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A Field Key to the Developmental Stages of Marine Turtles (Cheloniidae) with Notes on the Development of *Dermochelys*

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ABSTRACT. – Descriptions of the developmental stages of embryonic marine turtles are presented in the form of a dichotomous key supported by drawings to facilitate identifying stages of development in the field. The key emphasizes the sequential appearance or loss of external morphological structures that can be seen either with the unaided eye or with a ×10 hand lens and a handheld light. Stages are placed in the context of normal beach temperatures to facilitate estimation of laying date, emergence date, and events that cause embryonic mortality. Measurements of embryos are presented to assist determining stage.

KEY WORDS. – embryo; developmental stages; marine turtles; Cheloniidae; Dermochelyidae

The earliest descriptions of marine turtle embryos were made from specimens collected opportunistically to illustrate specific aspects of development. For example, embryos obtained at different times during development were described and illustrated for *Eretmochelys imbricata* (Voeltzkow 1903; Fuchs 1915; Deraniyagala 1939), *Chelonia mydas* (Parker 1880; Deraniyagala 1939; Penyapol 1958; Domantay 1968), *Caretta caretta* (Agassiz 1857; Mitsukuri 1894, 1896–1898; Jordan 1917; Fujiwara 1966; Kondo 1986; Kuratani 1999), *Lepidochelys olivacea* (Deraniyagala 1939), and *Dermochelys coriacea* (Deraniyagala 1933, 1939, 1953) as part of a variety of studies. Agassiz (1857), Mitsukuri (1894, 1896–1898), and Fujiwara (1966, 1971) examined aspects of ovipositional development. Raynaud et al. (1980) focused on the projections of the epithelia of the branchial arches of leatherback turtles (*D. coriacea*). Kuratani (1999) described the development of the chondrocranium in *C. caretta* embryos. Billett et al. (1992) used scanning electron microscopy to enhance the descriptions of *C. caretta* embryos. None of these studies provided a complete developmental sequence for any species of marine turtle.

The first standard developmental sequence for a marine turtle from oviposition to hatching was produced by Crastz (1982) for *L. olivacea*. Miller (1985b) combined descriptions of embryos of the Cheloniidae to define developmental stages from fertilization through preemergence for all species of marine turtles. More recently, Kaska and Downie (1999) used Miller's postovipositional stages to describe green and loggerhead turtle embryos in the Mediterranean. Embryonic development of the leatherback was described in detail by Renous et al. (1989) based on Miller (1985b). Al-Mukhaini et al. (2010) used Miller's definitions as a foundation to describe development in green turtle embryos at 30°C.

PRACTICAL APPLICATIONS OF A STAGING KEY

Staging tables provide a description of ontogenetic changes of embryos incubated under defined conditions (Hamburger and Hamilton 1951; Ewert 1985; Miller 1985a; Hopwood 2007) that can be used to assess development under various conditions, such as natural, experimental, and unknown (e.g., *C. caretta*, Özdemir et al. 2008; *Carettochelys insculpta*, Beggs et al. 2000; *Crocodylus porosus*, Magnusson and Taylor 1980; Webb et al. 1983).

Embryonic development occurs within the complex environment of the nesting beach (Ackerman 1997). As a result, nest site selection has a significant impact on incubation because the environment experienced by the developing embryos depends on the location selected by the nesting female (Mortimer 1982; Wood and Bjorndal 2000; Miller et al. 2003; Serafini et al. 2009). The physical characteristics of the substrate mediate thermal and hydric insulation and gas exchange between the environment and the developing embryos within the nest (Mortimer 1990; Ackerman 1997; Hewavisenthi and Parmenter 2002; Ackerman and Lott 2004).

Field assessment of the stage and time during incubation at which embryos died can help to identify mortality factors, such as subsand flooding (Caut et al. 2010), excessive rainfall (Ragotzkie 1959), inundation (Foley et al. 2006), collapse of egg chambers during pipping and hatchling emergence (Mortimer 1990), and

extreme temperatures (Valverde et al. 2010), that affect embryonic survival in the nesting beach. Herein we present a simplified key to developmental stages of marine turtles, which in conjunction with knowledge of beach temperature and/or duration of incubation, helps bracket when mortality occurred, thereby helping to identify mortality factors.

METHODS USED TO GENERATE THE KEY

Miller (1985b) defined 31 stages in the development of marine turtle embryos, of which stages 1–5 occur inside the oviduct of the female and stages 6–31 occur in the nest after oviposition. The five preovipositional stages described by Miller (1985b) are not included in the key. For stages 6–31, only those external morphological characters that can be seen by the unaided eye or by using a ×10 hand lens and a handheld light are presented in the key. The original stage descriptions were a composite compiled from examination of multiple individuals of each species incubated under natural and controlled conditions (Miller 1982, 1985b). Descriptions of characters that relate to only one species have been de-emphasized in favor of general ones that place the specimen in an appropriate stage regardless of species. Drawings were made from specimens and photographs. Volume of embryos and their yolks was determined by water displacement in a graduated cylinder (± 2.5 cc). Measurements were made using Vernier calipers (± 0.1 mm) on fresh and preserved specimens.

Eggs were collected at oviposition and moved to a protected hatchery area or into incubators (temperatures: 26°C ± 0.5°C, 29°C ± 0.5°C, 32°C ± 0.5°C). The majority were moved within 1 hr (Limpus et al. 1979). Eggs of *C. mydas*, *Natator depressus*, *C. caretta*, and *D. coriacea* were incubated under both laboratory and beach conditions; eggs of other species were incubated in beach hatcheries (Miller 1982). The *L. olivacea* embryos examined were unhatched remnants of emerged clutches; these specimens were compared with descriptions by Crastz (1982) to assign appropriate stages.

In the following key, the chronology of the stages is given as a percentage of the developmental time based on eggs incubated at 29°C. Although not providing exact timing of when a stage occurred, the use of a percentage accommodates variation in the duration of development at different temperatures under field conditions. The use of 29°C as the baseline is justified because the temperature is 1) near the middle of the embryonic tolerance limits (Ackerman 1997) and 2) near the pivotal temperature for sexual differentiation for most species (except for *Lepidochelys*) (Wibbels 2003).

Measurements of specific characteristics are presented by species to augment the determination of a stage. Total disc length was measured as the straight distance between the anterior and posterior of the embryonic disc; crown-to-rump length was measured as the straight distance from the top of the curled embryo to the curl at the base of the tail. Forelimb length was measured as the straight distance between the proximal and distal ends of the flipper manus of the developing embryo. Straight carapace length was measured as the straight distance between the anterior and posterior ends of the carapace of the developing embryo. Straight carapace width was measured as the straight distance across the carapace of the developing embryo. Interclaw distance was measured as the straight distance between the claws of the fore flipper. Development time is defined as the interval from oviposition to pipping. Pipping takes place when the embryo ruptures the eggshell. Hatching occurs when the embryo exits the eggshell. Emergence is defined as when the hatchling appears on the beach surface.

RESULTS: THE KEY

The following dichotomous key to the stages of development of the Cheloniidae (and in general to development of *Dermochelys*) (Figs. 1 and 2) is based on developmental stages defined by Miller (1985b), using embryos of *C. mydas* (*n* = 733), *N. depressus* (*n* = 375), *C. caretta* (*n* = 1303), *Eretmocheleys imbricata* (*n* = 567), *L. olivacea* (*n* = 51), and *Dermochleys coriacea* (*n* = 96) (Miller 1985b).

Dichotomous Key to the Embryonic Stages of Marine Turtles when Eggs Have Been Removed from a Nest on the Beach or Other Conditions of Incubation

(Based on developmental stage definitions by Miller 1985b. %DT [development time] = % of incubation time from oviposition to pipping for eggs incubated at 29°C.)

1a. Embryo recognizable as a turtle with pigment on the carapace 23
1a. Embryo other than with pigmented carapace 2
2a. Embryo with limbs twisted flat against the sides of the body and with iris pigmentation 21
2b. Embryo other than above 3
3a. Embryo with definite head and eyes and with laterally projecting limb buds 17
3b. Embryo other than above 4
4a. Embryo mostly disk shaped, lacking eye bulges 5
4b. Embryo elongate with definite eye bulges 13
5a. Blastopore shaped as a transverse slit or as a wide, anteriorly opening crescent ..... **Oviposition Stage 6** [0.5 ± 0.5 %DT]
5b. Embryonic area not as above 6
6a. Blastopore shaped as a posteriorly opening crescent ..... **Stage 7** [1.2 ± 0.5 %DT]
6b. Embryonic area not as above 7
7a. Blastopore shaped as an inverted "U"; head fold indicated ..... **Stage 8** [2.8 ± 0.5 %DT]
7b. Embryonic area not as above 8
8a. Blastopore shaped as an inverted "U"; head fold shaped as a posteriorly opening crescent; no somites present ..... **Stage 9** [3.8 ± 0.5 %DT]
8b. Not as above 9
9a. 2 or 3 pairs of somites present; neural crests touch at posterior end of head ..... **Stage 10** [4.8 ± 0.5 %DT]
9b. More than 4 pairs of somites present 10

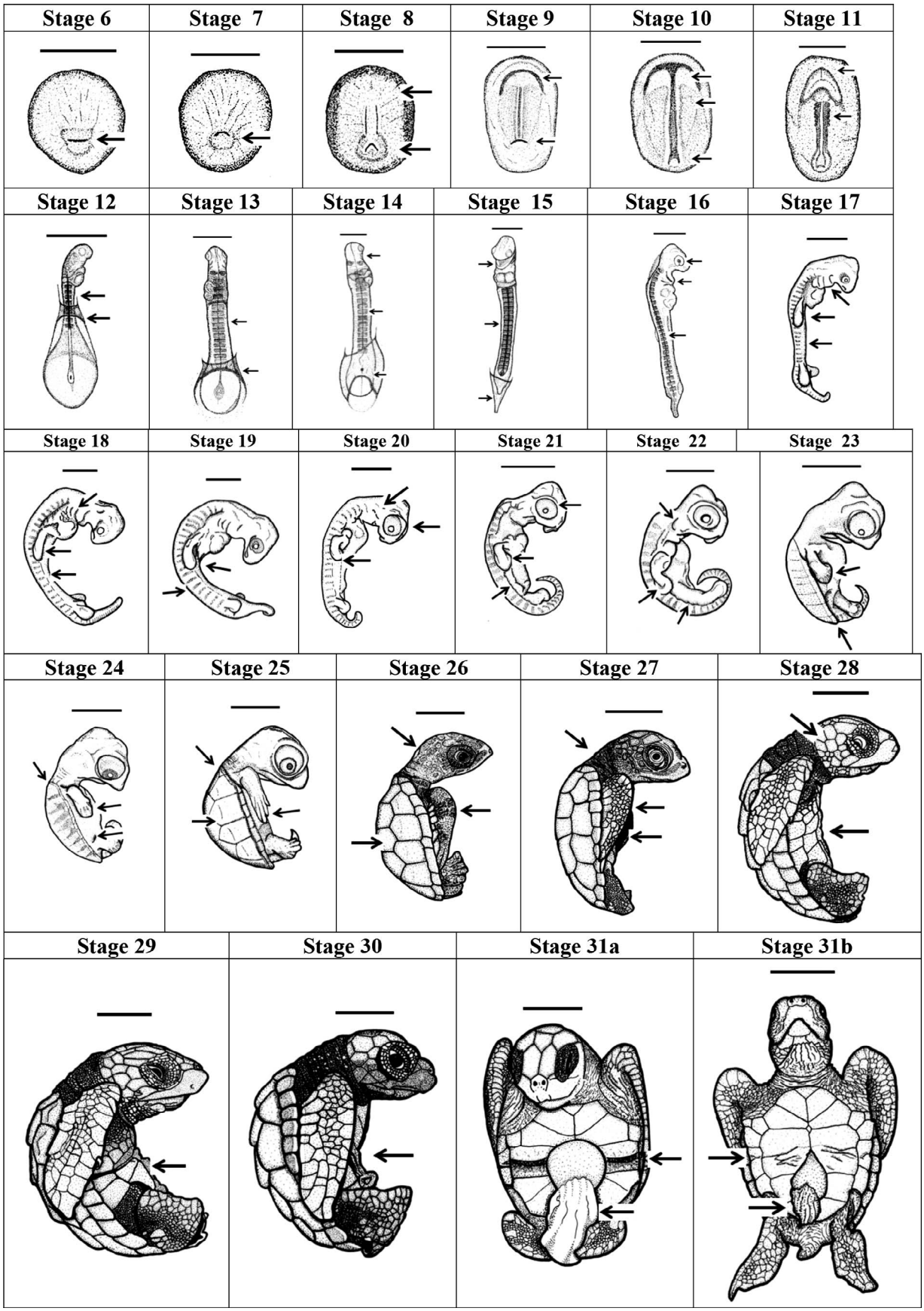

Figure 1. Illustrations of the embryonic stages of marine turtles based on developmental stage definitions by Miller (1985b). DT (development time) = time from oviposition to pipping. Arrows indicate key characteristics. Bar = 1 mm: stages 6–20; 5 mm: stages 21–24; 10 mm: stages 25–31.

