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Age Determination in Turtles: Evidence of Annual Deposition of Scute Rings

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Determining the age of individuals in a turtle population is a useful tool for understanding their ecology (e.g., demography, growth rates, age at sexual maturity, senescence). Even recording age of only a portion of a population is important, especially if the age of younger individuals can be determined accurately. Most useful for long-term studies is a technique that does not require individuals to be killed or harmed. Counting the number of rings formed by deposition of epidermal scute layers in turtles has been used by many researchers to determine age without harming individuals. Several reviews (e.g., Gibbons, 1976; Graham, 1979; Castanet, 1988; Zug, 1991) have supported this technique to determine the age of young turtles, but recent papers have questioned its use (Stott, 1988; Cox et al., 1991; Tracy and Tracy, 1995; Kennett, 1996; Brooks et al., 1997). Although there are an impressive number of studies that have used scute annuli to estimate age of turtles, Kennett (1996) stated "growth annuli on many species have proved unreliable in determining ages of individuals." Further, there is concern that researchers do not validate the use of scute layers (Galbraith and Brooks, 1987; Brooks et al., 1997). The underlying concern is whether or not growth rings on scutes represent layers that are deposited annually or not. We provide a current review to investigate the evidence for and against the use of scute rings for age determination and compare its advantages and limitations.

Historical Use of Scute Annuli

The use of scute annuli to determine ages of turtles extends from Agassiz (1857) who used them to determine ages of *Chrysemys picta*. Discussing the general nature of scute layering in turtles, Agassiz (1857:259) stated "hence it follows that we find upon the surface of each scale, around a small angular central plate, (the scale of the first years' 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." He also discussed the use and appearance of scute annuli in several tortoise species, including *Gopherus polyphemus*, *Geochelone radiata*, and *Psammobates geometricus*, as well as several aquatic species. Coker (1906) was the next to use scute annuli to determine age of a turtle species, *Malaclemys terrapin*. Other early pioneers of this technique were Benedetti (1926) working on *Testudo graeca*, Storer (1930) on *Clemmys marmorata*, Townsend (1931) on *Geochelone vicina*, Risley (1933) on *Sternotherus odoratus*, Sergeev (1937) on *Emys orbicularis*, Ewing (1939) and Nichols (1939) on *Terrapene carolina*, and Liu and Hu (1940) on *Chinemys reevesii*. Cagle was the first to extensively use scute annuli as a means of determining age of *Trachemys scripta* (1946, 1948a, 1948b, 1950), *Chrysemys picta* (1954a), *Malaclemys terrapin* (1952b), and several species of *Graptemys* (1952a, 1953, 1954b). Sexton (1959) showed how to determine age of *C. picta* even when some of the early annuli were missing due to wear. Carr (1952) pointed out some of the problems associated with using scute annuli to determine age of turtles, but believed that they were a useful tool.

Multiple authors have used scute annuli to determine age of at least some portion of populations of turtle or tortoise species (Table 1). The most frequently studied species were *Chrysemys picta*, *Clemmys insculpta*, *Trachemys scripta, Testudo graeca, Chelydra serpentina,* and *Emydoidea blandingii*. We have not presented this table to justify the use of scute annuli merely because others have used this method. We recognize that the hypothesis that scute rings are formed annually has not been tested in all of these studies, but it has been verified for numerous

Table 1. Studies that have used scute annuli to determine age of individual turtles. Numbers in parentheses are the maximum number of scute rings reported by those authors and were either given in the text or determined from graphs. Numbers in brackets are unusually high number of scute rings found only in one individual. Question marks mean the number is highly uncertain. Taxonomy follows Ernst et al. (1994) and Ernst and Barbour (1989).

PELOMEDUSIDAE
- *Podocnemis expansa*
  - Pritchard and Trebbau, 1984

CHELIDAE
- *Chelodina rugosa*
  - Kennett, 1996 (5)
- *Chelodina mccordi*
  - Rhodin, 1994
- *Elseya dentata*
  - Kennett, 1996 (8)
- *Pseudemydura umbrina*
  - Burbidge, 1981
- *Phrynops rufipes*
  - Magnusson et al., 1997
- *Chelus fimbriatus*
  - Pritchard and Trebbau, 1984

CHELYDRIDAE
- *Chelydra serpentina*
  - Christiansen and Burken, 1979 (20); Iverson et al., 1997 (29); Gibbons, 1968a; Hammer, 1969; Graham and Perkins, 1976; Galbraith and Brooks, 1987; Galbraith and Brooks, 1989; Gibbons, 1987; Congdon et al., 1992; Congdon et al., 1994
- *Macroclemys temminckii*
  - Dobie, 1971 (36-37); Tucker and Sloan, 1997 (45); Powders, 1978; Morris and Sweet, 1985

KINOSTERNIDAE
- *Sternotherus odoratus*
  - Risley, 1933 (10); Tinkle, 1958 (9); Mahmoud, 1969 (10); Mitchell, 1988 (10); Mahmoud, 1967; Ernst, 1986; Gibbons, 1987; Mitchell, 1985c; Harding, 1997
- *Sternotherus depressus*
  - Tinkle, 1958 (4)
- *Sternotherus minor*
  - Tinkle, 1958 (10); Etchberger and Ehrhart, 1987; Etchberger and Stovall, 1990
- *Sternotherus carinatus*
  - Tinkle, 1958 (8); Mahmoud, 1969 (10)
- *Kinosternon subrubrum*
  - Mahmoud, 1969 (10); Iverson, 1979a (8); Mahmoud, 1967; