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# ESTIMATING AGE OF TURTLES FROM GROWTH RINGS: A CRITICAL EVALUATION OF THE TECHNIQUE

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ABSTRACT: The technique of counting growth rings to estimate age of turtles is widespread in the scientific literature. Review articles to date have provided primarily lists of authors who have found the technique useful or not, but these reviews have failed to evaluate properly how well the technique actually works. In an attempt to examine how well the published literature supports a biologically meaningful relationship between age and number of growth rings, we surveyed 145 scientific papers that have used counts of rings on scutes to estimate age of individual turtles.

Of the 145 papers surveyed, the authors of 44 papers, which comprised 49 case studies, presented data testing the use of growth ring counts for a population of turtles. Of these 49 case studies, 6 reported that the use of the technique was reliable for aging their turtle species past sexual maturity, 15 reported its use to be reliable for aging turtles to young adult (i.e., sexual maturity), 8 reported its use to be reliable for aging juvenile turtles, 2 found it to be reliable with no age limit given, and 8 reported its use unreliable as a method for aging their turtles. The remainder of the case studies presented data that were difficult for us to interpret as reliable or unreliable. Although 22 papers addressed the pattern of growth ring deposition, only four case studies had sufficient data to indicate that a consistent number of rings was added each year. In this paper, we illustrate how the widespread use of this technique ultimately has led to its acceptance without the rigor of tests of its validity or accuracy. We conclude that (a) studies attempting to calibrate the relationship between growth rings and age are few, (b) a majority of the papers that we surveyed referenced other papers that did not themselves include a test justifying growth ring counts as an estimate of turtle age, (c) aging turtles from counts of growth rings might be feasible in some types of studies, for some species at some locations, but only after calibrating the relationship between ring counts and age for each circumstance, and (d) there is currently no justification for generalizing the use of growth rings to estimate turtle age for many species.

*Key words:* Age; Body size; Demography; Growth annuli; Growth rings; Life history; Scutes; Testudines; Turtles

COUNTS of growth rings have been used to assess the age of turtles since Agassiz's (1857) foundational studies on the natural history of turtles (Germano and Bury, 1998). Agassiz stated that, "... we find upon the surface of each scale, around a smaller angular central plate, (the scale of the first year's growth,) a smaller or greater number of concentric stripes or regular annual rings, as they are exhibited on a transverse section of an old tree" (Agassiz, 1857:259). This aging technique is regarded as a convenient, non-destructive method for assessing age of turtles. The validity of its use for some species has long been questioned, however. For example, Miller (1932) concluded that counts of growth rings were not an accurate technique for assessing age of desert tortoises (*Gopherus agassizii*), and Nichols (1939) found that, of 18 individual *Terrapene carolina*, only five showed a one-to-one relationship between age and number of growth rings (but see Legler, 1960). Cagle (1946) found that counts of growth rings were accurate up to 3 yr in *Pseudemys scripta*, but ultimately he concluded that "annuli are of little value as age indicators since they disappear at a relatively early age" (Cagle, 1946:726).

Several literature reviews have evaluated the efficacy of aging turtles from counts of growth rings (e.g., Castanet, 1988; Dunham et al., 1988; Germano and Bury, 1998; Gibbons, 1976; Graham, 1979; Zug, 1991). Our analysis of the literature is not solely in the nature of a review, but it also evaluates how well the published literature supports the hypothesis that a relationship exists between age and number of growth

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rings that could be useful in estimating age. Our objectives are fourfold: (1) to determine whether each paper that we surveyed presented data to test the relationship between counts of growth rings and age, (2) to summarize the data that those papers presented and evaluate the efficacy of the aging technique, (3) to evaluate whether papers that presented data addressed the pattern of growth ring deposition and/or the stimulus that triggers growth ring deposition, and (4) to evaluate whether the data presented to date allow for discrimination between the hypothesis that growth rings are formed in relation to age and an alternative hypothesis that the number of growth rings is simply a function of body size, not age.

## Anatomy and Physiology of Growth Ring Deposition

A turtle's shell is composed of a dorsal carapace, a ventral plastron, and a lateral bridge, all composed of fused dermal bony elements. Except in soft-shelled (Trionychidae) and marine leathery turtles (Cheloniidae, Dermochelyidae), the outer surface of the bony shell is covered by epidermal laminae, or scutes, that are composed of cornified layers of the epidermal epithelium (Pough et al., 2001; Romer, 1997). The overlying epidermal scutes are fewer in number than the underlying dermal bones, and therefore the sutures of the scutes and bones, in most instances, do not align themselves evenly. The misalignment of epidermal and dermal sutures may add strength to the shell (Pough et al., 2001; Romer, 1997).

The formation (development) of growth rings has been described for *Terrapene ornata* (Legler, 1960) and *P. scripta* (Moll and Legler, 1971), and others have reviewed scute formation (Graham, 1979; Zug, 1991). The description here is based largely on these studies and discussions with these authors. However, it is important to note that, to date, there have been no detailed investigations of the histology or development of the keratinized coverings of turtle shells, and, thus, the mechanisms described here should be considered hypotheses that remain to be confirmed.

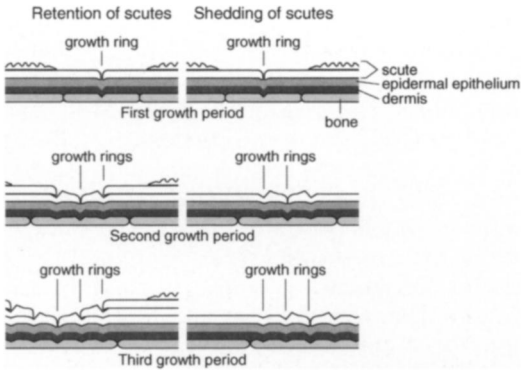


FIG. 1.—Formation of epidermal scute rings. The scutes are homologous with the scales of other reptiles and are formed from the epidermis that covers the bony shell. The margins of the scutes (i.e., seams between scutes) are formed from grooves in the epidermis that correspond to sulci in the bone tissue. As the epidermis grows, the outer cells die and become keratinized, forming a layer of scute. After a cessation of growth, an entire new layer is formed underneath the old. In some turtles (e.g., *Terrapene*), the old layers are retained and growth rings can be seen as the successively larger layers of scute. In other turtles (e.g., *Pseudemys*), the old scutes are shed and somehow leave an impression on the new scute (the growth rings). The figure represents a turtle at the end of its first (upper), second (middle), and third (lower) growth periods for a species that retains its scute layers (left) and one that sheds its scute layers (right). Growth periods may or may not be annual, depending on species and environmental conditions (see text).

The scutes covering turtle shells are homologous with the scales of squamate reptiles and are composed of dead, keratinized layers of the epidermal epithelium that covers the entire shell. The seams between each scute form along grooves in the epidermal tissue that fit into depressions, or sulci, in the underlying bone tissue (Fig. 1). The tissue bounded by these grooves is the individual scute. The growing edge of the scute and the seams between scutes are thus formed by the fold of epithelium in the groove. In some species, only the latest sulcus is retained, while in other species, several sulci that correspond to the location of epidermal scute layers are apparent on the bones of the shell.

It remains unknown what triggers the formation of new scute layers, but they ap-

pear to be formed primarily after a major cessation of growth, such as during hibernation, prolonged drought, or heavy rainfall (Berry, 2003; Legler, 1960; Moll and Legler, 1971). In some turtles (e.g., *Pseudemys*), a fracture zone forms and the older keratin layer is shed or sloughed when a new layer is deposited from below (Legler, 1960). In those species that shed their scutes, impressions from growth rings are retained on the shell for an indeterminate length of time, although the mechanism for this is not understood (Moll and Legler, 1971; Zug, 1991). Ernst et al. (1994) noted a thickening of the keratin layer at the edge of a scute. This thickening may result in an additional depression in the epidermal tissue or underlying bone that could result in a slight depression in subsequent scute layers. In those species that retain the old scutes, the margins of the old scute layers form the growth rings, similar to a pyramid of successively larger layers (although the pyramidal shape of the scutes of some turtle species is primarily caused by the shape of the underlying bone). During periods of slower growth, it appears that a thinner layer of epidermis is keratinized, thus forming a depression in the scute that may appear as an incomplete ring, making it difficult to distinguish between rings formed from new layers of keratin and those formed from depressions. These incomplete rings have been termed "pseudoannual growth zones" (Ewing, 1939), "minor growth-rings" (Legler, 1960), "subannual rings" (Bourn and Coe, 1978), "accessory lines (annuli)" (Sexton, 1959; Zweifel, 1989), and "false rings" (Germano, 1988). This terminology, however, tacitly implies that "complete" rings represent "true" rings and further implies that complete rings are produced annually. These terms do not necessarily reflect the environmental, developmental, and/or behavioral events that act to create different ring types.

In part, the controversy surrounding the use of growth rings for aging turtles may stem from the confusion surrounding the suggestive terminology used to describe these epidermal laminae. The term "annuli" (singular: annulus) is often (and correctly) used when describing the concentric rings formed periodically on each scute. However, it is easy to confuse the Latin root of "annuli," *annularis* (ring), for the Latin word *annualis* (year) and, therefore, incorrectly equate "annuli" with "annual" (Moll and Legler, 1971). For simplicity, therefore, we will use the term "growth rings" in this paper instead of growth annuli (or growth annulus).

## Philosophical Issues: Pattern Versus Cause

There are two phenomenologically different aspects to the question of whether counts of growth rings can be used to determine age in turtles: (1) is there a consistent and reliable "pattern" of growth ring deposition in relation to age and, if so, (2) what factor or factors cause the observed pattern of growth ring deposition (e.g., drought, rainfall, hibernation)? For example, Moll and Legler (1971) studied growth of *P. scripta* at a site in the tropics. They found no consistent pattern of growth ring addition each year; several marked sliders added 3–4 growth rings per year. It appeared, however, that the factor driving growth ring formation was heavy amounts of rainfall; turtles grew when it was sunny and slowed or ceased growth when it rained heavily. Moll and Legler (1971) concluded that the pattern of sunshine and rainfall was associated with juvenile slider growth cycles, but other, intrinsic factors appeared to affect growth in adult sliders. For instance, when juvenile growth was maximal, adult growth was minimal because, during this period, adults allocated their energy to reproductive activity, not growth. Therefore, although the factor driving growth ring formation was identified at this tropical study site, the pattern of deposition differed between juveniles and adults. Because many factors may play a role in the production of growth rings, different patterns of ring deposition may result, making it difficult to generalize observed patterns among sites, species, or even growth stages of the same species.

Questions about pattern are relatively simple, requiring either a count of growth

rings on a group of turtles of a known age or a recount of growth rings after a precisely measured interval of time. An analysis of these data should be performed to determine the extent to which there is a regular and predictable relationship (pattern) between the number of growth rings and age. It is important to anticipate several alternative patterns of the relationship between growth ring number and age. If the average number of growth rings counted on known age turtles is known age ±1 ring, then it is possible to conclude that, on average, one ring is added each year. Because defining a pattern of growth ring deposition requires only the recapture of turtles over some elapsed time period (snapshot study), the findings of such a study do not necessarily demonstrate that growth rings are added such that one ring is added each year. For example, eight growth rings counted on a turtle known to be 8-yr old may mean that one ring was added each year or it may mean that two rings were added in years 2, 3, 5, and 6, and no rings were added in years 1, 4, 7, and 8. Depending on the nature and scope of the study, this distinction may or may not be important, but it is necessary to recognize that differences in the pattern of growth ring accumulation may exist because these patterns reflect differences in the ecological processes that affect growth.