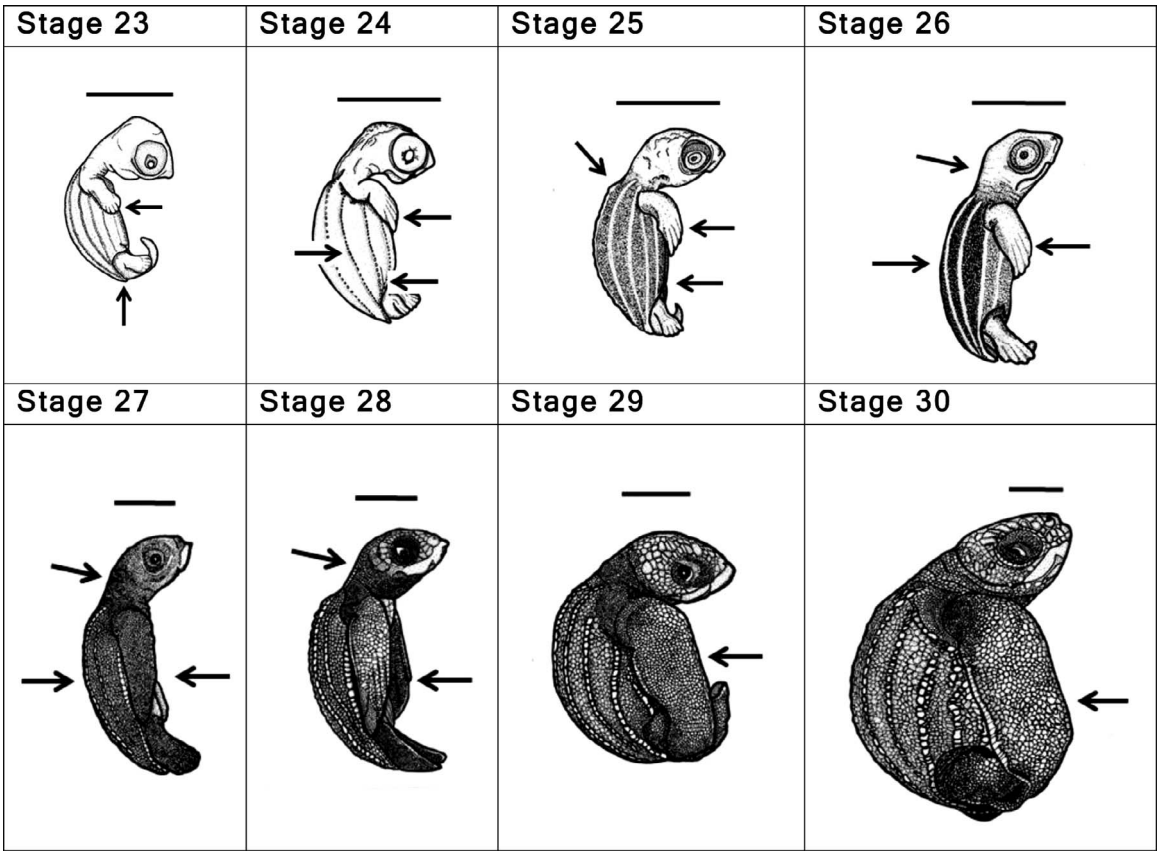

Figure 2. Developmental stages 23–30 of *D. coriacea* embryos based on Miller (1985b). Arrows indicate key characteristics. Bar = 10 mm: stages 23–30.

10a. 5 or 6 pairs of somites present; neural crests touching or fusing along midline of head ..... **Stage 11** [5.7 ± 0.5 %DT]
10b. More than 6 pairs of somites present 11
11a. 8–10 pairs of somites present; amnion covers about one-half of the total length ... **Stage 12** [6.7 ± 0.5 %DT]
11b. More than 11 pairs of somites present 12
12a. 12–14 pairs of somites present; neurocentric canal bounded posteriorly by a low ridge; amnion covers about three-fourths of total length ..... **Stage 13** [7.6 ± 0.5 %DT]
12b. More than 14 pairs of somites present 13
13a. 15–17 pairs of somites present; mouth not open; amnion covers neurocentric canal ..... **Stage 14** [8.6 ± 0.5 %DT]
13b. More than 17 pairs of somites present 14
14a. 19–21 pairs of somites present; mouth open as a deep "V"; first pharyngeal cleft open; posterior amnionic tube formed ..... **Stage 15** [11.5 ± 1 %DT]
14b. More than 21 pairs of somites present 15
15a. 23–25 pairs of somites present; lens differentiated in the eye, pharyngeal clefts 1 and 2 open; small limb buds visible on lateral body wall ..... **Stage 16** [13.4 ± 1 %DT]
15b. More than 26 pairs of somites present 16
16a. 29–34 pairs of somites present; limb buds bulge lateroposteriorly; all pharyngeal clefts open ..... **Stage 17** [16.3 ± 1 %DT]
16b. More than 35 pairs of somites present 17
17a. 35–40 pairs of somites present; digital plates not free of body wall; flaps have developed on anterior borders of all pharyngeal clefts ..... **Stage 18** [19.2 ± 1 %DT]
17b. More than 40 pairs of somites present 18
18a. 40–45 pairs of somites present; digital plates free from body wall and project laterally ..... **Stage 19** [22.0 ± 1 %DT]
18b. More than 45 pairs of somites present 19
19a. Digital plates partially or completely twisted flat against the body wall; iris unpigmented; pharyngeal clefts nearly closed ..... **Stage 20** [25.0 ± 1 %DT]
19b. Not as above 20
20a. Iris pigmented along its posterior border; carapace rudiment is a ridge on the lateral body wall and extends above the bases of the limbs; digital plates without serrations; digital plate not separated from limb by a ridge ..... **Stage 21** [29.5 ± 1 %DT]
20b. Not as above 21
21a. A distal ridge defines the limit of the limb from the digital plate; marginal ridge of carapace marked by small, low serrations; pharyngeal clefts closed ..... **Stage 22** [34.5 ± 1 %DT]
21b. Not as above 22
22a. Posterior border of carapace complete at least by a low ridge; anterior border incomplete; digital serrations present indicated as shallow ridges and grooves..... **Stage 23** [39.4 ± 1 %DT]
22b. Not as above 23
23a. Anterior border of carapace indicated by at least a low ridge across neck; posterior border of inframarginal area is defined; anterior is not; scutes of carapace indicated; flecks of pigmentation may occur on carapace; digital serrations present as ridges and grooves..... **Stage 24** [45.0 ± 1 %DT]
23b. Not as above 24

Table 1. Embryo volume and yolk volume relationships in late stage marine turtle embryos incubated at 29°C.

Relationship	Embryo:yolk volume	Stage	Days of incubation	% of incubation
Embryo volume less than yolk volume	EV < YV	27	34–39	70.6 ± 2
Embryo volume about equal to yolk volume	0.8–1.3:1	28	40–43	78.3 ± 2
Embryo volume greater than yolk volume	1.5–4:1	29	44–47	86.0 ± 2
Embryo volume much greater than yolk volume	5–11:1	30	47–50	96 ± 2
Yolk mass mostly withdrawn and mostly covered with pigmented tissue	EV >> YV	31	49–52	100

24a. Periphery of carapace complete anteriorly and posteriorly; all scutes have differentiated; body and flipper scales undifferentiated; tagging scales may be indicated; digital serrations elongate; claw rudiment present ..... **Stage 25** [53.0 ± 2 %DT]
24b. Not as above 25
25a. Scutes of carapace becoming pigmented; head scales, except over ear, and cutaneous papillae present; all flipper scales present; tops of scales may be pigmented; tagging scales present..... **Stage 26** [62.0 ± 2 %DT]
25b. Not as above 26
26a. Unpigmented scales over ear region except pigmented in hawksbill; all flipper scales present and pigmented; transverse plastronal fold indicated as a bend perpendicular to axis of body; yolk volume greater than specimen ..... **Stage 27** [70.6 ± 2 %DT]
26b. Not as above 27
27a. Scales over ear pigmented; transverse plastronal fold forms oblique angle between abdominal and thoracic scutes; specimen volume about equal to yolk volume ..... **Stage 28** [78.3 ± 2 %DT]
27b. Not as above 28
28a. Tansverse plastronal fold forms acute angle; inframarginal scutes form groove; hatchling pigmentation and morphology present; specimen volume greater than yolk volume ratios 1.5 to 4:1..... ..... **Stage 29** [86.0 ± 2 %DT]
28b. Not as above 29
29a. Remaining yolk mass covered with pigmented membrane; inframarginal scutes folded near plastron; yolk mass less than one-half the volume of unpipped specimen ..... **Stage 30** [94.7 ± 2 %DT]
29b. Embryo pipped with at least front flippers out of eggs shell..... 30
30a. Embryo pipped; yolk mass mostly withdrawn into abdomen; transverse plastronal fold forms an acute angle; moist membranes still attached; specimen not ready to emerge ..... **Stage 31a** [100 ± 2 %DT]
30b. Embryo out of eggshell; yolk mass absent; transverse plastronal fold forms an oblique angle or nearly absent; any attached membranes appear abraded; specimen ready to emerge ..... **Stage 31b** [102 ± 2 %DT]

Although stages of development are discrete and separated by unambiguous changes in morphology, development is a continuous process, and specimens may exhibit characters intermediate between two stages. In these cases, adding a + to the stage number to indicate that the embryo exhibits a set of characteristics that is more advanced than the stage description helps to better define the position of the specimen in the developmental sequence (e.g., stage 16+ indicates a specimen that exhibits 26 pairs of somites but has only 2 pharyngeal clefts open). Where specific staging is required, the key should be used in conjunction with the detailed descriptions of Miller (1985b) to determine the stage of development.

