Cambridge Street, Manchester M15 6FH, England.

stressed by Clarke (1888, 1891), Voeltzkow (1892, 1899) and Reese (1907, 1915) all of whom experienced considerable difficulty in working with young crocodilian embryos.

In fact, crocodilian embryos have undergone considerable development by the time of egg-laying (Reese 1907, 1915, 1931; Voeltzkow 1892, 1899; Clarke 1888, 1891; Wettstein 1954; Ferguson 1982, 1985; Webb *et al.* Chapter 43). Reese (1915, 1931) obtained eggs immediately after laying and, in addition, killed gravid female *A. mississippiensis* in order to obtain oviducal eggs. In both instances the embryos recovered were well formed and the stage at egg-laying was equivalent to stage 1 of this study. Voeltzkow (1899) illustrates a somewhat later stage at egg-laying for *C. niloticus*, but his descriptions do include those of a stage 1 embryo. [It is unclear if he recovered this from a nest or if he obtained it through a slit cut in the body wall of a captive, gravid female].

Extensive observations of many *A. mississippiensis*, *C. johnstoni* and *C. porosus* embryos recovered within a few hours of egg-laying have confirmed that the stage at laying (stage 1 here) is uniform both within and between species. Variations are principally in the numbers of somite pairs (14-20: 16-18 are particularly common) and the degree of delineation of the dorsal body wall from the blastoderm.

DEVELOPING THE STAGING SYSTEM

In my preliminary work with *A. mississippiensis* embryos, I tried to combine 'aging' and 'staging' by making the stages numerically equivalent to the number of days after egg-laying, with incubation at 30°C and 100% humidity (Ferguson 1982). However, such stages proved cumbersome to use, particularly with the older embryos in which most external structures have developed and the embryo is merely enlarging with time. In addition, after studying the embryology of *C. johnstoni* and *C. porosus*, it became evident that the morphology of these developing embryos was remarkably similar to those of *A. mississippiensis*; only the timing varied, particularly in the later stages. It was therefore possible to construct a crocodilian staging scheme based on morphology which was applicable to most if not all species, and to treat age separately.

The approach adopted was threefold. First, a detailed morphological crocodilian staging scheme was prepared in which species specific characters were noted, but the diagnostic criteria for designating particular stages were "crocodilian" and species independent. Second, many of the embryos used for these series were derived from specified incubation conditions and thus a chronological age or age range for each stage could be given, which is applicable to embryos incubated under the same conditions. Data on both of these are presented here. The third

approach was to take 13 different standard measurements (total length, eye length, snout length, snout width, etc.) on hundreds of embryos of all stages for *A. mississippiensis*, *C. johnstoni* and *C. porosus*, supplemented by data on egg dimensions and the extent of the opaque egg-shell banding (Ferguson and Webb, unpublished data). These measurements will allow the relationship between embryo size, egg size and opaque band development to be quantified within and between species. They also highlight interspecific differences in body proportions: for example *C. porosus* embryos are larger and have longer tails than the other two species; *C. johnstoni* embryos have longer limbs and narrower snouts; and, *A. mississippiensis* embryos have a greater proportion of absorbed abdominal yolk at hatching and have retarded development of the external genitalia.

Measurements and morphometric ratios can also be used to predict age given standardized incubation conditions (see Webb *et al.* Chapter 50), although this is not pursued here. A "morphological age" scale [similar to published analyses for rat embryos (Ferguson 1978a)] is of particular value in the later stages of incubation (stages 20-28), when the time interval between numbered stages is prolonged.

The two systems (numbered stages based on morphology and, age in days under standard uncubation conditions) are complementary and can be used together. For example an embryo may be classified as "stage 24 morphological age 58.5 days". In general, stages based on external morphological criteria are accurate for "aging" up to stage 20, because development is fast and the time interval between stages is small (diagnostic criteria are easy to identify and the embryos are small and difficult to measure). However, after stage 20, morphological age predicted from morphometric ratios may allow finer identification of the stage of development than is possible from the numbered stages alone.

No morphometric data are included in the crocodilian morphological staging system (Mormentafel) presented here. For each stage I have listed the most important diagnostic morphological criteria first, and for this reason the order of described structures is not the same for all stages. The essential features of each stage are illustrated in Figures 1-4 which are photographs of *A. mississippiensis* embryos. Figure 5 depicts diagrammatically the appearances of the right forelimb and left hindlimb at all stages of their development: limb appearance is particularly useful in ascribing stages. Some stages are subdivided by reference to other criteria. For example stages 1-6 are supplemented with somite counts (referred to as stage 1/20s embryo), and stages 17-19 with a measure of the degree of palatal closure. The stages were not defined by these criteria (for example somite counts) because they are somewhat variable

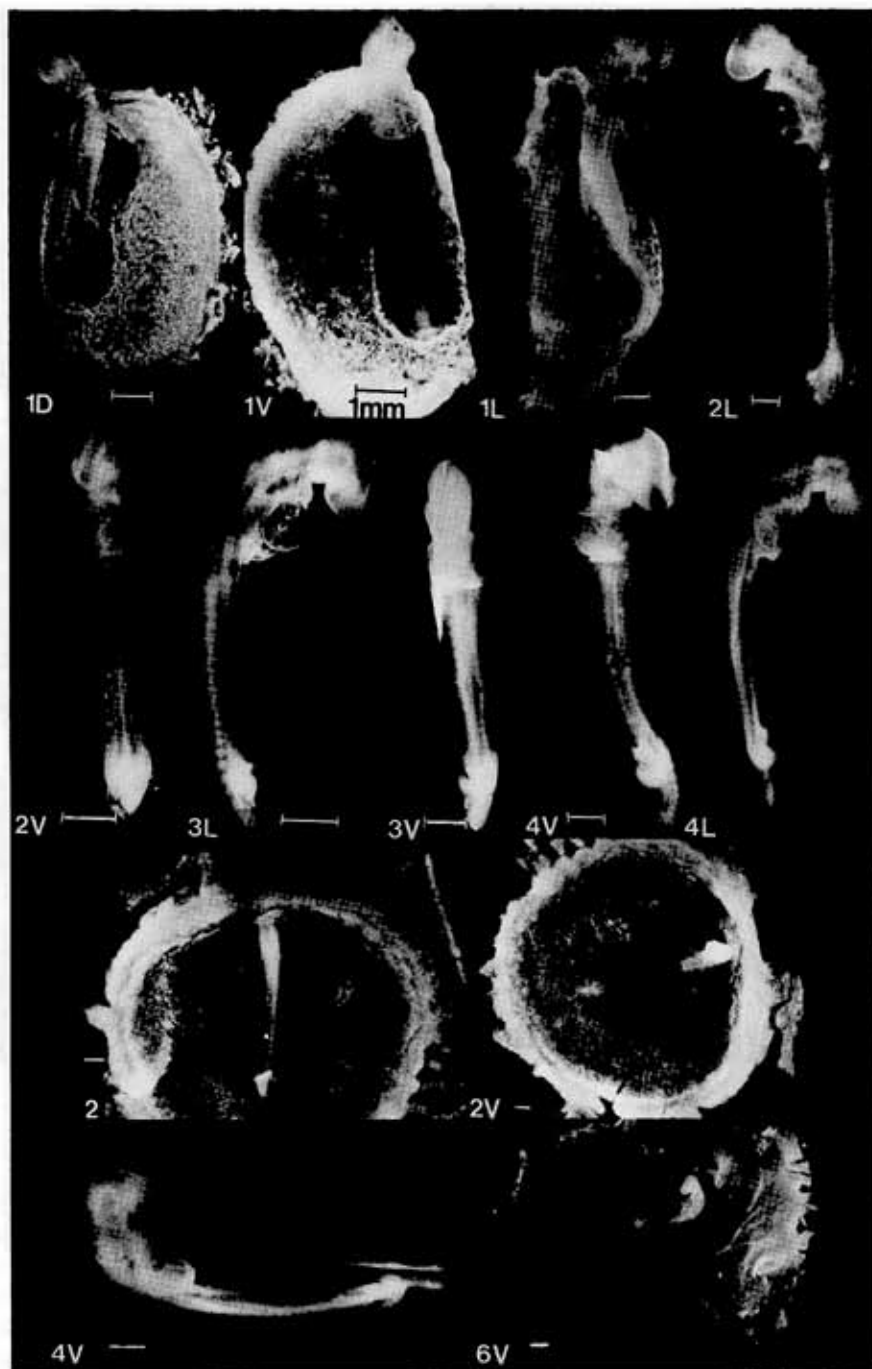


Fig. 1. Stages 1-4 of embryonic development in *Alligator mississippiensis*. Numbers indicate the stages (see text for their descriptions). D=dorsal view, L=lateral view, V=ventral view. Dorsal (2D) and ventral (2V) views of a Stage 2 embryo illustrate its attachment and vertical relationship (i.e. no body torsion) to the blastoderm. Body torsion commences at Stage 4 (4V) when the cranial end has rotated; it is complete by Stage 6 where a ventral view (6V) illustrates its relationship to the overlying chorion. Scale bars=1 mm. Reproduced from Ferguson (1985) by kind permission of J. Wiley and Sons, New York.

in relation to other features; some embryos develop by enlarging the size of existing somites before they form new ones, whilst others may form more somites before enlargement takes place (such variations are commonly seen with differing incubation temperatures).