Regression analysis can be used to describe the pattern between growth ring counts and age when variation exists in the number of growth rings and age. Regression analysis allows calculation of confidence limits around predictions of age made this way. With a calibration curve, it would be possible to estimate the age of a turtle with five growth rings, for example, but the confidence limits around the regression line may indicate that the age is 5 ± 3 yr. Because of the nature of regression analysis, the error surrounding the regression will be larger toward the end of the analyzed range, making estimates of turtle age for individuals with many growth rings less precise. For some species, the uncertainties in the relationship may be so large that estimates of age from counts of growth rings are effectively (or biologically) meaningless. For instance, although Litzgus and Brooks (1998) found a statistically significant relationship between change in ring counts and change in years between counts, the variance of the relationship was so large that they questioned the biological relevance of the relationship.

If a consistent and predictable pattern of growth ring deposition is found, it is necessary to determine whether that pattern holds for the entire lifespan of the turtle or whether the pattern changes ontogenetically. For example, as a turtle reaches sexual maturity, its growth rate slows and a consistent juvenile pattern of growth ring deposition may change or disappear entirely. Thus, it is necessary to determine patterns of growth ring development over different stages of the lifespan of a turtle species to identify when there may be limitations in the use of growth ring counts to age turtles (e.g., Mushinsky et al., 1994).

Although it is not necessary to know how or why growth rings form to demonstrate their usefulness in aging turtles, the greatest certainty about the relationship between age and growth ring counts, and thus the greatest power to generalize, would come from knowing not only the pattern but the factors responsible for growth ring formation as well. The only way to be confident about consistency of pattern is to perform longitudinal studies where individuals are recaptured repeatedly over many years. Ideally, it would be necessary to recapture individuals more frequently than growth rings are deposited, thus allowing a precise measure of when, and under what circumstances, a ring is formed. With frequent counts of growth rings on an individual, in conjunction with monitoring such factors as hibernation state, growth, feeding behavior, and size (length and mass), it would be possible to determine what physical, physiological, and environmental conditions lead to the formation of growth rings. For instance, if new scute layers are deposited at the end of a spring growing season, as has been hypothesized for many North American species (e.g., Zug, 1991), then there

TABLE 1.—Relationship between plastral growth rings and known age (in years) of juvenile desert tortoises housed in a seminatural enclosure at the Ft. Irwin Study Site, Mojave Desert, California. Plastral growth rings were counted 30 April 1997 and known age was calculated based on fall hatching.

| Turtle number | Plastral growth rings | Known age | Turtle number | Plastral growth rings | Known age |
|---|---|---|---|---|---|
| 21 | 4 | 6.8 | 131 | 4 | 5.7 |
| 23 | 5 | 6.8 | 133 | 3 | 5.7 |
| 25 | 5 | 6.8 | 138 | 3 | 5.7 |
| 29 | 4 | 6.8 | 141 | 3 | 5.7 |
| 36 | 6 | 6.8 | 146 | 4 | 5.6 |
| 39 | 4 | 6.7 | 149 | 3 | 5.6 |
| 42 | 4 | 6.7 | 168 | 3 | 4.7 |
| 66 | 4 | 5.8 | 173 | 5 | 4.6 |
| 68 | 3 | 5.8 | 175 | 2 | 3.8 |
| 73 | 3 | 5.8 | 177 | 2 | 3.8 |
| 76 | 4 | 5.8 | 186 | 1 | 1.7 |
| 80 | 4 | 5.8 | 191 | 1 | 1.7 |
| 89 | 3 | 5.8 | 197 | 0 | 1.6 |
| 93 | 2 | 5.8 | 201 | 4 | 5.7 |
| 95 | 3 | 5.8 | 202 | 4 | 5.7 |
| 96 | 4 | 5.8 | 204 | 2 | 1.6 |
| 97 | 4 | 5.8 | 208 | 2 | 1.6 |
| 108 | 5 | 5.7 | 209 | 1 | 1.6 |
| 110 | 3 | 5.7 | 211 | 1 | 1.6 |
| 114 | 3 | 5.7 | 223 | 0 | 0.7 |
| 119 | 3 | 5.7 | 224 | 1 | 0.7 |
| 121 | 4 | 5.7 | 233 | 1 | 0.7 |
| 128 | 6 | 5.7 | 235 | 1 | 0.7 |
| 130 | 2 | 5.7 | 240 | 0 | 0.7 |

would be a single layer deposited every spring. In field studies, it also would be important to perform the longitudinal study over several years, in the event that the production of new growth rings is not annual. Single-year studies may not capture variation in the rate of growth ring deposition that may occur over longer periods as a result of environmental variation or other external cues. Comparisons of wild juvenile desert tortoises at several study sites in the Mojave and Colorado Deserts, California, USA, showed that the frequency of growth rings produced annually varied significantly (Berry, 2003). The formation of growth rings was positively correlated with total annual precipitation and to a lesser extent available forage, both of which were patchily distributed both spatially and temporarily.

Alternative mechanistic explanations have been proposed to explain how growth rings could be added. The widely held explanation is that growth rings form after growth spurts (Germano, 1988, 1998; Moll and Legler, 1971). An alternative explanation hypothesizes that growth rings could be added as a function of body size, not age (Litzgus and Brooks, 1998; Tracy and Tracy, 1995). Growth rings may form as the turtle grows as a structural adaptation to strengthen scutes, making it more difficult for the scutes to bend or to be pulled off the shell. According to this hypothesis, growth ring deposition may not show a consistent pattern with age but, instead, would relate to body size. Of course, age and size are usually correlated (turtles usually get larger as they get older); however, growth rates of turtles can vary both spatially and temporally and can lead substantially to different conclusions about the regularity of the pattern of deposition of growth rings. For example, counts of plastral growth rings tended to underestimate the known age of juvenile desert tortoises born and housed in semi-natural enclosures near Barstow, California, USA, without any supplemental food or water (Table 1). In "good" years, when ground forage was abundant, they grew and added one or more growth rings per year. In "bad" years, however, when forage was sparse, they did not show any measureable growth (in fact, some juveniles actually showed negative growth, shrinking in size!) and no growth rings were added (K. Spangenberg, personal communication).