The first group of postovipositional stages (6–10) was defined by changes in the shape of the blastopore and by differentiation of the notochord, neural folds, and head folds (Fig. 1). Stages 11–22 were defined by the number of somites, differentiation of the head, pigmentation of the eyes, and pharyngeal clefts. Later stages (23–31) were defined by carapace formation, development of pigmentation and scales, and the change in volume of the embryo relative to the volume of the yolk (Table 1).

The interval between the mean times of stage 6 (oviposition) and stage 7 may exceed 18 hrs because eggs

Table 2. Elapsed days from first pipping to last hatching among eggs incubated at different temperatures (see also Christens 1990; Godfrey and Mrosovsky 1997; Houghton and Hays 2001; Koch et al. 2008). SD = standard deviation; df = degrees of freedom. NS = not significant.

			Elapsed no. of days							
	Temp (°C)	*n*	Mean	SD	Min	Max	Pair tested	*t*-test	df	Significance
Flatback	32 ± 0.5	4	1.5	0.5773	1	2				
	29 ± 0.5	8	2.6	0.5175	2	3	32 × 29	3.35	10	0.01
	26 ± 0.5	7	2.8	0.9279	2	5	29 × 26	0.4256	13	NS
Green	32 ± 0.5	9	2.9	0.9279	2	4				
	29 ± 0.5	10	2.9	0.7378	1	4	32 × 29	0.0522	17	NS
	26 ± 0.5	9	5.6	2	3	9	29 × 26	3.984	17	0.001
Loggerhead	32 ± 0.5	13	2.8	1.012	2	5				
	29 ± 0.5	14	3.1	1.099	2		32 × 29	0.9323	25	NS
	26 ± 0.5	11	3.9	1.445	2	7	29 × 26	1.0732	23	NS

Table 3. Duration of incubation of eggs from 3 species of marine turtles at 3 different constant temperatures. Degree-days equals difference in mean days divided by difference in degrees.

Species (groups of 10 eggs)	Temp (°C)	Mean (d)	SD	Min–max	Range (d)	Difference in mean days	Difference in degree-days
Flatback							
(6)	32 ± 0.5	45.6	1.94	44–49	5		
(9)	29 ± 0.5	52.8	1.054	51–55	4	7.2	2.4
(5)	26 ± 0.5	75.2	0.707	74–77	3	22.4	7.5
Loggerhead							
(11)	32 ± 0.5	47.5	0.934	46–49	3		
(15)	29 ± 0.5	56.3	1.447	54–58	4	8.8	2.9
(6)	26 ± 0.5	77.8	1.231	76–79	3	21.5	7.2
Green							
(8)	32 ± 0.5	48.1	1.885	46–51	5		
(10)	29 ± 0.5	55.2	1.549	53–58	5	7.1	2.4
(9)	26 ± 0.5	80.8	3.257	77–85	8	25.6	8.5

must equilibrate to the temperature of the sand and be released from their oviducal diapause (sensu preovipositional arrest; Rafferty and Reina 2012). For eggs incubated at 29°C, the mean times of stages 7 and 8 are separated by approximately 10 hrs. The mean intervals between stages 8 and 12 were short, being about 6–8 hrs each. One-day (24-hr) intervals occurred between stages 12 and 14. The mean interval increased to 1.5 d between stages 14 and 19; stages 19–24 were separated by intervals of 2 d. For stages 24–30, the mean interval between the mean times of the stages was slightly over 4 d (4.2 d). The sum of these intervals equaled 50 d of embryonic development. The interval between rupturing (pipping) and exiting the eggshell was between 1.5 and 5.6 d and varied with temperature (Table 2). Digging out of the nest chamber to emerge onto the beach surface varied with temperature (Table 3) and may involve an additional 1–7 or more days (Christens 1990; Godfrey and Mrosovsky 1997; Houghton and Hays 2001; Koch et al. 2008). In total, this schedule predicts that hatchlings should emerge onto the beach approximately 55 d (range, 51–59 d) following oviposition for eggs incubated at 29°C.

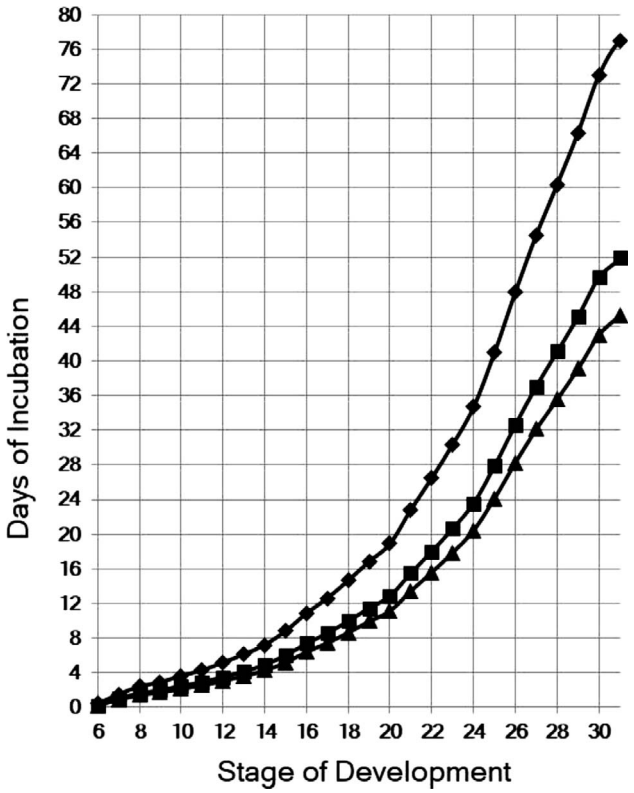

Figure 3. Expected days of incubation through pipping to reach the middle of a specific stage of development at 26°C (diamonds), 29°C (squares), and 32°C (triangles). Additional time is required for hatchling to emerge onto the beach surface.

The timing of the occurrence of a stage within the embryonic sequence depended on the temperature during development (Fig. 3; Table 3). At 26°C, the mean duration of incubation to emergence for the 3 species (77.9 d) was 23.2 d longer than at 29°C, which was 7.7 d longer than at 32°C. The duration of incubation was shortened by 2.6 d for each degree between 29°C and 32°C, whereas the duration was shortened by 7.7 d per degree between 26°C and 29°C.

Measurements of embryos (Tables 4–7) can be used to provide confirmation of the stage of development determined using the key. Total disc length (Table 4) is the first measureable characteristic exhibited by early stage embryos (stages 6–10). The mean total disc length of embryos of 4 species is about 0.2 cm. Crown-to-rump length (Table 4) became measurable as the head fold developed (stage 11) and continued to be useful through stage 20. The forelimb (Table 5) began to differentiate enough to be measured at stage 18; it continued to be useful as a confirmation of stage until stage 30, after which its length did not change. Straight carapace length (Table 6) became measurable during stage 23, when the posterior margin of the carapace was indicated; it was useful after the anterior margin of the carapace formed over the neck (stage 24) as a confirmation of stage until stage 28, after which its length did not change because of the embryonic curvature imposed by the eggshell.

Measurements of flatback and green turtle embryos (Tables 4–6) can be used as a general proxy to help estimate the stage of young leatherback embryos during

Table 4. Measurements of selected embryonic characteristics: total disc length (mm) and crown-to-rump length (mm). Stages from Miller (1985b); measurements from Miller (1982). Total disc length was measured as the straight distance between the anterior and posterior of the embryonic disc; crown-to-rump length was measured as the straight distance from the top head of the curled embryo to the curl at the base of the tail. SD = standard deviation.