Complications arise from the independent variation of different characters (for example development of the branchial arches may lag behind that of the limbs in some embryos), and as a consequence, certain characteristics are of no diagnostic value (the degree of head flexion, the amnion, the allantois

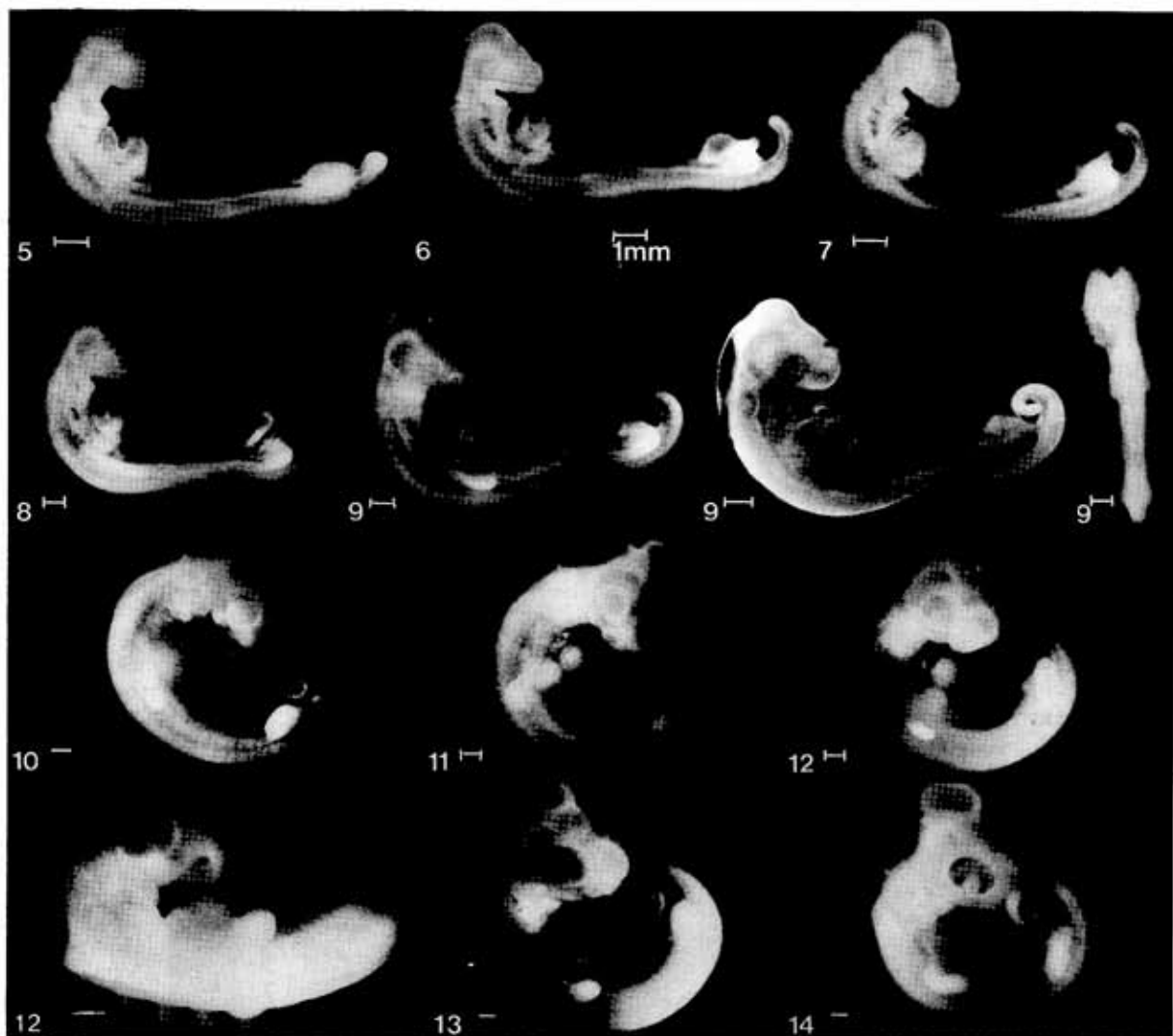


Fig. 2. Stages 5-14 of embryonic development in *A. mississippiensis* (see text for descriptions). Scale bars=1 mm. Reproduced from Ferguson (1985) by kind permission of J. Wiley and Sons, New York.

after stage 8, the number of somite pairs beyond 40). Independent variation in the development of different structures is particularly marked at the extremes of incubation temperatures (28°C and 34°C). I have tried to establish 'standard types' by comparing a number of embryos at each stage and selecting for illustration those which appeared typical. All embryos examined were fixed in 10% formal saline and all were photographed with oblique incident illumination using a Wild M8 stereophotomicroscope. The staging scheme is based on the examination of some 1500 embryos of *A. mississippiensis* and 300 each of *C. porosus* and *C. johnstoni*.

The given ages (in days) for embryos of *A. mississippiensis* are based on a number of standard series collected within three hours of egg-laying and artificially incubated at 30°C and approximately 90-100% humidity. In the case of *C. johnstoni* and *C. porosus*, the standard series were incubated by Grahame

Webb (as described in Webb *et al.* 1983a,b) at 30°C and 90-100% humidity. All the embryos they reported on (and many others) were re-examined by me, and thus the ages and morphology presented here are derived from the data and specimens [rather than from the field guide diagrams (Webb *et al.* 1983a,b) which contain a few inaccuracies and omissions as far as staging is concerned].

For *A. mississippiensis* an age is given for every stage, because large numbers of eggs were incubated and recovered in the standard series. For *C. porosus* and *C. johnstoni* age assignment is sporadic because a limited number of known age embryos were available. Remarkably, the timing of development in relation to stages is virtually identical in all three species up to stage 24 (throughout the period when new structures are appearing), and it is only in the later stages (24-28), when only growth is occurring, that species specific aging differences become very apparent. I would therefore speculate that the



Fig. 3. Stages 15-21 of embryonic development in *A. mississippiensis* (see text for descriptions). Scale bars=2 mm. Reproduced from Ferguson (1985) by kind permission of J. Wiley and Sons, New York.

ages given for *A. mississippiensis* at each stage up to 24 would be extremely similar in all crocodylian species.

For each stage I have also given "equivalence values" for the figures in Voeltzkow's (1899) work on *C. niloticus* and for the stages in Reese's (1915) work on *A. mississippiensis* [which includes Clarke's (1891) illustrations]. I did attempt to give equivalent Hamburger and Hamilton (1951) stages for chick development, but avian and crocodylian embryos are too dissimilar in appearance to make this a useful exercise. Reese's (1908, 1915) drawings of the macroscopic appearances of *A. mississippiensis* embryos are inaccurate and little attention should be

paid to them. Contrariwise, Voeltzkow's (1899) drawings are fairly accurate — remarkably so considering when they were executed — but still contain errors. Where possible, I have selected figure numbers from Voeltzkow (1899) which are representative and contain few, if any, errors. Others have been omitted (for example Figs 39b and 43 which show body torsion to the right as opposed to the left), or where this was not possible, because there was no other illustration of that stage, I have indicated that there is a "major error" in his figure.