## LITERATURE SURVEY: AGE VERSUS GROWTH RINGS

In an effort to synthesize the primary scientific literature, we evaluated research papers that used counts of growth rings as a technique for determining the age of terrestrial and freshwater (including brackish water) turtle species. The contents of each paper were examined and initially placed into one of three groups: (1) papers in which the author(s) presented some data to support their use of the technique (ranging from a single data point to multiple recaptures over several years), (2) papers in which the author(s) stated that they had data to support their use of the technique, but did not present it, and (3) pa-

TABLE 2.—Papers that used the technique of counting growth rings to age turtles. Papers are divided into those that contained data and those that did not contain data testing the validity of the technique for use in their study.

| | |
|---|---|
| Papers that present a test of the method; $n$ = 44 | Aresco and Guyer, 1998; Benedetti, 1926; Berry, 2003; Bourn and Coe, 1978; Brooks et al., 1997; Burbidge, 1981; Bury and Germano, 1998; Cagle, 1946; Castanet and Cheylan, 1979; Coker, 1906; Congdon et al., 1992, 1993; Ewing, 1939; Galbraith and Brooks, 1987, 1989; Germano, 1988, 1998; Grubb, 1971; Harding and Bloomer, 1979; Iverson, 1988, 1991; Jones and Hartfield, 1995; Kennett, 1996; Lambert, 1982, 1993; Litzgus and Brooks, 1998; Miller, 1932, 1955; Moll and Klemens, 1996; Moll and Legler, 1971; Mushinsky et al., 1994; Nichols, 1939; Rowe, 1997; Schwartz et al., 1984; St. Clair, 1998; St. Clair et al., 1994; Stickel, 1978; Stickel and Bunck, 1989; Stott, 1988; Stubbs et al., 1985; Townsend, 1931; Tracy and Tracy, 1995; van Loben Sels et al., 1997; Zweifel, 1989 |
| Papers that do not present a test of the method; $n$ = 101 | Auffenberg and Weaver, 1969; Balcombe and Licht, 1987; Bayley and Highfield, 1996; Blair, 1976; Branch, 1984; Brooks et al., 1992; Buhlmann, 1995; Cagle, 1948, 1950, 1952, 1953, 1954*b*; Christiansen and Burken, 1979; Christiansen and Dunham, 1972; Christiansen and Moll, 1973; Dobie, 1971; Doroff and Keith, 1990; Ernst, 1971, 1975, 1977, 1986; Ernst and Ernst, 1973; Ernst et al., 1973; Etchberger and Ehrhart, 1987; Farrell and Graham, 1991; Frazer et al., 1991*a,b*; Gaymer, 1968; Germano, 1992, 1994; Germano and Joyner, 1988; Gibbons, 1967, 1968*a,b*, 1969, 1970, 1983; Gibbons and Coker, 1977; Gibbons and Lovich, 1990; Gordon and MacCulloch, 1980; Graham, 1970, 1971, 1995; Graham and Doyle, 1977; Graham and Perkins, 1976; Hailey, 1988, 1990; Hammer, 1969; Hulse, 1976; Inozemtsev and Pereshkolnik, 1994; Iverson, 1979*a*, 1982, 1989; Iverson et al., 1991; Judd and Rose, 1983; Kofron, 1991; Kuchling and Bloxam, 1988; Lahanas, 1982; Lambert, 1995; Landers et al., 1982; Lindeman, 1996; Liu and Hu, 1939; Long, 1986; Lovich et al., 1990, 1998; MacCulloch and Secoy, 1983; Magnusson et al., 1997; Mahmoud, 1967, 1969; Meek, 1985, 1989; Mitchell, 1985, 1988; Mitchell and Pague, 1990; Mitchell and Rhodin, 1996; Moll, 1973, 1976; Morris and Sweet, 1985; Pilgrim et al., 1997; Powders, 1978; Quinn and Christiansen, 1972; Rickard et al., 1989; Risley, 1933; Ross, 1989; Ross et al., 1991; Rowe, 1992; Sexton, 1959; Shealy, 1976; Spearman, 1969; Storer, 1930; Stubbs et al., 1984; Swingland and Coe, 1979; Swingland et al., 1989; Tinkle, 1958; Tucker, 1978; Tucker and Sloan, 1997; Tucker et al., 1995*a,b*; Vogt, 1980; Webb, 1961; Wilbur, 1975 |

pers in which the author(s) neither presented nor referred to having their own data to support using scute ring counts (most studies cited previously published papers). Some authors have published several papers on a particular species of turtle at a specific location. For example, several papers have been published on *Emydoidea blandingi* at the E. S. George Reserve study site (e.g., Congdon and van Loben Sels, 1991; Congdon et al., 1993) and on *Pseudemys* (*Trachemys*) *scripta* at the City Lake study site (Cagle, 1946, 1948). Because the methods used in each group of papers were similar (e.g., same species, same study area, etc.) and the data sets were subsets of each other or identical, we only included one of the publications in our survey to avoid redundancy. Three of the papers that we examined included growth ring data on two turtle species. Each of these papers was treated as two separate case studies, unless the author(s) combined the results for both species ($n$ = 1), whereby the paper was treated as one case study. Also, two papers included growth ring data on both captive and wild individuals of the same species. Because captive and wild individuals do not experience the same environmental conditions and this can influence the pattern of ring deposition (Moll and Legler, 1971), we considered the wild and captive data from these papers as separate studies.