	Loggerhead turtle			Hawksbill turtle			Green turtle			Flatback turtle		
Stage	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
Total disc length (mm)												
6	2.0	0.27	94	2.0	0.21	49	1.9	0.30	48	2.0	0.30	17
7	2.1	0.29	24	1.9	0.10	20	1.6	0.25	4	2.1	0.24	8
8	2.3	0.18	16	2.0	0.07	12	2.1	0.39	5	2.3	0.00	1
9	2.1	0.12	3	2.1	0.16	19	2.1	0.40	9	4.0	0.71	2
10	2.4	0.33	9	3.1	0.55	14	1.5	0.00	1	2.5	0.00	1
Crown-to-rump length (cm)												
11	2.5	0.22	15	3.0	0.95	10	2.1	0.58	8	3.0	0.71	2
12	3.7	0.61	20	3.7	0.54	16	4.2	0.76	7	3.8	0.82	6
13	4.6	0.98	30	5.2	0.37	24	3.6	1.12	9	4.3	1.61	3
14	4.7	0.83	30	5.7	0.50	15	4.9	0.98	15	6.3	1.10	3
15	5.5	1.54	33	6.1	0.77	25	5.4	0.92	18	6.5	1.47	4
16	6.4	1.84	32	7.7	0.89	27	5.5	0.89	15	6.8	0.52	6
17	6.2	1.74	21	9.1	0.71	14	6.9	1.32	17	7.5	1.87	4
18	8.0	1.37	26	9.6	0.85	19	7.9	1.47	29	8.5	1.73	6
19	8.1	1.45	26	1.0	0.82	4	7.8	0.80	8	10.5	1.58	4
20	9.3	1.32	63	0.5	1.10	38	8.7	1.57	17	8.3	2.36	12

Table 5. Measurements of selected embryonic characteristics: forelimb length (mm). Stages from Miller (1985b); measurements from Miller (1982). Forelimb length was measured as the straight distance between the proximal and distal ends of the flipper manus of the developing embryo. SD = standard deviation.

	Loggerhead turtle			Hawksbill turtle			Green turtle			Flatback turtle		
Stage	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
18	1.2	0.23	25	1.3	0.17	16	1.2	0.25	29	0.9	0.10	6
19	1.4	0.33	22	1.5	0.06	4	1.5	0.42	8	1.5	0.42	4
20	1.8	0.45	64	2.4	0.34	38	2.1	0.38	18	1.7	0.66	11
21	2.5	0.56	38	3.2	0.50	11	2.8	0.29	26	2.3	0.52	11
22	3.3	0.56	67	3.7	0.19	20	3.8	0.75	30	3.6	0.55	21
23	4.3	0.76	70	4.4	0.78	11	4.8	0.91	46	4.5	0.95	17
24	5.9	1.42	63	6.7	0.52	25	7.8	1.50	27	7.6	1.91	10
25	9.9	2.13	68	10.1	1.00	31	11.3	2.09	28	11.8	2.36	16
26	12.9	3.30	32	14.1	2.48	8	14.9	1.09	14	20.7	1.16	3
27	23.1	1.81	15	21.5	0.92	24	27.4	2.93	13	28.7	2.11	5
28	27.8	2.26	13	25.5	1.66	27	31.3	3.33	26	27.2	2.62	5
29	30.5	1.22	15	27.5	1.77	26	38.4	1.72	22	40.2	2.11	6
30	32.5	1.90	16	28.6	1.10	13	40.0	0.77	17	43.2	0.32	4

Table 6. Measurements of selected embryonic characteristics: straight carapace length (mm). Stages from Miller (1985b); measurements from Miller (1982). Straight carapace length was measured as the straight distance between the anterior and posterior ends of the carapace of the developing embryo. SD = standard deviation.

	Loggerhead turtle			Hawksbill turtle			Green turtle			Flatback turtle		
Stage	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
23	4.3	0.76	70	4.4	0.78	11	4.8	0.91	46	4.5	0.95	17
24	5.9	1.42	63	6.7	0.52	25	7.8	1.50	27	7.6	1.91	10
25	9.9	2.13	68	10.1	1.00	31	11.3	2.09	28	11.8	2.36	16
26	12.9	3.30	32	14.1	2.48	8	14.9	1.09	14	20.7	1.16	3
27	23.1	1.81	15	21.5	0.92	24	27.4	2.93	13	28.7	2.11	5
28	27.8	2.26	13	25.5	1.66	27	31.3	3.33	26	37.2	2.62	5
29	30.5	1.22	15	27.5	1.77	26	38.4	1.72	22	40.2	2.11	6
30	32.5	1.90	16	28.6	1.10	13	40.0	0.77	17	43.2	0.32	4

Table 7. Selected measurements for later stage leatherback embryos of *D. coriacea*. Stages from Miller (1985b); measurements from Miller (1982). Straight carapace length was measured as the straight distance between the anterior and posterior ends of the carapace of the developing embryo. Straight carapace width was measured as the straight distance across the carapace of the developing embryo. Forelimb length was measured as the straight distance between the proximal and distal ends of the flipper manus of the developing embryo.

	Straight carapace length (mm)			Straight carapace width (mm)			Forelimb (mm)		
Stage	Mean	Range	*n*	Mean	Range	*n*	Mean	Range	*n*
23	13.0	12.8–13.2	2	7.0	6.6–7.4	2	4.0	3.6–4.4	2
24	14.5	14.0–15.0	2	8.7	8.3–9.2	2	5.5	5.1–5.9	2
25	19.0	18.4–19.6	2	12.6	12.2–13.0	2	8.3	8.0–8.6	2
26	25.1	24.7–25.5	2	18.1	17.8–18.4	2	13.2	13.0–13.4	2
27	35.9	34.2–37.6	2	23.1	22.5–22.7	2	24.2	22.9–26.5	2
28	38.1	37.2–39.0	2	28.6	28.1–29.1	2	27.1	26.6–27.7	2
29	41.8	41.5–42.1	2	32.4	31.9–32.5	2	44.4	43.2–45.6	2
30	43.3	42.7–43.9	2	32.8	32.1–33.1	2	48.4	47.3–48.9	2

stages 6–22 because these embryos are larger than those of the other Cheloniide species. To assess older leatherback embryos (stages 23–31), the selected measurements shown in Table 7 can be used. Late stage embryos (stages 27–31) of all species can be staged by determining the ratio of the volume of the embryo (exclusive of yolk and membranes) to the yolk as the embryo progresses through these stages (Table 1).

DISCUSSION

Traditionally, a standard series of embryonic stages describes sequential morphological changes coordinated with the chronological age and size of the embryo incubated under defined conditions and provides illustrations of the embryonic stages (Yntema 1968; Mahmoud et al. 1973; Ewert 1985; Ferguson 1985; Miller 1985a, 1985b; Renous et al. 1989). Although the numbering and interval between stages, as well as the morphological characteristics that are described in a stage, vary somewhat among the several standard staging schemes for turtles, the selection of morphological characteristics used to define stages is not arbitrary (e.g., opening of pharyngeal clefts, formation of limbs, expression of scales, and pigmentation) because turtle embryos exhibit the same general suite of morphological characters in the same general sequence during development (Agassiz 1857; Yntema 1968; Mahmoud et al. 1973; Crastz 1982; Ewert 1985; Miller 1985b; Greenbaum 2002; Greenbaum and Carr 2002; Werneburg 2009).

All turtles oviposit their eggs during middle gastrulation (Ewert 1985; Werneburg 2009), and as a result, most staging tables for turtles begin at oviposition (e.g., stage 0 for *Chelydra serpentina*; Yntema 1968) even though development begins at fertilization in the oviduct. In contrast, the 5 preovipositional stages described for sea turtles (Miller 1985b) placed oviposition at stage 6; consequentially, we used stage 6 for oviposition in the key.