In some cases my cross referencing between Voeltzkow's (1899) macroscopic drawings of whole embryos and individual regions is different from his,

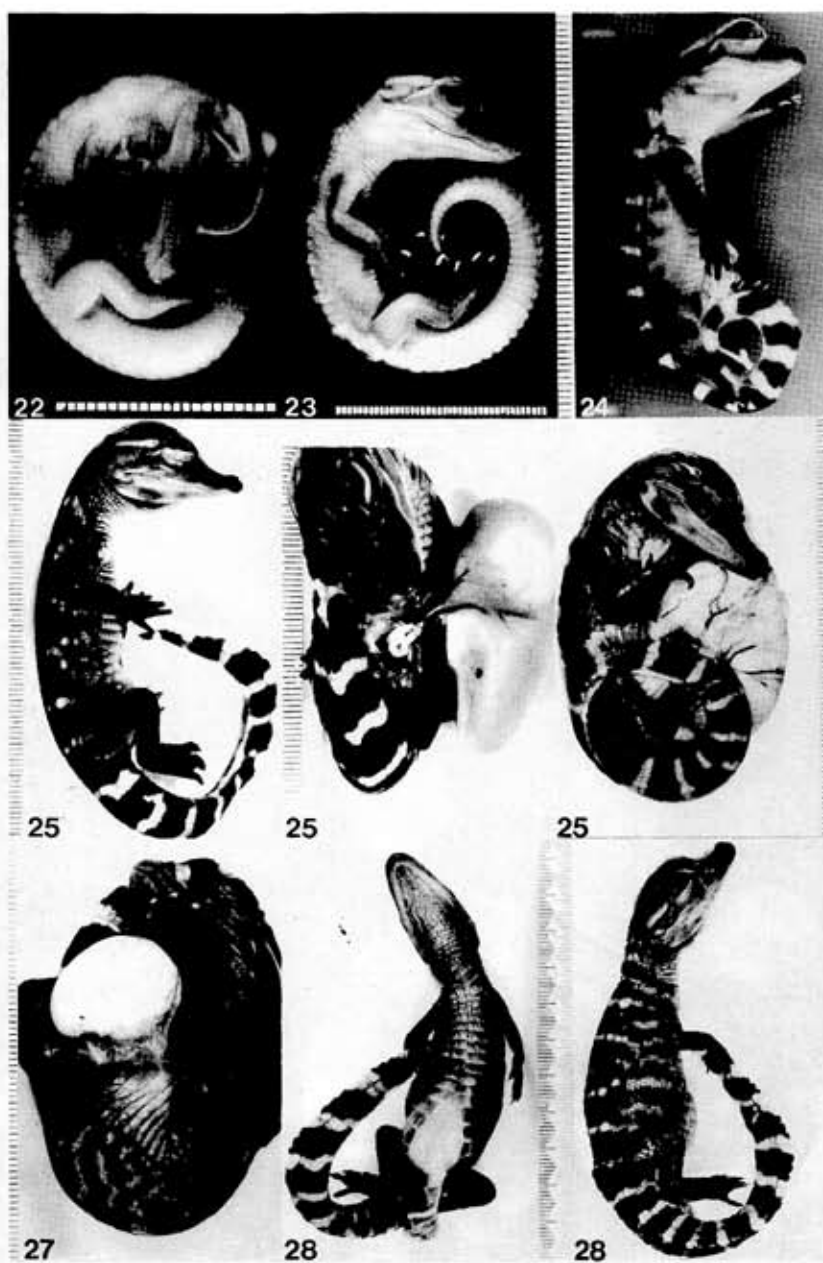


Fig. 4. Stages 22-28 of embryonic development in *A. mississippiensis* (see text for descriptions). Millimeter scale. Reproduced from Ferguson (1985) by kind permission of J. Wiley and Sons, New York.

and I believe mine reflect more closely the appearances at specified stages. Not all errors in Voeltzkow's (1899) figures are listed here, and so discrepancies between his figures and the photographs presented here may still arise. Judgement should favour the present photographs, which are known to be accurate for *A. mississippiensis*, *C. porosus* and *C. johnstoni*. Voeltzkow's (1899) ages are often inaccurate and inconsistent (for example his Figs 49 and 58 are of the same embryo, yet they are aged two months and four weeks after egg-laying respectively), and thus no ages are given for *C. niloticus* here. However, some of Voeltzkow's (1899) data do suggest that the relationship between

age and stage of development for *C. niloticus* is very similar to that for *C. porosus* and *C. johnstoni* (and to that for *A. mississippiensis* up to stage 24).

At the time of writing, few data were available on the relationship between chronological age and stage of development at incubation temperatures other than 30°C (but see Webb *et al.* Chapter 50). In *A. mississippiensis* increasing incubation temperature (within viable limits) accelerates development in the early phases of organogenesis (up to stage 20) to a much greater extent than it does in the later stages of growth and maturation of already formed

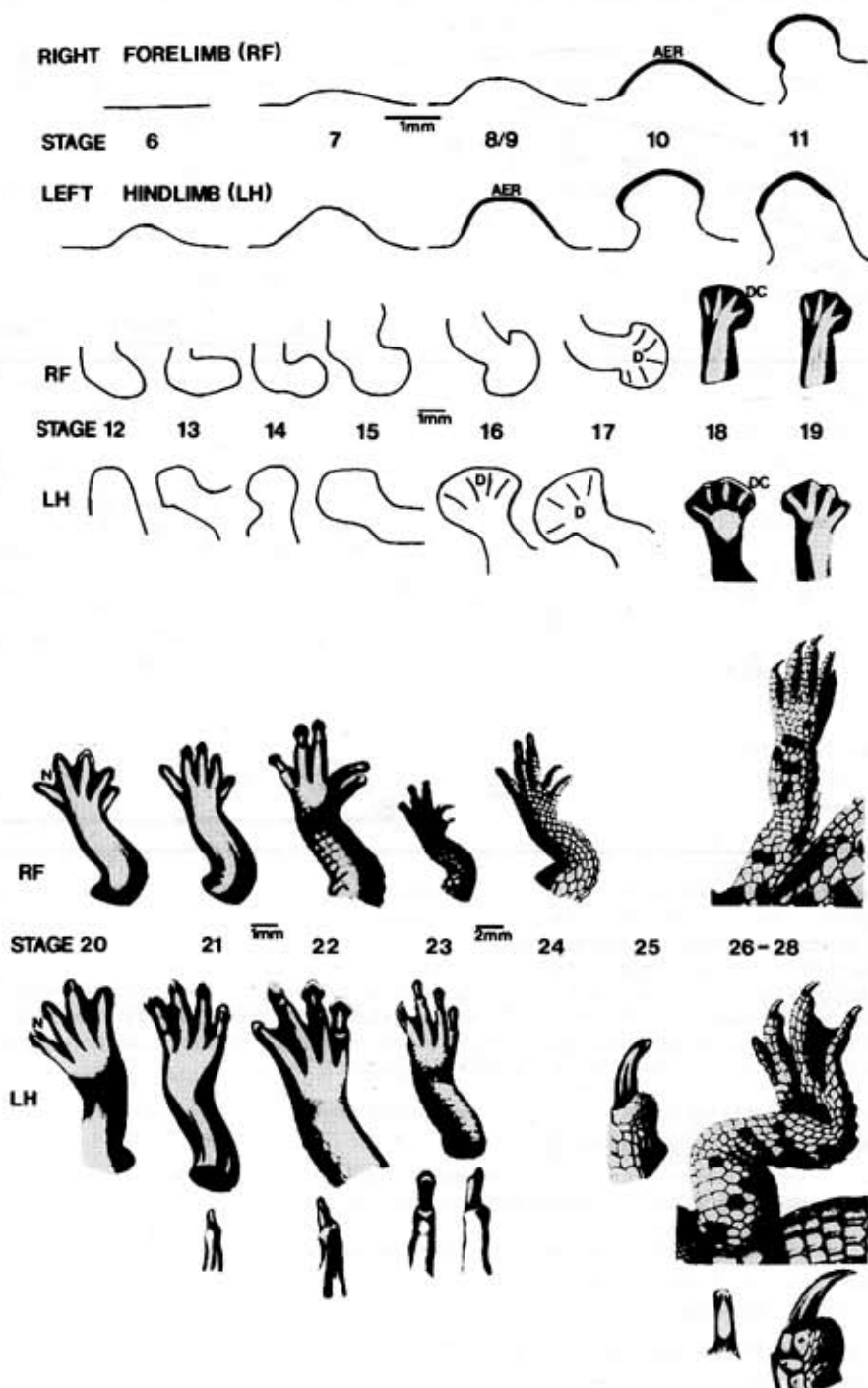


Fig. 5. The typical (diagnostic) appearances of crocodilian right fore- and left hindlimbs (including hands, feet and nails) at various stages of development. Stages 6 to 11 are views from the dorsal aspect of the embryo and depict the projection of the limb anlage from the flank. Stages 12 to 17 are lateral views of the sides of the embryo and depict the proximal and distal elements of the limb anlage. Stages 18 to 28 are views of the hands, feet and nails. Up to Stage 17, no structures except the digital mesodermal condensations (at Stages 16 and 17) are visible macroscopically in the limbs, thereafter anlage for the limb and digit cartilages, for the nails and for the interdigital webbing are evident, hence the change in diagram style at Stage 18. Based on observation of *Alligator mississippiensis*, *Crocodylus porosus* and *C. johnstoni*, with some (Stages 18 to 28) drawings adapted from Voeltzkow's (1899) work on *C. niloticus*. AER, Apical ectodermal ridge; D, mesodermal condensations for the digits; DC, digit cartilages; N, nail anlage. Reproduced from Ferguson (1985) by kind permission of J. Wiley and Sons, New York.