We examined a total of 150 case studies from 145 papers that used counts of growth rings to estimate the age of individual turtles (Table 2). Six families of tur-

TABLE 3.—Summary of papers that presented data (or implied data existed) testing the relationship between growth rings and age.

| Taxon | Turtles—wild or captive | Sample size (age class[a]) | Duration of study (yr) | Frequency of recapture (yr) | Author(s) general conclusion of study | Category (see text) | Source |
|---|---|---|---|---|---|---|---|
| Chelidae | | | | | | | |
| *Chelodina longicollis* | W | 1 (?) | 3 | 3 | six rings added 3.8 yr later | UN | Stott, 1988 |
| *Chelodina rugosa* | W | 9 (?) | 1 | 1 | ring counts reliable to 3 yr of age | JUV | Kennett, 1996 |
| *Elseya dentata* | W | 14 (?) | 1 | 1 | ring counts reliable to 9 yr of age | SM | Kennett, 1996 |
| *Pseudemydura umbrina* | W | ? | ? | ? | ring counts present to 4–6 yr of age[b] | DTI | Burbidge, 1981 |
| Chelydridae | | | | | | | |
| *Chelydra serpentina* | W | 8 (J), 24 (A) | 10 | 3–10 | juveniles add rings at rate of 1.07/yr[c,d] | JUV | Brooks et al., 1997 |
| *Chelydra serpentina* | W | 18 (A) | 3 | 1 | observer variation exists in ring counts[e] | DTI | Galbraith and Brooks, 1989 |
| *Chelydra serpentina* | W | 4 (J), 51 (A) | 3 | 1 | ring counts reliable to sexual maturity[d] | SM | Galbraith and Brooks, 1987 |
| *Chelydra serpentina* | W | ? | 15 | 1–15 | ring counts reliable to young adult | SM | Congdon et al., 1992 |
| Emydidae | | | | | | | |
| *Chrysemys picta* | W | ? | 15 | 1–15 | ring counts reliable to young adult | SM | Congdon et al., 1992 |
| *Chrysemys picta* | W | 88 (J) | 6 | 1 | ring counts reliable to 3 yr of age[f] | JUV | Brooks et al., 1997 |
| *Chrysemys picta* | W | ? | 3 | ? | ring counts equal years elasped | SM | Rowe, 1997 |
| *Chrysemys picta* | W | ? | 3 | 1–3 | ring counts reliable to young adult | SM | St Clair et al., 1994 |
| *Chrysemys picta* | W | >100 | 18 | 1–18 | ring counts reliable to 3 yr of age[b] | JUV | Zweifel, 1989 |
| *Clemmys guttata* | W | 51 (J,A) | 11 | 1–11 | one to six rings added 1 yr later | UN | Litzgus and Brooks, 1998 |
| *Clemmys insculpta* | W | ? | 9 | 1–9 | ring counts reliable to 15 yr of age | SM | Harding and Bloomer, 1979 |
| *Clemmys marmorata* | W | 36 (J,A) | 5 | 1–2 | reliable to sexual maturity[g] | SM | Bury and Germano, 1998 |
| *Emydoidea blandingii* | W | ? | 15 | ? | ring counts reliable to young adult | SM | Congdon et al., 1993 |
| *Graptemys geographica* | W | 8 (?) | ? | ? | one ring added each year | NAL | Iverson, 1988 |
| *Graptemys oculifera* | W | 33 (?) | 3 | 1–3 | ring counts reliable to 3 yr of age[h] | JUV | Jones and Hartfield, 1995 |
| *Malaclemys terrapin* | C | 2 (J) | 2 | 2 | ring counts reliable to 3 yr of age[b] | JUV | Coker, 1906 |
| *Terrapene carolina* | W | 18 (J,A) | 12 | 1–12 | ring counts equal years elasped 33%[i] | DTI | Nichols, 1939 |
| *Terrapene carolina* | W | 52 (J,A) | 8 | 1–8 | ring counts equal years elasped 40%[j] | DTI | Stickel and Bunck, 1989 |
| *Terrapene carolina* | W | 70 (J,A) | 20 | 1–20 | ring counts equal years elasped 32%[k] | DTI | Stickel, 1978 |
| *Terrapene carolina* | W | ? | ? | 1–? | rings countable until sexual maturity | DTI | Ewing, 1939 |
| *Terrapene carolina* | W | 303 (J,A) | 19 | 1–19 | ring counts reliable to 9 yr of age | SM | Schwartz et al., 1984 |
| *Terrapene carolina, Terrapene ornata* | C | 61 (J,A) | 3 | 1–3 | ring counts equal years elasped 61%[l] | DTI | St. Clair, 1998 |
| *Trachemys scripta* | W | ? | 4 | 1–4 | three to four rings added 1 yr later | UN | Moll and Legler, 1971 |
| *Trachemys scripta* | W | 28 (J,A) | 3 | 1–3 | ring counts reliable to 3 yr of age[b] | JUV | Cagle, 1946 |
| Kinosternidae | | | | | | | |
| *Kinosternon flavescens* | W | ? | ? | ? | ring counts reliable to 12 yr of age[m] | SM | Iverson, 1991 |
| *Kinosternon sonoriense* | W | ? (J) | 4 | ? | ring counts reliable to 9 yr of age | SM | van Loben Sels et al., 1997 |

TABLE 3.—Continued.