This key is based on the assumptions 1) that development of external morphological characters is similar among all species of marine turtles (Miller 1985b) and 2) that under the same conditions of incubation, the variation in the rate of development and the timing of the expression of morphological characteristics among embryos within eggs of the same clutch is small and the variation between clutches reduced (Miller 1985b). These assumptions are supported because throughout early and middle development, the embryos of all species of marine turtles are remarkably similar. As development progresses, clear differences between taxonomic groups appear at the following points: between the 2 families at stage 23 and among the genera at stage 25. Species characteristics become evident at stage 26, at which point adult identification keys can be used to identify species of embryos based on scalation (e.g., Bustard 1972; Pritchard and Mortimer 1999).

Following stage 27, the main embryonic changes involve growth (i.e., expressed as increased embryonic volume and corresponding decreased yolk volume) and the formation of the transverse plastronal fold caused by the bending of the embryo as it increases in size within the confines of the eggshell. Consequently, during the last $\sim$ 20% of the developmental period, staging relies on assessing the ratio of the volume of the embryo to that of the remaining yolk and the general angle displayed by the transverse plastronal fold. Crastz (1982) used embryonic volume as a measure of development and found that it had a reasonable correlation to days of development ($R^2 = 0.96$). Stage 31a represents an embryo that has completed embryonic development and is in the process of extricating itself from the ruptured (pipped) eggshell. At stage 31b, the embryo has exited the eggshell, has begun to uncurl its body from the curved position it maintained inside the eggshell, and has withdrawn most of the remnant yolk into its abdomen; abraded extraembryonic membranes may still be attached.

The various species of marine turtles produce eggs of different sizes (i.e., diameter and mass) that, in turn, produce hatchlings of different sizes (Van Buskirk and Crowder 1994; Miller 1997). It follows that embryos of the various species will differ in size even though they

express the same representative characteristics of a given embryonic stage. Even within a species, using a suite of morphological criteria to define a stage is more consistent than measurements (Yntema 1968). Therefore, measurements of specific characters (e.g., carapace length and crown-to-rump length) are not used to define a developmental stage in the key. However, measurements of embryos (Tables 4–7) can be used to provide confirmation of the stage of development determined using the key. Measurements of single characteristics are useful, but a combination of multiple characteristics provides better definition of the stage.

Because morphological changes occur rapidly at first and then more slowly as development proceeds, the initial stages span shorter time periods than the later stages. At 29°C, the sum of the time intervals between stages equals approximately 50 d from oviposition (stage 6) to pipping (stage 31a). Allowing for variation as a result of 1) temperature fluctuations during development, 2) the time required for pipping and leaving the eggshell, and 3) the time needed to dig out of the nest chamber, hatchlings are predicted to emerge onto the beach approximately 55 d following oviposition. Although incubation time varies among species and within a species at different locations (Hirth 1980; Van Buskirk and Crowder 1994; Limpus 2009), the 55-d schedule approximates the incubation time to emergence for most of the Cheloniidae (e.g., average 55.6 d and range 47–90 d in Queensland, Australia; Limpus 2009). In contrast, leatherback hatchlings, which typically emerge from deeper nests, usually require more time to reach the surface of the sand (approximately 60 d; Eckert et al. 2012).

In field studies, the "duration of incubation" is usually defined as the period from oviposition to the emergence of the hatchlings onto the beach surface (Márquez et al. 1976; Balazs 1980; Dodd 1988; Márquez 1994; Witzell 1983; Godfrey and Mrosovsky 1997; Hirth 1997; Limpus 2009; Eckert et al. 2012). In contrast, the "end of the embryonic period" occurs when the embryo pips and exits the eggshell (sensu Ewert 1979), which is several days prior to the emergence of the hatchlings onto the beach surface (Godfrey and Mrosovsky 1997). Temperature, as well as characteristics of the beach substrate, can modify the interval between hatching in the egg chamber and emergence onto the beach by several days (Table 2) (Christens 1990; Godfrey and Mrosovsky 1997; Houghton and Hays 2001; Koch et al. 2008). For this reason, rupturing of the eggshell (pipping) is a better measure of the end of incubation than is emergence from the nest (Gutzke et al. 1984). Taking into account reported interval variation, Godfrey and Mrosovsky (1997) suggested using 5 d as a reasonable estimate of the interval between pipping and emergence onto the beach, but this can vary between nesting sites and needs to be assessed on a site-by-site basis.

The key provided here addresses a need so that extrapolation from staging tables from nonmarine species and the associated problems can be avoided. Although many of the morphological criteria derived from nonmarine turtle species are applicable to marine turtle development, problems may occur when direct comparisons are attempted (Blanck and Sawyer 1981). Yntema and Mrosovsky (1982) applied Yntema's (1968) stages for *C. serpentina* successfully to *C. caretta* embryos. Determining the timing of developmental events, however, is difficult because staging tables for nonmarine turtle species have been based on embryos incubated (at least in part) at temperatures lower than those at which marine turtle eggs normally incubate (e.g., 20°C, *C. serpentina*, Yntema 1968; 21°C and 23°C, *Chrysemys picta belli*, Mahmoud et al. 1973).

In addition, as a result of the insulating effect of the substrate on the interactions among the hydric, gaseous, and temperature conditions experienced by the embryos, a delay of several hours or more may occur before changes in environmental conditions impact the embryos (Lolavar and Wyneken 2015). In the context of fluctuation in the environmental conditions of the beach, the variation in the prediction of developmental schedule is acceptable because these exogenous events do not have an instantaneous impact on the embryos.

A combination of determining hatching success (sensu Miller 1999) and assessing the stage of development of marine turtle embryos contained in eggs that did not hatch can contribute to an understanding of mortality factors operating on the nesting beach (Özdemir et al. 2008) or in a managed hatchery. Although retrieving a middle to late stage embryo is usually straight forward (albeit messy), autolysis of tissues in early stage embryos that died within the oviduct or within hours of oviposition (stages 2–10; Miller 1985b) can make it difficult to identify the presence of the embryo when a dead egg is opened some 2 mo later following the emergence of hatchlings from the nest (Wyneken et al. 1988). Therefore, the failure to find an embryo in such eggs does not necessarily equate to the egg not being fertilized.

When this simplified key to developmental stages is used in conjunction with knowledge of beach temperature and duration of incubation, it can aid estimation of when mortality occurred. In conjunction with review of data available for environmental parameters such as nest depth, position on the beach, tidal cycle, storm patterns, and rainfall, use of the key can help identify likely causes of mortality and can help with the design and assessment of field-based experiments.

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LITERATURE CITED

ACKERMAN, R.A. 1997. The nest environment and the embryonic development of sea turtles. In: Lutz, P.L. and Musick, J.A. (Eds.). The Biology of Sea Turtles. Volume 1. Boca Raton, FL: CRC Press, pp. 83–106.

ACKERMAN, R.A. AND LOTT, D.B. 2004. Thermal, hydric and respiratory climate of nests. In: Deeming, D.C. (Ed.). Reptilian Incubation Environment, Evolution and Behaviour. Nottingham, UK. Nottingham University Press, pp. 15–43.

AGASSIZ, L. 1857. Contributions to the Natural History of the United States of America. Monograph I. Part III. Embryology of the Turtle. Boston: Little, Brown & Co.

AL-MUKHAINI, N., BA-OMAR, T.A., MAHMOUD, I.Y., AND AL-BARWANI, S. 2010. Embryonic staging of green turtles, *Chelonia mydas* (Linnaeus, 1758). Zoology of the Middle East 51:39–50.

BALAZS, G.H. 1980. Synopsis of biological data on the green turtle in the Hawaiian Islands. NOAA Tech. Memor. NMFS-SWFC-7, pp. 1–141.

BEGGS, K., YOUNG, J., GEORGES, A., AND WEST, P. 2000. Ageing the eggs and embryos of the pig-nosed turtle, *Carettochelys insculpta* Chelonia: Carettochelydidae, from northern Australia. Canadian Journal of Zoology-Revue Canadienne De Zoologie 783:373–392.