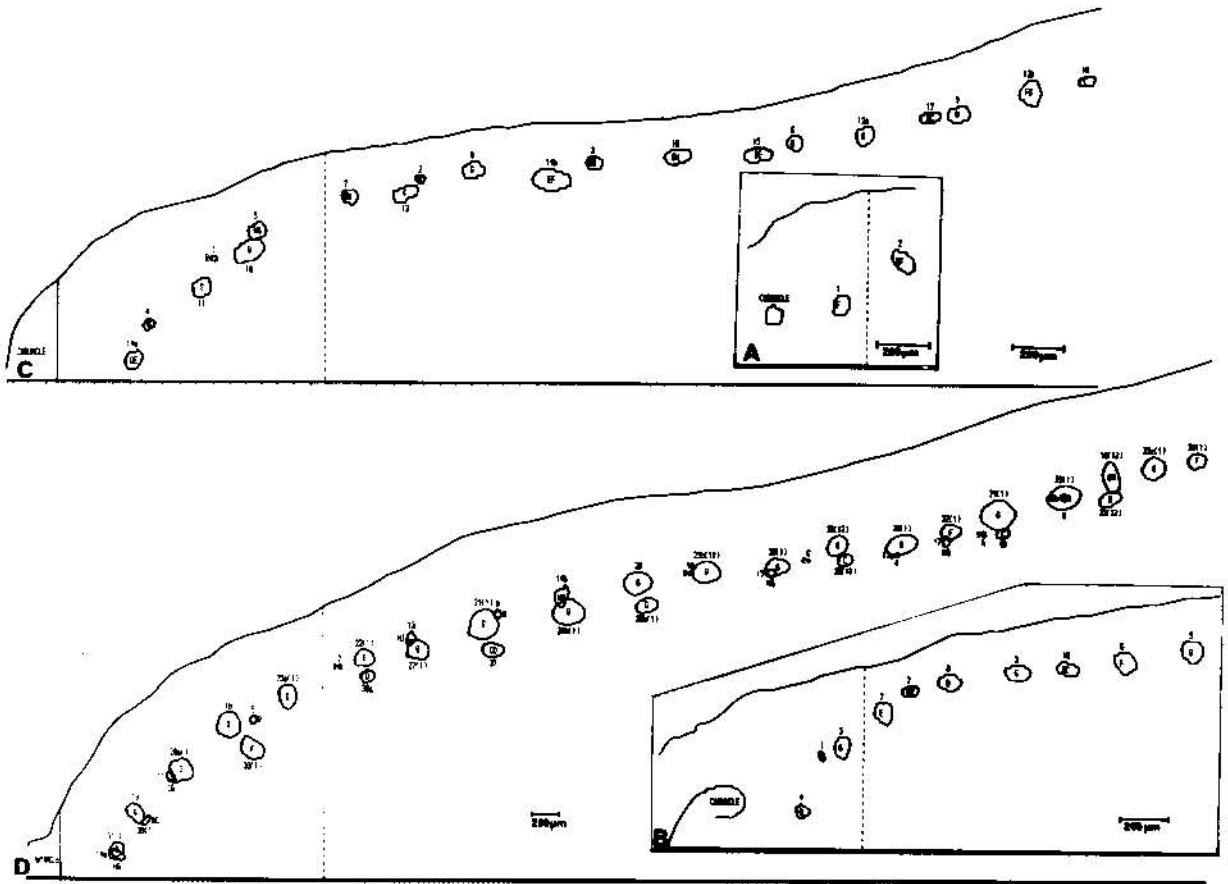


Fig. 6. Maps generated from serially sectioned heads of *A. mississippiensis* indicating the development of the left upper dentition: (A) Stage 15, (B) Stage 18, (C) Stage 20, (D) Stage 23. None of the teeth present at Stage 20 becomes functional. Early teeth are not initiated in regularly spaced front to back sequences (Zahnreihen *sensu* Edmund) nor in perfect alternation (as described by Woerdenman — see Edmund 1962, 1969). Development of the early dentition is similar to that in the gecko *Cnemaspis kandiana*; comparison shows that the tooth numbered 14a in Figures C and D is homologous with the geckonid eggtooth (one tooth in each jaw half) and probably also with the eggteeth of other reptiles (Westergaard, in prep.). At Stage 23 all 20 post-hatching tooth positions are established. The number of early nonfunctional teeth is approximately 25, although variation in the specimens investigated suggests a maximum range of 22-30, but certainly not 92 as postulated by Edmund (1962, 1969).

- Thick lines: jaw outlines and outer surfaces of inner enamel epithelium.
 Dashed lines: premaxillary-maxillary junction.
 Numbers: the initiation sequence of tooth germs calculated by mapping the dentition in a close series of *A. mississippiensis* embryos from Stage 14 (first tooth present) to Stage 28 (hatching).
 (I): first functional teeth.
 (I?): teeth which become functional in some individuals but nonfunctional in others.
 Capital letters: tooth development stages.
- A: bud stage;
 B: $h < 1/2w$ (cap Stage 1), no tooth matrix;
 C: $1/2w \leq h < w$ (cap Stage 2), no tooth matrix;
 D: $w \leq h < 1 1/2w$ (bell Stage 1), no tooth matrix;
 E: $1 1/2w \leq h$ (bell Stage 2), no tooth matrix;
 F: start of dentine matrix formation;
 G: $w_m < 1/3wt$;
 H: $1/3wt \leq w_m < 1/2wt$;
 I: $1/2wt \leq w_m < 2/3wt$;
 Q: inner enamel epithelium degenerated, little or no resorption of tooth matrix, numerous odontoblasts in pulp;
 R: resorption of tooth matrix, few or no odontoblasts in pulp;

h = tooth height at the outer surface of the inner enamel epithelium; w = tooth width at the outer surface of the inner enamel epithelium; w_m = width of the total tooth matrix measured at half the tooth height; w_t = width of the tooth, as measured by the distance between the outer surfaces of the matrix at half the tooth height. Data from Westergaard and Ferguson (1986, 1987).

structures. Similar observations have been made on embryonic chickens (Romanoff 1967), snakes (Zehr 1962) and turtles (Yntema 1968; Ewert 1979). However, not all structures have their development accelerated to the same extent, and for example gonadal development is actually retarded at 34°C, relative to 30°C, when compared on a stage by stage basis. This makes it difficult to make precise statements on the effects of varying incubation temperatures on the "embryonic development rate", as the latter is often tissue specific. It also introduces difficulties when trying to adjust regression equations for temperature variations during incubation in order to predict embryonic age (or hatching dates) from morphometric ratios (Webb *et al.* 1983a,b).

Development of *A. mississippiensis* embryos up to stage 20 proceeds approximately 1.2-1.8 times as fast at 34°C as it does at 30°C, and approximately 1.6-2.0 times as fast at 30°C as it does at 28°C. However, after stage 20 the rates of development at different temperatures show less variation: *A. mississippiensis* eggs incubated at 34°C may hatch after 55-60 days incubation, those at 30°C after 62-67 days and those at 28°C after 70-75 days. In crocodylians with longer incubation periods, the effects of incubation temperature on total incubation time may be more pronounced (see Webb *et al.* Chapter 50), largely as a result of increased times spent in the egg between stages 24 and 28.