| Taxon | Turtles—wild or captive | Sample size (age class[a]) | Duration of study (yr) | Frequency of recapture (yr) | Author(s) general conclusion of study | Category (see text) | Source |
|---|---|---|---|---|---|---|---|
| Testudinidae | | | | | | | |
| *Geochelone gigantea* | C | ? | ? | 1 | rings fade in older adults | DTI | Bourn and Coe, 1978 |
| *Geochelone gigantea* | W | ? | ? | 1 | rings fade in older adults | DTI | Bourn and Coe, 1978 |
| *Geochelone gigantea* | W | 5 (?) | 3 | 3 | three rings added 3 yr later | NAL | Grubb, 1971 |
| *Geochelone nigra vicina* | C | 1 (J), 2 (A) | 2, 11, 15 | 2, 11, 15 | ring counts equal years elasped | PSM | Townsend, 1931 |
| *Geochelone sulcata* | C | 1 (J) | 18 | 18 | 17 rings added 18 yr later | PSM | Lambert, 1993 |
| *Gopherus agassizi* | C | 4 (J) | 3 | 1–3 | ring counts unreliable | UN | Miller, 1932 |
| *Gopherus agassizi* | C | 2 (J) | 2 | 2 | four to five rings added 2 yr later | UN | Miller, 1955 |
| *Gopherus agassizi* | C | 16 (J) | 2 | 1–2 | 0–7 rings added 1 yr later | UN | Tracy and Tracy, 1995 |
| *Gopherus agassizi* | W | 13 (A) | >20 | >20 | ring counts reliable 20–25 yr of age | PSM | Germano, 1988 |
| *Gopherus agassizi* | C | 6 (J) | 8 | 7–8 | ring counts equal known age | PSM | Germano, 1988 |
| *Gopherus agassizi* | C | 13 (J,A) | ? | ? | ring counts reliable 20–25 yr of age[n] | PSM | Germano, 1998 |
| *Gopherus agassizi* | W | 192 (J) | 9 | <1–9 | 0–3 rings added 1 yr later[o] | UN | Berry, 2003 |
| *Gopherus polyphemus* | W | >50 (J,A) | 10 | 1–10 | ring counts reliable to 13 yr of age | SM | Mushinsky et al., 1994 |
| *Gopherus polyphemus* | W | 39 (J,A) | 6 | 1–5 | ring counts equal time elasped to 15 yr | SM | Aresco and Guyer, 1998 |
| *Malachocherus tornieri* | W | 3 (A) | 1.4 | 1.4 | two to four rings added 1.4 yr later | UN | Moll and Klemens, 1996 |
| *Testudo graeca* | C | 1 (J) | 37 | 37 | 35 rings added 37 yr later | PSM | Lambert, 1982 |
| *Testudo graeca* | C | 94 (?) | 2 | 2 | young only | JUV | Benedetti, 1926 |
| *Testudo hermanni* | W | >100 (J,A) | 2 | 2 | ring counts equal years elasped 29%[p] | DTI | Stubbs et al., 1985 |
| *Testudo hermanni,* | W | 4 (J), 14 (A) | ? | ? | ring counts reliable to sexual maturity[q] | SM | Castanet and Cheylan, 1979 |
| *Testudo graeca* | W | 9 (J), 4 (A) | ? | ? | | | |

[a] J = juvenile, A = adult, ? = unknown.
[b] Repeated shedding of scutes causes annuli to disappear.
[c] Among observer variation in ring counts for juveniles ranged from 3–10 yr.
[d] Most adults do not add annual rings.
[e] Did not test relationship between ring counts and age, just observer variation in counting rings.
[f] Ring counts ranged from −2 to +3 of previous years count for 6 and 7 yr olds.
[g] $n$ = 29, one ring added 1 yr later; $n$ = 6, two rings added 2 yr later; $n$ = 1, one ring added 2 yr later.
[h] 55% had added annual rings and 45% had lost part or all of rings.
[i] Ring counts ranged from −7 to +1 of years elasped.
[j] Ring counts 1 too high 13%, 1 too low 19%, maximum difference was 3 too high or too low; for turtles with 13 or fewer scute rings at first capture.
[k] Ring counts within 1 yr or less 77%, 2 yr or less 92%, 3 yr or less 97%, 4 yr or less 99%, 5 yr or less 100%.
[l] Ring counts fewer than expected 33% and higher than expected 7%.
[m] Two annuli may appear as one in years of no growth.
[n] Ring counts within 1 to 2 yr of known age for adults.
[o] Number of rings added each year positively correlated with total annual precipitation.
[p] Tortoises <15 yr accuracy rose to 36%; 89% of turtles +/− 2 scute rings of years elasped.
[q] Reports good correlation exists between known age turtles to 7 yr and ring counts but provides no data.

tles, including 24 genera and 53 species, were represented. Of these 53 species, 36 were freshwater, 15 were terrestrial, and 2 were brackish-water species. Most of the case studies ($n$ = 101) fell into our third grouping, i.e., that no data were presented to support the use of the technique. The authors of these 101 case studies either cited other studies to support using growth ring counts for their population of turtles or simply assumed that this technique works (Table 2). The remaining 44 papers (49 case studies) fell into one of the first two categories, i.e., the authors presented data (or implied that data existed) on growth rings and age (Table 3). After carefully reading these 49 case studies, we placed them into one of the following six categories: PSM, the authors found the technique reliable for aging turtles "past the age of sexual maturity" ($n$ = 6); SM, the authors found the technique reliable for aging turtles up to young adult (i.e., "sexual maturity," $n$ = 15); JUV, the authors found the technique reliable for aging "juvenile" turtles ($n$ = 8; 6 of the 8 to age 3); NAL, the authors found the technique reliable but "no age limit" was given ($n$ = 2); UN, the authors found the technique "unreliable" as a method for aging turtles ($n$ = 8); and DTI, the authors presented data that we found "difficult to interpret" ($n$ = 10) (Table 3). The studies that we categorized as DTI either reported only the percent of instances in which ring counts equaled years elapsed (e.g., 33%, Nichols, 1939; 40%, Stickel and Bunck, 1989; 29%, Stubbs et al., 1985; Table 3), did not themselves draw any general conclusions as to the usefulness of the technique for their species studied, and/or stated simply that growth rings were "countable" until sexual maturity but did not test the relationship between counts and age (e.g., Ewing, 1939). The primary objective of most of the papers presenting data on growth rings and age was to examine some aspect of the ecology and/or life history of a particular turtle species, and not to test the relationship between growth rings and turtle age. Therefore, papers with data that tested the relationship between growth rings and age usually involved small sample sizes, short durations of study, and/or use of captive animals to infer a pattern in a wild population (Table 3).