BILLETT, F.S., COLLINS, P., GOULDING D.A., AND SUTHERLAND, J. 1992. The development of *Caretta caretta*, at 25–34°C, in artificial nests. Journal of Morphology 2132:251–263.

BLANCK, C.E. AND SAWYER, R.H. 1981. Hatchery practices in relation to early embryology of the loggerhead sea turtle, *Caretta caretta* Linne. Journal of Experimental Marine Biology and Ecology 49:163–177.

BUSTARD, H.R. 1972. Sea Turtles: Natural History and Conservation. Sydney: Collins, 220 pp.

CAUT, S., GUIRLET, E., AND GIRONDOT, M. 2010. Effect of tidal overwash on the embryonic development of leatherback turtles in French Guiana. Marine Environmental Research 694:254–261.

CHRISTENS, E. 1990. Nest emergence lag in loggerhead sea turtles. Journal of Herpetology 244:400–402.

CRASTZ, F. 1982. Embryological stages of the marine turtle *Lepidochelys olivacea* Eschscholtz. Revista de Biologia Tropical 302:113–120.

DERANIYAGALA, P.E.P. 1933. Notes on the development of the leathery turtle, *Dermochelys coriacea*. Spolia Zeylanica. Ceylon Journal of Science 17:73–102.

DERANIYAGALA, P.E.P. 1939. Tetrapod Reptiles of Ceylon. Volume I. Testudinates and Crocodilians. Ceylon Museum Natural History Series, Ceylon Journal of Science, 412 pp.

DERANIYAGALA, P.E.P. 1953. A Coloured Atlas of Some Vertebrates from Ceylon. Volume 2. Tetrapod Reptilia. Colombo: Ceylon Government Press, 102 pp.

DODD, C.K. 1988. Synopsis of the biological data on the loggerhead sea turtle *Caretta caretta* (Linnaeus 1758). US Fish and Wildlife Service Biological Report 88(14), pp. 1–110.

DOMANTAY, J.S. 1968. Notes on the development and breeding habits of *Chelonia mydas*. Acta Manilana 4:87–109.

ECKERT, K.L., WALLACE, B.P., FRAZIER, J.G., ECKERT, S.A., AND PRITCHARD, P.C.H. 2012. Synopsis of the Biological Data on the Leatherback Sea Turtle *Dermochelys coriacea*. Biological Tech. Pub. BTP-R4015-2012. US Department of Interior, Fish and Wildlife Service, Washington, DC, 172 pp.

EWERT, M.A. 1979. The embryo and its egg: development and natural history. In: Harless, M. and Morlock, H. (Eds.). Turtles: Perspectives and Research. New York: Wiley & Sons, pp. 333–413.

EWERT, M.A. 1985. Embryology of turtles. In: Gans, C., Billett, F., and Maderson, P. (Eds.). Biology of the Reptilia. Volume 14A. New York: Wiley-Interscience, pp. 75–267.

FERGUSON, M.W.J. 1985. The reproductive biology and embryology of crocodilians. In: Gans, C., Billett, F., and Maderson, P.F.A. (Eds.). Biology of the Reptilia. Volume 14A. Development. New York: Wiley-Interscience, pp. 329–491.

FOLEY, A.M., PECK, S.A., AND HARMAN, G.R. 2006. Effects of sand characteristics and inundation on the hatching success of loggerhead sea turtle (*Caretta caretta*) clutches on low-relief mangrove islands in southwest Florida. Chelonian Conservation and Biology 5(1):32–41.

FUCHS, H. 1915. Über den Bau und Endwicklung des Schädels der *Chelone imbricata*. Ein Beitrag zur Entwicklungsgeschichte und vergleichenden Anatomie des Wirbeltierschädels. Erster Teil: Das Primordialskelett des Neurocraniums und des Kieferbogens. In: Voeltzkow, A. (Ed.). Reise in Ostafrika in den Jahren 1903–1905. Wissenschaftliche Ergebnisse Volume 5. Stuttgart: Schweizerbart, pp. 1–325.

FUJIWARA, M. 1966. The early development of the marine turtle with special reference to the formation of germ layers in Amniota. Bulletin of Tokyo Gakugai University 18 Ser. IV: 45–60.

FUJIWARA, M. 1971. Perforation of the chordomesodermal canal in the Pacific roggerhead [*sic*] turtle. Acta Herpetologica Japonica 4:16–17.

GODFREY, M.H. AND MROSOVSKY, N. 1997. Estimating the time between hatching of sea turtles and their emergence from the nest. Chelonian Conservation and Biology 24:581–585.

GREENBAUM, E. 2002. A standardized series of embryonic stages for the emydid turtle *Trachemys scripta*. Canadian Journal of Zoology 808:1350–1370.

GREENBAUM, E. AND CARR, J.L. 2002. Staging criteria for embryos of the spiny softshell turtle, *Apalone spinifera* testudines: Trionychidae. Journal of Morphology 2543:272–291.

GUTZKE, W.H.N., PAUKSTIS, G.L., AND PACKARD, G.C. 1984. Pipping versus hatching as indices of time of incubation in reptiles. Journal of Herpetology 184:494–496.

HAMBURGER, V. AND HAMILTON, C. 1951. A series of normal stages in the development of the chick embryo. Journal of Morphology 888:231–272.

HEWAVISENTHI, S. AND PARMENTER, C.J. 2002. Incubation environment and nest success of the flatback turtle *Natator depressus* from a natural nesting beach. Copeia 2002:302–312.

HIRTH, H.F. 1980. Some aspects of the nesting behavior and reproductive biology of sea turtles. American Zoologist 20: 507–523.

HIRTH, H.F. 1997. Synopsis of the biological data on the green turtle *Chelonia mydas* Linnaeus 1758. US Fish and Wildlife Service Biological Report 97(1), pp. 1–129.

HOPWOOD, N. 2007. A history of normal plates, tables and stages in vertebrate embryology. International Journal of Developmental Biology 51:1–26.

HOUGHTON, J.D.R. AND HAYS, G.C. 2001. Asynchronous emergence by loggerhead turtle (*Caretta caretta*) hatchlings. Naturwissenschaften 88:133–136.

JORDAN, H.E. 1917. Embryonic history of the germ cells of the loggerhead turtle *Caretta caretta*. Publications of the Carnegie Institution for Science, Contributions in Embryology 251: 313–344.

KASKA, Y. AND DOWNIE, R. 1999. Embryological development of sea turtles *Chelonia mydas*, *Caretta caretta* in the Mediterranean. Zoology in the Middle East 19:59–65.

KOCH, A.U., GUINEA, M.L., AND WHITING, S.D. 2008. Asynchronous emergence of Flatback Seaturtles, *Natator depressus,* from a beach hatchery in Northern Australia. Journal of Herpetology 42(1):1–8.

KONDO, Y. 1986. *Caretta caretta olivacea* (Escholtz). Hiwasa: Chelonian Museum.

KURATANI, S. 1999. Development of the chondrocranium of the loggerhead turtle, *Caretta caretta*. Zoological Science 16:803–818.

LIMPUS, C.J. 2009. A Biological Review of Australian Marine Turtles. Brisbane, Queensland, Australia: Queensland Environmental Protection Agency, 324 pp.

LIMPUS, C.J., BAKER, V., AND MILLER, J.D. 1979. Movement induced mortality of loggerhead eggs. Herpetologica 35:335–338.

LOLAVAR, A. AND WYNEKEN, J. 2015. Effect of rainfall on loggerhead turtle nest temperatures, sand temperatures and hatchling sex. Endangered Species Research 28:235–247.

MAGNUSSON, W.E. AND TAYLOR, J.A. 1980. A description of developmental stages in *Crocodylus porosus*, for use in aging eggs in the field. Australian Wildlife Research 7:479–485.