The extent to which the later stages of growth and yolk internalization are accelerated by increased incubation temperatures is unclear. Field nests increase gradually in temperature throughout incubation (Webb and Smith 1984) and one can speculate that this increase would facilitate development, yolk internalization and hatching. It is an area worthy of detailed investigation for many reasons. Are there selective pressures resulting from constrained climatic environments such that all or some crocodylians hatch in the minimum time possible? Or do crocodylians in tropical environments receive advantages from staying in the egg longer? If crocodyles remain in the egg longer between stages 24-28 than do alligators, do they need higher incubation temperatures at those stages to accelerate yolk utilization and growth? Should such regimes be provided for in artificial incubators?

Hatching is a difficult endpoint to use with crocodylian staging in any precise way, because it is initiated by factors other than just the completion of development. Viable embryos incubated under constant conditions can hatch over a range of 5-10 days and with varying degrees of yolk absorption.

EMBRYOLOGICAL STAGES

The stages given below are republished from Ferguson (1985), which includes a comprehensive

review of crocodylian reproduction and development.

Stage 1 (Fig. 1)

Blastoderm: blastoderm and embryo lie on top of the yolk and are not attached to the overlying eggshell membrane. Blood vessels are not evident in the blastoderm.

Somites: 12-20 pairs (16 and 18 are very common at the time of egg-laying) which commence caudal to the otic placode.

Delineation of the embryo from the blastoderm: approximately the caudal third of the dorsal body wall is not delineated from the blastoderm; i.e. in a 15S embryo the body is delimited to the level of the 7th somite, in a 16S embryo to the 8th somite, in an 18S embryo to the 12th somite and in a 20S embryo to the 16th somite.

Branchial arches: the first branchial arch is just visible.

Heart: a simple S-shaped tube in the midline of the embryo.

Sensory placodes, pits, etc.: both the optic and otic placodes are evident and may even be considered pits at this stage. The optic and otic vesicles are also obvious. The optic placodes and vesicles are more obvious than the otic ones.

Flexures and rotation: the embryo lies at right angles to the yolk surface, i.e. body torsion has not yet commenced. The head and brain are retort shaped and the brain is not obviously regionalized.

Blastopore: both the blastopore and primitive streak are obvious.

Gut: the gut is incomplete caudally and open ventrally along its entire length.

Somitomeres: three pairs of cranial somitomeres are evident macroscopically, cranial to the otic vesicle.

Organs: the notochord is evident.

Alligator mississippiensis (AM) — 0-1 days (after egg-laying)

Crocodylus johnstoni (CJ) — 0-1 days

Crocodylus porosus (CP) — 0-1 days

Voeltzkow (1899) (V) — Tafel VI Figs 37a, b

Reese (1915) (R) — Stage VIII and IX

Stage 2 (Fig. 1)

Blastoderm: the dorsal surface of the blastoderm is attached to the overlying eggshell membrane. The embryo is thus tethered to the innermost upper surface of the eggshell membrane at this and all subsequent stages of development. Blood vessels are now evident in the blastoderm. One pair emerges

from the embryo at approximately the caudal level of the heart, whilst another (larger) pair run down the lateral walls of the embryo to emerge at approximately the level of the 20th somite pair.

Somites: 21-25 pairs (decreasing markedly in size caudally).

Delineation of the embryo from the blastoderm: dorsally the embryo is almost completely delineated except for a very small circular area at the extreme caudal tip. Ventrally the definitive caudal and caudo-lateral boundaries of the embryonic body wall are established.

Branchial arches: the first and second arches and the first branchial cleft are visible.

Heart: an extra vertical loop has developed making a total of three loops. It lies in the centre of the embryo.

Sensory placodes, pits, etc.: the lens placode and optic cup are present and the otic pit is distinctly patent.

Brain: the hindbrain becomes evident as a clear transparent region.

Flexures and rotation: no body torsion, the embryo is still at right angles to the yolk. The cranial end of the embryo is flexed at approximately the level of the heart with the head lying at approximately 45° to the plane of the body.

AM 2 day
CJ 2 day
V Tafel VI Figs 38a, b, c
R Stage X and XI

Stage 3 (Fig. 1)

Somites: 26-30 pairs.

Delineation of the embryo from the blastoderm: complete.

Branchial arches: three branchial arches, the first branchial cleft, the second branchial groove and the branchial sinus are all present.

Tail: the tail end of the embryo is defined as a tail bud, which contains no somites.

Brain: the brain is regionalized into a forebrain, midbrain and hindbrain, the latter appearing as a distinct clear/transparent region.

Sensory placodes, pits, etc.: the optic cup is now the shape of an elongated horseshoe which extends below the lens vesicle on to the roof of the primitive oronasal cavity (floor of the brain).

Blastopore: neither the blastopore nor the primitive streak are now visible.

Extraembryonic membranes: the amnion is attached ventrally to the lateral body walls, cranially to the borders of the pericardium about the level of the 7-8th somite and caudally to the cranial margin of the fold of tail bud.

Flexures and rotation: no body torsion. Head approximately at right angles to the body.

AM 3 day
CJ 3 day
CP 3 day
V Tafel VI Fig. 40, Tafel VIII Fig. 51a
R Stage XII

Stage 4 (Fig. 1)

Somites: 31-35 pairs. The first somite is beginning to disappear but is included in this count.

Tail: distinct straight tail containing 3-5 somites in its base, the tail tip is unsegmented.

Flexures and rotation: body torsion has commenced. The cranial half of the embryo is rotated so that its right surface is in contact with the eggshell membrane and its left surface parallel to the underlying yolk. The caudal half of the embryo is not rotated and still lies at right angles to the shell surface and yolk.

Heart: displaced to the left side of the embryo and large.

Allantois: small elevation for the allantois is just visible immediately caudal to the cranial limit of the ventral tail fold; i.e. at approximately somite 27.

Branchial arches: three branchial arches, the first branchial cleft, the second and third branchial grooves and the branchial sinus are present. The cranial nerves to branchial arches 1-3 (mandibular division of trigeminal, facial and glossopharyngeal respectively) are very evident if the embryo is illuminated obliquely or viewed with transmitted light.

AM 4 day
CJ 4 day
CP 4 day
V Tafel VII Fig. 43, Tafel VIII Fig. 51a

Stage 5 (Fig. 2)

Somites: 36-40 pairs. Only traces of the first somite can be detected, although it is included in this count.

Tail: the tail tip is bent ventrally at right angles to the body of the embryo and it contains 6-10 somites at its base; the tail tip is unsegmented.

Flexures and rotation: body torsion is complete except for the tail. The head is further flexed with the roof of the brain at approximately 25° to the plane of the body.

Allantois: the allantoic bud is a distinct swelling, smaller in height than the tail.

Sensory placodes, pits, etc.: the external opening of the otic pit is closing. The otic pit is dorsal to the junction of the second and third branchial arches.

AM 5 day
CJ 5 day
CP 5 day
R Stage XIII

Stage 6 (Figs 1 and 2)

Sensory placodes, pits, etc.: nasal placodes present. Otic pit closed to the exterior surface.

Limbs: hindlimb buds are just visible on each side, the right hindlimb bud being marginally advanced over the left. No forelimb buds are present (see Fig. 5).

Flexures and rotation: body torsion is complete. The roof of the brain is at approximately 45° to the plane of the body while the floor of the brain (roof of the oronasal cavity) is horizontal and parallel to the body plane.

Brain: the olfactory bulbs, forebrain, midbrain and hindbrain are distinct. Four to six neuromeres are evident macroscopically in the clear hindbrain area.

Tail: the tip is starting to curl but is unsegmented. Somites are only present in the basal region of the vertically oriented tail.

Allantois: the allantoic anlage is larger but still smaller in height than the tail.

Gut: the foregut and hindgut are formed, but the midgut is incomplete ventrally where it is in contact with the yolk.

Extraembryonic membranes: blood vessels are now more prevalent in the vitelline and yolk sac membranes, the major ones emerging at the level of the 18th somite pair and other smaller ones at the sixth and 11th somite levels.

AM 6 day
CJ 6 day
CP 6 day

Stage 7 (Figs 2 and 5)

Limbs: distinct hindlimb bud, forelimb bud just visible as a thickened sinusoidal elevation (Fig. 5). The forelimb bud is longer craniocaudally (extending over approximately somites 12-15) than the hindlimb bud (which extends over somites 26-28) particularly in *Crocodylus johnstoni*.