We categorized each case study containing growth ring data as to whether it addressed pattern of growth ring deposition and/or the causal factors behind growth ring deposition. We found three case studies that supported the pattern that counts of growth rings equaled the exact age of the turtles studied (Aresco and Guyer, 1998; Coker, 1906; Germano, 1988); Coker (1906) and Germano (1988) used small samples of captive turtles. Several case studies ($n$ = 22) concluded that, on average, a consistent number of growth rings were added each year; however, many of these authors pointed out that this pattern only held for certain ages (e.g., only reliable for juvenile turtles). Only five case studies had sufficient data to provide a better understanding of what physiological/environmental cues are responsible for deposition of growth rings from new epidermal layers (Berry, 2003; Bourn and Coe, 1978; Bury and Germano, 1998; Galbraith and Brooks, 1987; St. Clair et al., 1994); however, three of these five case studies were either on captive turtles or were of relatively short duration (3 yr).

## Literature Survey: Size Versus Growth Rings

To test the hypothesis that body size, rather than age, may be a better predictor of the number of growth rings on a turtle (Tracy and Tracy, 1995), we examined the papers we reviewed for those reporting data that could be used to determine both age versus growth ring and body size versus growth ring relationships. Some authors presented the relationships graphically without reporting correlation coefficients. In these cases, we used Data Thief® to capture data from published figures and then computed correlation coefficients for these relationships.

We found five papers that provided data on the relationship between counts of growth rings and both body size and age for a total of six turtle species (Table 4). We then compared the amount of variance

explained by regressions of both age and size against the number of rings. Arbitrarily assuming that a difference in $r^2$ values of 0.1 represented a real difference in the predictive ability, we found that, for one species, age was a better predictor of the number of rings than size; for one species, size was a better predictor than age; and for the other four species, neither variable was a better predictor.

TABLE 4.—Relationships between scute rings and age (or elapsed time) and scute rings and body size.

| Species | $r^2$-age | $r^2$-size | Source |
|---|---|---|---|
| *Clemmys guttata* | 0.46 | 0.54 | Litzgus and Brooks, 1998 |
| *Gopherus agassizii* | 0.77 | 0.87 | Germano, 1988 |
| *Gopherus polyphemus* | 1.00 | 0.98 | Aresco and Guyer, 1998 |
| *Terrapene carolina* | 0.54 | 0.98 | Nichols, 1939 |
| *Testudo hermani* | 0.91 | 0.61 | Castanet and Cheylan, 1979 |
| *Testudo graeca* | 0.75 | 0.73 | Castanet and Cheylan, 1979 |

## DISCUSSION

The majority (67%) of the surveyed papers that used counts of growth rings to age turtles presented no data supporting the use of the technique. Most of the authors of these papers either assumed that the technique worked or cited other studies as validation of its use in their study. Many researchers cited Sexton (1959) as validation of the use of counts of growth rings to age turtles. Sexton's paper, however, never tested the relationship between growth rings and age in any species; it simply described a method of using age-size data to estimate the age of older individuals that had lost growth rings by shedding or shell wear. Additionally, Sexton (1959) directly stated that the assumption that growth rings are deposited annually must be tested and verified before using his technique. Reviewers of techniques for estimating age of turtles have pointed out that this assumption should be tested before employing Sexton's technique or ring counts in general (e.g., Graham, 1979; Zug, 1991), but these cautions have been largely ignored.

Some authors cited papers that used growth ring counts to age turtle species other than the species in their study (e.g., Dobie, 1971; Graham and Doyle, 1977; Lindeman, 1996). One could argue that scute development is likely a phylogenetically conservative trait, i.e., nearly all turtle lineages form scutes that are apparently developmentally similar. Thus, closely related species could be expected to have the same pattern of ring deposition. Studies have shown, however, that environmental variation plays a role in the pattern of growth ring formation (e.g., Berry, 2003; Moll and Legler, 1971). In order to rely on this phylogenetic conservatism argument, therefore, it would be necessary to show that scute ring formation in related species responds the same way to environmental variation. The potential effects of environmental variation could be demonstrated by conducting studies of multiple species that co-occur in several areas that vary in local environmental conditions. Alternatively, an understanding of the fundamental physiological triggers for ring formation would allow us to predict how species would respond to geographic variation in environmental conditions and, thus, give more confidence in assumptions about the relationship between ring counts and age.

Previous review articles on the use of growth rings to age turtles have listed numerous papers that have counted growth rings without evaluating whether the data contained within these papers support a relationship between ring counts and age (e.g., Castanet, 1988; Germano and Bury, 1998; Gibbons, 1976). The widespread use of any technique should not be considered sufficient evidence of its efficacy or accuracy. Although it may be possible to count growth rings on many turtle species, the ability to count rings on the shell of a turtle should not imply that ring counts are an accurate method for aging the turtle. Ironically, the recurring use of the technique by turtle biologists has been taken to be its validation despite a lack of actual scientific justification. However, several reviewers have suggested caution in employing ring counts (e.g., Carr, 1952; Graham, 1979; Zangerl, 1969; Zug, 1991) and sug-

gested that the effectiveness of using ring counts to estimate age may vary with location, species, and climatic patterns (Zug, 1991).

As we have shown, 33% of the papers (49 of 150) that we examined presented any data that could be used to discern the relationship between growth ring counts and age, and 18 of these 49 either presented no interpretable conclusions or concluded that the technique was not useful. Investigators, who concluded that the use of growth rings was not a reliable method to age their turtles, studied turtle species that spanned families from Chelidae to Testudinidae. Several investigators, however, found the technique to be useful for aging turtles at their study site and, from these papers, we can make some very general conclusions. Within families, considerable variation was observed in the usefulness of the technique, with the exception of the Kinosternidae; both species of *Kinosternon* studied could be aged using growth rings up to the age of sexual maturity. Only within the family Testudinidae could growth rings be used as an indication of age past the age of sexual maturity (Germano, 1988, 1998; Lambert, 1982). However, several studies on tortoises found the technique unreliable (Berry, 2003; Miller, 1932), useful for young only (Benedetti, 1926), or useful to sexual maturity only (Aresco and Guyer, 1998; Castanet and Cheylan, 1979; Mushinsky et al., 1994). For example, Mushinsky et al. (1994) found it difficult to age gopher tortoises past the age of sexual maturity (approximately 13 yr) because, as growth slowed, the growth rings tended to overlap, making them impossible to count. Even within a particular species, we found considerable variation in the usefulness of the technique. For example, of the five studies on *Chrysemys picta,* three found the technique useful in aging turtles to sexual maturity and two found it only useful in aging turtles to age 3 (Table 3).