MAHMOUD, I.Y., HESS, G.L., AND KLICKA, J. 1973. Normal embryonic stages of the western painted turtle, *Chrysemys picta belli*. Journal of Morphology 141:269–280.

MÁRQUEZ, M.R. 1994. Synopsis of biological data on the Kemp's Ridley Turtle, *Lepidochelys kempi* Garman, 1880. NOAA Tech. Memor. NMFS-SEFSC-343, pp. 1–91.

MÁRQUEZ, M.R., VILLANUEVA, O.A., AND PEÑAFLORES, S.C. 1976. Sinopsis de Datos Biológicos Sobre la Tortuga Golfina *Lepidochelys olivacea* Eschscholtz, 1829 en México. Sinopsis sobre la Pesca INP/S2, SAT, INP 2, 61 pp.

MILLER, J.D. 1982. Embryology of marine turtles. PhD Thesis, University of New England, Armidale, Australia.

MILLER, J.D. 1985a. Criteria for staging reptilian embryos. In: Grigg, G., Shine, R. and Ehmann, H. (Eds.). Biology of Australasian Frogs and Reptiles. New South Wales, Australia: Royal Zoological Society of New South Wales, pp. 305–310.

MILLER, J.D. 1985b. Embryology of marine turtles. In: Gans, C., Billett, F., and Maderson, P.F.A. (Eds.). Biology of the Reptilia. Volume 14A. Development. New York: Wiley-Interscience, pp. 269–328.

MILLER, J.D. 1997. Reproduction in sea turtles. In: Lutz P.L. and Musick, J.A. (Eds.). The Biology of Sea Turtles. Boca Raton, FL: CRC Press, pp. 51–79.

MILLER, J.D. 1999. Determining clutch size and hatching success. In: Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A., and Donnelly, M. (Eds.). Research and Management Techniques for the Conservation of Sea Turtles. IUCN/SSC Marine Turtle Specialist Group Publication No. 4, pp. 124–129.

MILLER, J.D., LIMPUS, C.J., AND GODFREY, M.H. 2003. Nest site selection, oviposition, eggs, development, hatching, and emergence of loggerhead turtles. In: Bolton, A.B. and Witherington, B.E. (Eds.). Loggerhead Sea Turtles. Washington, DC: Smithsonian Institution Press, pp. 125–143.

MITSUKURI, K. 1894. On the process of gastrulation in Chelonia. Journal of the College of Science, Imperial University of Tokyo, Japan 6:227–277.

MITSUKURI, K. 1896–1898. On the fate of the blastopore. The relations of the primitive streaks, and the formation of the posterior end of the embryo in Chelonia, together with remarks on the nature of meroblastic ova in vertebrates. Journal of the College of Science, Imperial University of Tokyo, Japan 10:1–116.

MORTIMER, J.A. 1982. Factors influencing beach selection by nesting sea turtles. In: Bjorndal, K.A. (Ed.). Biology and Conservation of Sea Turtles. Washington, DC: Smithsonian Institution Press, pp. 45–51.

MORTIMER, J.A. 1990. Influence of sand characteristics on the nesting behavior and hatching success of the green turtle (*Chelonia mydas*). Copeia 1990(3):798–813.

ÖZDEMIR, A., TÜRKOZAN, O., AND GÜCLÜ, O. 2008. Embryonic mortality in loggerhead turtle *Caretta caretta* nests: a comparative study on Fethiye and Göksu Delta Beaches. Turkish Journal of Zoology 323:287–292.

PARKER, W.K. 1880. Report on the development of the green turtle *Chelonia viridis* Schneid. In: Report of the Scientific Results of the Voyage of the H.M.S. Challenger during the years 1872–1876. Zoology 1 Part 5. London: Longmans, Green and Co., pp. 1–57.

PENYAPOL, A. 1958. A preliminary study of the sea turtles in the Gulf of Thailand. Natural History Bulletin of the Siam Society 17:23–36.

PRITCHARD, P.C.H. AND MORTIMER, J.A. 1999. Taxonomy, external morphology and species identification. In: Eckert, K., Bjorndal, K., Abreu-Grobois, F.A., and Donnelly, M. (Eds.). Research and Management Techniques for the Conservation of Sea Turtles. Washington, DC: IUCN Marine Turtle Specialist Group, pp. 21–38.

RAFFERTY, A. AND REINA, R. 2012. Arrested embryonic development: a review of strategies to delay hatching in egg-laying reptiles. Proceedings of the Royal Society B: Biological Sciences 279:2299–2308.

RAGOTZKIE, R.A. 1959. Mortality of loggerhead turtle eggs from excessive rainfall. Ecology 402:303–305.

RAYNAUD, A., FRETEY, J., AND CLERGUE-GAZEAU, M. 1980. Epithelial structures of temporary existence appended on branchial arches in the embryos of the leathery turtle *Dermochelys coriacea*. Bulletin Biologique de la France et de la Belgique 1980:72–99.

RENOUS, S., RIMBLOT-BALY, F., FRETEY, J., AND PIEAU, C. 1989. Embryonic development characteristics of the leatherback *Dermochelys coriacea* Vandelli, 1761. Annales des Sciences Naturelles, Zoologie 10:197–229.

SERAFINI, T.Z., LOPEZ, G.G., AND DA ROCHA, P.L.B. 2009. Nest site selection and hatching success of hawksbill and loggerhead sea turtles, Testudines, Cheloniidae, at Arembepe Beach, northeastern Brazil. Phyllomedusa 81:3–17.

VALVERDE, R.A., WINGARD, S., GÓMEZ, F., TORDOIR, M.T., AND ORREGO, C.M. 2010. Field lethal incubation temperature of olive Ridley sea turtle *Lepidochelys olivacea* embryos at a mass nesting rookery. Endangered Species Research 12:77–86.

VAN BUSKIRK, J. AND CROWDER, L.B. 1994. Life-history variation in marine turtles. Copeia 1994:66–81.

VOELTZKOW, A. 1903. Beiträge zur Entwicklungsgeschichte der Reptilien. VI. Gesichtsbildung and Entwicklungder äusseren Körperform bei *Chelone imbricata* Schweigg. Abhandlungen Senckenbergische Naturforschende Gesellschaft 27:179–190.

WEBB, G.J.W., BUCKWORTH, R., SACK, G.C., AND MANOLIS, S.C. 1983. An interim method for estimating the age of *Crocodylus porosus* embryos. Australian Wildlife Research 10:563–570.

WERNEBURG, I. 2009. A standard system to study vertebrate embryos. PLoS ONE 46:e5887.

WIBBELS, T. 2003. Critical approaches to sex determination in sea turtles. In: Lutz, P.L., Musick, J.A., and Wyneken, J. (Eds.).

The Biology of Sea Turtles. Volume III. Boca Raton, FL: CRC Press, pp. 103–134.

WITZELL, W.N. 1983. Synopsis of biological data on the hawksbill turtle *Eretmochelys imbricata* Linnaeus, 1766. Food and Agriculture Organization Fisheries Synopsis No. 137, pp. 1–78.

WOOD, D.W. AND BJORNDAL, K.A. 2000. Relation of temperature, moisture, salinity, and slope to nest site selection in Loggerhead sea turtles. Copeia 2000 1:119–128.

WYNEKEN, J., BURKE, T.J., SALMON, M., AND PEDERSEN, D.K. 1988. Egg failure in natural and relocated sea turtle nests. Journal of Herpetology 22(1):88–96.

YNTEMA, C.L. 1968. A series of stages in the embryonic development of *Chelydra serpentina*. Journal of Morphology 125:219–252.

YNTEMA, C.L. AND MROSOVSKY, N. 1982. Critical periods and pivotal temperatures for sexual differentiation in loggerhead sea turtles. Canadian Journal of Zoology 60:1012–1016.

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