Sensory placodes, pits, etc.: nasal placode is invaginating but has not yet formed a distinct pit.

Brain: the midbrain bulge is evident.

Tail: the tip of the tail is curled at approximately 90° to the remainder of the tail and contains somites.

Flexures and rotation: At the level of the heart the cranial end of the embryo is bent at approximately 90° to the plane of the rest of the body. The neck region is also flexed such that the roof of the brain is at approximately 60° to the body plane and the floor of the brain at 45°. This dichotomy in angulation accentuates the midbrain bulge.

Branchial arches: three branchial arches, the first branchial cleft and groove, the second and third branchial grooves and the branchial sinus are present.

AM 7 day
CP 7 day
V Tafel VII Fig. 44, Tafel VIII Figs 52 and 53, Tafel IX Fig. 66 major error, Fig. 74

Stage 8 (Figs 2 and 5)

Allantois: this is a large balloon-like sac, longer than the tail and containing allantoic blood vessels. It is not yet fused with either the amnion or the chorion.

External genitalia: a small elevation for the genital primordia (genital tubercle) is present.

Sensory placodes, pits, etc.: nasal pits are present on each side of the head, external to the swellings of the olfactory bulbs. Rathke's pouch is burrowing upwards towards the infundibular region of the brain. It is evidenced by a midline pit in the middle of the roof of the primitive oronasal cavity.

Limbs: the fore- and hindlimb buds are distinct, at the levels of somites 11-16 and 27-32 respectively (Fig. 5). The apical ectodermal ridge is developing on the hindlimb bud.

Tail: the tail tip is coiled through two 90° turns, and contains 12-18 somite pairs which extend to its tip. Flexion of the base of the tail has commenced.

AM 8 day
CJ 8 day
CP 8 day
V Tafel VII Fig. 45, Tafel VIII Fig. 54, Tafel IX Figs 67 major error, 75 and 76

Stage 9 (Figs 2 and 5)

Branchial arches: four branchial arches, the first and third branchial clefts and grooves, the second and fourth branchial grooves and the branchial sinus are visible. The branchial clefts are present only in the dorsal halves of the junctions between the first and second, and third and fourth arches, the ventral intervening tissue being continuous and forming the branchial grooves.

Facial processes: the maxillary process is distinct and extends forward as far as the mid-point of the eye. There are elevated rims of tissue around the nasal pits but these are not distinct enough to call the

lateral nasal and medial nasal processes at this stage. A remnant of the ingrowth of Rathke's pouch is visible in the roof of the primitive oronasal cavity.

Eye: the optic cup and central lens anlage are large and round but unpigmented.

Limbs: there is a distinct apical ectodermal ridge on the hindlimb bud, but not on the forelimb bud. The hindlimb bud extends out further from the body than the forelimb bud (Fig. 5).

Tail: the tail tip is curled through three 90° turns and the tail base is distinctly flexed from the lower lumbar region of the body. The tail contains approximately 20 somites.

Allantois: the allantois is large, fused to the amnion and chorion and is therefore of little further diagnostic value. The chorioallantoic membrane extends around approximately half of the eggshell.

Heart: the atria and ventricles are distinct. Both they and the lung primordia are visible through the transparent pericardial sac.

Gut and abdominal organs: the midgut and body walls are open ventrally from the caudal limit of the pericardial sac to two-thirds the way down the body; i.e. the distance between the upper and lower limb buds. The developing mesonephros and liver are just visible through the lateral body walls.

AM 9 day

CP 9 day

V Tafel IX Figs 68 and 77

Stage 10 (Figs 2 and 5)

Eye: pigment has just appeared in the iris. Consequently the eye appears light black except for the distinct central opaque lens. The right eye is usually pigmented earlier and more heavily than the left eye.

Branchial arches: five branchial arches, five branchial grooves and the branchial sinus are present. The first branchial cleft is dorsally located, immediately ventral to the otocyst. The third branchial cleft (between arches 3 and 4) is closing over. Branchial arches 1 and 2 are merged together in their ventral half and arch 2 has started to overgrow arch 3. Branchial arches 4 and 5 are very small. Viewed from the frontal aspect the first branchial arch is distinctly lobulated in the midline and is horseshoe shaped.

Facial processes: the medial and lateral nasal processes are obvious as distinct elevations on either side of the nasal pits. The maxillary process extends forward as far as the caudal junction of the medial and lateral nasal processes. The development of the maxillary process causes a distinct groove to form between it and the eye.

Limbs: the hindlimb bud has grown out further from the body wall than the forelimb bud. The

hindlimb bud is fan-shaped with a distinct apical ectodermal ridge (Fig. 5).

Tail: the tail is coiled through four 90° turns and is flexed from the lower lumbar region of the body.

Gut and abdominal organs: the mesonephros and liver are visible through the lateral body walls.

AM 10 and 11 days

CJ 10 day

CP 10 day

V Tafel VII Fig. 46, Tafel VIII Fig. 55 major error, Tafel IX Fig. 69 major error

Stage 11 (Figs 2 and 5)

Facial processes: the nasal pit slit is starting to form between the medial and lateral nasal processes. The maxillary process is club-shaped and extends to the junction of the medial and lateral nasal processes. It is continuous with the lateral nasal process.

Limbs: both fore- and hindlimb buds extend out caudally from the body wall, particularly the hindlimb buds. The forelimb has a distinct constriction signifying the differentiation of proximal and distal elements; this constriction is less marked in the hindlimb. Both limb primordia have distinct apical ectodermal ridges (Fig. 5).

Gut and abdominal organs: a loop of midgut tube is visible at the level of the umbilicus.

Branchial arches: the first branchial cleft is at the ventral aspect of the otocyst. The second branchial arch is overgrowing the third and arches 4 and 5 are starting to submerge.

Eye: distinct black pigment present in the iris.

Extraembryonic membranes: the chorioallantois extends as a band two-thirds the way around the breadth of the eggshell membrane.

AM 12 day

CP 12-13 days

Stage 12 (Figs 2 and 5)

Branchial arches: the first branchial cleft is sinusoidal in outline, situated above the otocyst and its margins show condensations for the auricular hillocks. The merged conglomerate of arches 1 and 2 is growing caudally towards the pericardium. It has overgrown arch 3 to reach the junction between the third and fourth branchial arches. This conglomerate forms the base of the lower jaw, which extends as far forward as the middle of the lens of the eye. Arches 4 and 5 are still visible but very small. The branchial sinus is patent.

Facial processes: the maxillary process is distinctly club-shaped, extending forwards as a large shelf of tissue beneath the eye to reach the junction of the medial and lateral nasal processes. The nasal pit slits

are deepening as the medial and lateral nasal processes enlarge. There is a distinct notch and furrow in the midline of the face between the medial nasal processes of each side.

Limbs: the forelimb has a definite constriction for proximal and distal elements. It is starting to bend in this area so that it lies closer to the flank of the embryo. The hindlimb is markedly elongated and shows little differentiation into proximal and distal elements. There is just a hint of foot plate formation in the lower limb, which still has a distinct apical ectodermal ridge (Fig. 5).

AM 13 and 14 days
 CJ 14 day
 CP 14-15 days
 R Stage XIV
 V Tafel VII Fig. 47, Tafel VIII Fig. 55, Tafel IX Fig. 69 major error

Stage 13 (Figs 2 and 5)

Facial processes: the nasal pit slits are very distinct. The maxillary processes are prominent and clearly continuous with the lateral nasal processes.

Limbs: the forelimb is now distinctly bent (towards the pericardium). The end of the hindlimb is flattened and slightly enlarged as the footplate becomes demarcated (Fig. 5).

Branchial arches: arch 3 is almost completely overgrown by arch 2 which now reaches the pericardium. Arches 4 and 5 are difficult to see. The branchial sinus has closed. The anterior margin of the lower jaw is becoming distinct as it grows out from the merged basal conglomerate of arches 1 and 2. The first branchial cleft is now more horizontally oriented and is hereafter called the external auditory meatus. The upper ear flap is sinusoidal with a midline bulge formed by the merging of the auricular hillocks. A groove runs craniocaudally along the basal (dorsal) aspects of the branchial arches and lower jaw.