The usefulness of growth ring counts as a technique for assessing age depends not only on the strength of the relationship, but upon the biological questions addressed using this technique. For some studies of turtle life history, it may not be necessary to know exact ages of individuals, but it may be sufficient to categorize animals into age classes (e.g., hatchling, juvenile, adult). In this type of study, the uncertainties in age estimates from growth ring counts may be unimportant. In other words, a lack of precision and accuracy of age estimates from growth rings may be an acceptable trade-off for the speed and ease of using this method.

On the other hand, accurate determination of age is critically important in some types of studies, particularly those with implications for conservation of rare or endangered species. In population viability analyses and demographic surveys of endangered species, incorrect estimates of age at maturity and population demographics could lead to improper decisions about management of sensitive biological resources. For example, overestimates of age at maturity in a turtle species that accumulates several growth rings per year may lead to the erroneous conclusion that generation time is much shorter than it actually is (Berry, 2003). This error, in turn, would lead to overestimates of potential population growth rates, imprudently easing concern about the low population size of that species.

Regardless of the accuracy in age estimates needed for a particular study, it is necessary to know how the relationship between growth ring counts and age changes with age. For species that shed scutes, age estimates may only be accurate for a few years (e.g., Brooks et al., 1997; Jones and Hartfield, 1995; Kennett, 1996), whereas growth ring counts may be accurate to sexual maturity in species that do not shed scutes (e.g., Galbraith and Brooks, 1987; Mushinsky et al., 1994). Knowledge of how growth ring deposition (and retention) changes with age for each particular species remains important even though close correlation between age and growth ring numbers may not.

Although some early studies describe how growth rings are formed (Legler, 1960; Moll and Legler, 1971), there has been no work detailing the histological and physiological mechanisms underlying the

deposition of scutes as layers. Unlike tree rings or bone rings, which are formed when new growth is added on top of existing tissue, growth rings are formed when an entirely new layer of tissue is added beneath existing tissue. This type of deposition results in a thicker scute than would result if the tissue simply expanded outward. A number of adaptive explanations can be postulated to explain the advantages of thickened scutes. However, without a clearer understanding of the factors responsible for growth ring formation, we can describe only the patterns observed in the relationship between growth rings and growth. This lack of information leads to inherent uncertainty in the accuracy of using growth ring counts to age turtles.

Significant differences in the number of growth rings present on an individual turtle have been observed by investigators (Galbraith and Brooks, 1989). The discrepancies in counts of growth rings appear to result from the ability (or inability) of the observer to distinguish so called "true rings" from "false rings." False rings are reported as forming shallower indentations on the epidermal surface than true rings and not forming completely around the scute like true rings (Germano and Bury, 1998; Legler, 1960). Because turtles are long-lived vertebrates, studies of some populations are conducted by different generations of investigators. Thus, more than one researcher will be involved in aging turtles in any given population. Under these circumstances, a permanent record of growth rings (e.g., plaster casts) for individual turtles should be obtained whenever possible (Germano and Bury, 1998). These records can then be used in a future test of validation of the technique for a particular population of turtles.

Some authors have used measurements of size (as opposed to counts) of growth rings to measure growth rates of turtles (e.g., Cagle, 1946, 1954*a*; Hart, 1982; Iverson, 1979*a*; Magnusson et al., 1997). Size of scutes certainly is related to size of turtles in some manner, but that discussion is beyond the scope of this paper. However, authors, who imply that size (width) of scutes can be used to measure growth of turtles from one age to another, should be wary of the assumptions implicit in that technique. Measurements of growth rate from growth rings implies that these rings are formed at a known time, which is exactly the assumption we have questioned in this review. Further, some reviews of ring-based techniques often fail to emphasize that the time between deposition of rings may not be consistent (e.g., 1 yr), even in cases where the same reviews have urged caution in using ring counts to estimate age (e.g., Carr, 1952; Graham, 1979). Authors who wish to use measures of growth rings to quantify growth over time should be aware of the issues that we have raised above (see Philosophical Issues: Pattern Versus Cause) and should have similar lines of evidence as those who wish to use growth ring counts to estimate age.

## CONCLUSIONS

Our literature review illustrates that (a) there is currently no basis for aging turtles from counts of growth rings that can be generalized across species and populations, (b) relatively few studies have attempted to calibrate the relationship between counts of growth rings and age, and (c) the preponderance of literature relies on an assumption that ring counts are an accurate estimate of turtle age, without testing that relationship or citing studies that verify the relationship. Moreover, the literature provides only a weak understanding of how growth rings are accumulated in turtles, and, as a result, it is not clear whether growth rings are accumulated in accordance with an individual's age or in accordance with its body size. Indeed, we know so little about growth ring production that we cannot distinguish between the hypothesis that growth rings are a non-adaptive consequence of periodic growth spurts or an adaptation for providing strength to scutes as they become larger and more vulnerable to bending and peeling.

Regardless of the factors responsible for growth ring formation, patterns in the number of growth rings in relation to age

can provide a statistical basis for estimating age for some species. In these circumstances, attempts to age turtles using counts of growth rings (a) require a calibration of the technique for each species in each environmental situation, and (b) also should include an estimation of statistical error associated with the age estimation. For some scientific questions, precision in determining age is not critically important, and rough estimates of age from growth rings are adequate. In other circumstances, unknown precision in the estimation of age in individuals will dangerously jeopardize, or limit, conclusions that can be drawn from data.

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