Extraembryonic membranes: the chorioallantois now extends as a ring around the inner circumference of the eggshell membrane in the centre of the egg.

AM 15 day
 CP 16-17 days
 R Stage XV and XVI
 V Tafel IX Figs 70 and 79, Tafel XV Fig. 134

Stage 14 (Figs 2 and 5)

Facial processes: the nasal pit slit is closed by merging of the medial nasal, lateral nasal and maxillary processes. The medial nasal processes project markedly and have anterodorsal external bulges. These grow forward to displace the external nares

dorsally at later stages of development. The medial nasal processes also have two anterior intra-oral bulges signifying the onset of primary palate development. The maxillary processes have sinusoidal intra-oral margins signifying the onset of secondary palate development. The internal nares are distinct.

Limbs: the foot and hand plates are distinct, the foot plate being obviously advanced over the hand plate (Fig. 5).

Branchial arches: the second branchial arch has overgrown the third, fourth and fifth arches which have now disappeared. This merged conglomerate (including the first arch) forms the base of the lower jaw and the neck. A craniocaudal groove is still present along the dorsal margins of the merged first and second arches.

Lower jaw: the lower jaw is one-quarter the way beneath the upper jaw. It is broad and round in *A. mississippiensis* but more pointed in *C. johnstoni*.

Ear: the upper ear flap is overgrowing the opening of the external ear. White opacities are evident in the region below the ear opening. These represent internal condensations for ear development.

Denticles: one denticle is present on each side of the developing primary palate (merged medial nasal processes) margins.

Flexures and rotation: the embryonic face rests on the large bulge of the thorax (pericardial sac).

Gut and abdominal viscera: a large loop of gut is herniated out through the narrow umbilical stalk and touches the underlying yolk. The abdominal viscera (e.g. liver and mesonephros) are prominently visible through the body walls.

Tail: the tail tip has a terminal kink and the tail is markedly coiled.

External genitalia: in *A. mississippiensis* this is still a small tubercle-like elevation but in *C. porosus* and *C. johnstoni* it is much larger.

Embryonic reflexes: contralateral withdrawal reflexes are present.

AM 16 and 17 days
 CJ 16 day
 CP 18-19 days
 R Stage XVII

Stage 15 (Figs 3 and 5)

Lower jaw: extends one-third to half the way beneath the upper jaw. Dorsal to the lower jaw complex, there are three furrows and surface elevations, which appear to be dorsal representations of the branchial arches, which have now coalesced ventrally.

Denticles: two denticles are present on the anterior upper jaw margins of each side. One is on the margin of the primary palate, the other on the maxillary process just behind the closure zone.

Eye: pigmented dark black stria in the iris radiating out from around the central lens. There is an elevated rim of tissue above each eye delineating the orbit and forming the anlage for the upper eyelid.

Limbs: distinct proximal and distal elements, foot and hand plates (but no digit rays) on both the fore- and hindlimbs (Fig. 5).

Facial processes: the anterodorsal bulges of the medial nasal processes have coalesced in the midline and displaced the external nares dorsally. The primary palate is present but still retains two anterior bulges. There is a distinct hollow in the face beneath the anterior third of the eye. The tectoseptal process is evident in the roof of the primitive oronasal cavity.

AM 18-20 days
 CJ 18 day
 CP 20-23 days
 R Stage XVIII
 V Tafel VII Fig. 48, Tafel VIII Fig. 56,
 Tafel IX Figs 71 and 80, Tafel X Fig. 84a,
 Tafel XV Fig. 135

Stage 16 (Figs 3 and 5)

Limbs: faint condensations for the digits present in the foot plate but not in the hand plate (Fig. 5).

Lower jaw: extends two-thirds of the way beneath the upper jaw.

Denticles: three pairs on the upper jaw margins; one on the primary palate and two on the maxillary processes.

Facial processes: the upper jaw is hook-shaped, being moulded around the bulge of the pericardial sac. Small secondary palatal shelves are present immediately behind the posterolateral margins of the primary palate.

AM 21 day
 CP 24 day
 V Tafel IX Figs 72 and 81

Stage 17 (Figs 3 and 5)

Limbs: mesodermal condensations for the digits are present on both the foot and hand plates (Fig. 5). There are five digits in the hands and four in the feet.

Lower jaw: the lower jaw is behind the primary palate bulges. The furrows and elevations dorsal to the lower jaw have disappeared.

Denticles: four pairs on the upper jaw margins; one on the primary palate and three on the maxillary

processes. Six pairs of mandibular denticles are present.

Egg caruncle: two small elevations, widely separated, have appeared on the anterior tip of the snout.

Palate: the secondary palatal shelves are distinct as lateral extensions of the maxillary processes. They are closest to each other anteriorly behind the primary palate, but are not yet in contact. The tectoseptal processes are closing in the posterior half of the oronasal cavity.

Scales, scutes, etc.: the somite pattern is distinct particularly on the dorsal aspects of the body and tail. This heralds the onset of scale differentiation. Anlage for the abdominal ribs are also visible.

Flexures and rotation: the head is extended off the bulge of the pericardial sac due to elongation of the neck.

Ear: the external ear flap is distinct and the adult format of the external ear is established.

AM 22 and 23 days
 CJ 23 day
 CP 25-26 days
 R Stage XIX
 V Tafel VIII Fig. 57, Tafel IX Fig. 82,
 Tafel X Fig. 85a

Stage 18 (Figs 3 and 5)

Limbs: the digit rays on the hand and foot plates are now distinct cartilaginous condensations as opposed to mesodermal ones. The margins of the interdigital tissues are straight, giving the profiles of the hand and foot plates a crenellated as opposed to a rounded appearance (Fig. 5).

Lower jaw: the lower jaw lies beneath the anterior primary palate bulges.

Denticles: there are five pairs of maxillary denticles, the anterior pair of which are regressing.

Egg caruncle: two widely spaced blebs on the anterior tip of the snout. They are white in colour.

Palate: the secondary palatal shelves are one-quarter closed at the earliest phase of stage 18 and three-quarters closed at the latest phase. This stage can be accurately subdivided by specifying the extent of secondary palate closure. The upper jaw margin has a straighter, less hooked profile.

Eye: the margins of the upper eyelid anlage extend over the superior rim of the iris. There is a distinct groove between the margins of the eyelid anlage and the eye into which small instrument probes can be passed.

Scales, scutes, etc.: scalation is now marked, particularly dorsally.

Pericardial sac: the bulge of the transparent pericardial sac is starting to be submerged into the ventral thoracic wall. The lower jaw no longer rests on the pericardial sac.

AM 24-26 days
 CJ 26 day
 CP 27-30 days
 V Tafel VII Fig. 49, Tafel VIII Fig. 58,
 Tafel X Fig. 86a, Tafel XI Fig. 105

Stage 19 (Figs 3 and 5)

Eye: the lower eyelid is distinct as well as the upper one. The anterior nictitating membrane anlage is present in the anterior corner of the eye.

Egg caruncle: the two elevations of the egg caruncle have approximated each other at the tip of the snout. The tissue between them is thin and often appears transparent under incident illumination.

Lower jaw: the lower jaw is behind the anterior margin of the upper jaw. If the premaxillary bulges are large this results in an opening of the mouth. The tongue and floor of the mouth contents sag downwards beneath the margins of the lower jaw.

Limbs: the cartilaginous digit anlagen are distinct and interdigital clefting has commenced. This is represented by slight notches in the margins of the interdigital tissues particularly in the foot plates (Fig. 5).

Palate: the palate is almost completely closed.

Colouration: white flecks are obvious on the margins of the upper and lower jaws and around the ears. These represent marked underlying ossification.

External genitalia: the end of the external genitalia has developed a globular swelling.

Denticles: seven pairs of denticles are present on the lower jaw. At this and later stages the numbers of denticles are too variable to be useful as diagnostic indices of stages.

Species differences: in *C. johnstoni* and *C. porosus* the nostrils are elevated on a nasal disc, and the lateral jaw margins have a distinct notch in the region where the primary palate closed with the secondary palate. This notch later accommodates the large fourth dentary tooth.

AM 27-28 days
 CP 31-33 days
 V Tafel X Figs 87a and 88a

Stage 20 (Figs 2 and 5)

Limbs: nail anlagen are present on the most medial three digits of the hands and feet (Fig. 5). The nail anlage first appears on the most medial digit of the foot, then on the other two foot digits, the most medial digit of the hand and finally on the medial three digits of the hand. This developmental

sequence is rapid and occurs early in Stage 20. Interdigital clefting now extends along approximately one-quarter of the length of the digits (Fig. 5). The outer two digits of the hand and the outer digit of the foot never develop nails.

Egg caruncle: the egg caruncle is now a more solid structure due to a consolidation of the central area between the two initial swellings.

Lower jaw: the lower jaw is in its adult relationship with the upper jaw.

External genitalia: the end of the external genitalia is now more pointed with a distinct elevation on the cranial half of its tip.

Palate: the palate is completely closed but the basihyal valve is not yet present.

Pericardial sac: the pericardial sac containing the heart, lungs, etc., is now one-quarter withdrawn into the ventral body cavity.

Tail: the tail has a hook-like kink at its extreme tip.

Colouration: white flecks of ossification are present along the margins of the upper and lower jaws, around the external auditory meatus, and in the proximal and distal elements of the limbs.

Scales and scutes: scale formation is marked dorsally and scutes are beginning to appear in the neck region behind the skull.

AM 29-30 days
 CJ 30 day
 CP 34-36 days
 R Stage XX
 V Tafel VII Fig. 50, Tafel VIII Fig. 59,
 Tafel XI Figs 95 and 106, Tafel XV Fig. 136

Stage 21 (Figs 3 and 5)

Limbs: nails are clearly present on the medial three digits of the hands and feet (Fig. 5). Interdigital clefting extends three-quarters the way along the digits — almost to its adult position. Phalanges can be distinguished in the digits (Fig. 5).

Scales and scutes: scales are now evident on the ventral aspect of the body of the embryo as well as dorsally on the snout, neck, body and tail. The dorsal neck scutes are clearly defined.

Egg caruncle: the egg caruncle is a solid mass of tissue on the tip of the snout but the tissue around the base of the caruncle is not yet differentiated from the remainder of the snout scales.

Palate: the superior basihyal valve flap is present at the posterior margin of the palate (and the inferior flap at the base of the tongue) and a plexus of palatal blood vessels is conspicuous.

Pericardial sac: the pericardial sac is half withdrawn into the body cavity.

External nares: elevations for the constrictor nares muscles are evident.

Eye: a white ring in the iris surrounds the outline of the lens of the eye and is overlapped by both upper and lower eyelids.

AM 31-35 days
 CJ 33 day
 CP 37-45 days
 V Tafel VIII Fig. 60, Tafel XI Figs 107a, b

Stage 22 (Figs 3 and 5)

Colouration: pigmentation commences. It is first visible in the margins of the upper jaw, along the ventral aspect of the flank and in the proximal and distal elements of the limbs. There is little or no pigmentation dorsally at this stage.

Limbs: the nails are distinctive and the interdigital clefting is at its adult level (Fig. 5). Scalation is difficult to see on the limbs.

Eye: the eyelids are frequently closed at this and subsequent stages.

Pericardial sac: this is two-thirds withdrawn into the body cavity.

AM 36-40 days
 CP 46-53 days
 R Stage XXI
 V Tafel VIII Figs 61 and 62

Stage 23 (Figs 4 and 5)

Colouration: pigmentation is more extensive. Dorsally the striped pigmentation pattern is present and varies within and between species. This is associated with definitive scale and scute patterns. Pigment is also present ventrally and in all elements of the limbs. The pigment is not dense so that embryos are a light brown colour.

Limbs: scales are present on the proximal and distal elements. The nails on the feet have a slight elevation at their tips (Fig. 5).

Jaws: sensory papillae are present along the lateral jaw margins and scales are evident on the skin covering the floor of the mouth.

Egg caruncle: the egg caruncle is located on a white smooth (i.e. no sensory papillary elevations) base at the tip of the snout.

Brain: the midbrain is evident as a white bulge at the back of the cranium. The skin overlying it is poorly pigmented and the developing cranial bones have not yet enclosed it.

Pericardial sac: this is three-quarters withdrawn into the body cavity.

Palate: an extensive plexus of blood vessels and sensory papillae are present.

Species differences: in *C. johnstoni* and *C. porosus* the scales along the jaw margins are triangular in shape with the apex of the triangle towards the jaw margins, giving the latter a serrated appearance. The external genitalia are larger and more advanced in their differentiation.

AM 41-45 days
 CJ 41 day
 CP 54-62 days
 V Tafel XI Fig. 96

Stage 24 (Figs 4 and 5)

Colouration: pigmentation is now extensive and denser so that embryos appear blacker in colour. Various patterns are present both within and between species.

Limbs: the nails on the hand also have elevations at their tips (Fig. 5) and these elevations are starting to form the curves at the tip of the nails.

Brain: the midbrain is enclosed by bone and the skin overlying it is pigmented.

Pericardial sac: this is fully withdrawn into the body cavity and the ventral thoracic wall is closing in the midline.

Yolk: a large volume of yolk lies external to the embryo and the umbilical area on the ventral aspect of the embryo is large.

Scales and scutes: the scales and scutes are now very evident as elevations on all aspects of the embryo including the snout.

AM 45-50 days
 CP 63-70 days
 V Tafel XI Fig. 97

Stage 25 (Figs 4 and 5)

The embryo is like a miniature version of a hatching, with a considerable volume of external yolk and a large umbilical region. The nails have a hooked appearance which becomes more pronounced towards hatching (Fig. 5). Musk glands are visible along the posterior lateral margins of the floor of the lower jaw. The egg caruncle is a bifid elevation on a smooth base similar in structure to that at hatching, although perhaps a little less pigmented (this is variable). Few macroscopic changes are visible at this and later stages so that aging is best done by morphometric ratios such as volume of external yolk, length of embryo, etc.

AM 51-60 days
 CP 72-87 days
 R Stage XXII
 V Tafel VIII Fig. 63, Tafel XI Figs 98a, b

Stage 26

This stage does not occur in *Alligator mississippiensis*. Embryos of *C. johnstoni* and *C. porosus* at this stage are identical to those at Stage 25 except that teeth have erupted and the characteristic sensory elevations on the scales are present. Teeth of *A. mississippiensis* rarely erupt before hatching, and if they do, it is at Stage 28.

CJ 71-75 days
CP 72-88 days

Stage 27 (Figs 4 and 5)

This stage is characterized by the withdrawal of remaining yolk into the abdominal cavity of the embryo. It commences with the ventral body wall growing out to enclose the herniated embryonic intestines, yolk sac and yolk, and ends with the absorption of the latter into the abdominal cavity. Ventral skin then forms across the yolk scar.

AM 60-63 days
CJ 75-80 days
CP 89-92 days
V Tafel XI Figs 99 and 100

Stage 28 (Figs 4 and 5)

At this stage the yolk scar diminishes in length and width as the absorbed abdominal yolk is utilized. There are considerable variations both between and within species as to the volume of absorbed yolk and the size of the yolk scar at hatching. The temperature of egg incubation influences the parameters (Ferguson and Joanen 1982, 1983). Hatching occurs at this stage and may be initiated by a variety of external factors.

AM 64-70 days
CJ 81-87 days
CP 92-97 days
R Stage XXIII
V Tafel VIII Fig. 64, Tafel XI Fig. 108

Further Characterization of Stages 24-28

It is obvious that later in development, one embryonic stage covers a large range of embryonic ages. For this reason I have attempted to further refine these stages, for example, by reference to tooth eruption. However, counting the numbers of erupted teeth in crocodilian embryos is not reliable unless close attention is paid to the position of such teeth in the jaw quadrants. Crocodilians develop and resorb at least 25 embryonic teeth before establishing a functional, erupted dentition (Westergaard and Ferguson 1986, 1987). Furthermore, some teeth, once erupted, only remain functional for a few days before being resorbed and falling out (Westergaard and Ferguson 1986, 1987). Thus, merely counting the

teeth erupted gives no idea of continuing development. It is, however, possible to accurately stage later crocodilian embryos by carefully analysing their dentitions, either by radiography or by reconstruction of the dentition from serial histological sections of the head. Westergaard and Ferguson (1986, 1987) provide extensive details about the development of the dentition in *Alligator mississippiensis* from first initiation to hatching. This includes detailed fate maps from which embryos can be staged: examples of four such fate maps are given in Figure 6. For further details of crocodilian embryology readers are referred to the above publications and to Ferguson (1985).

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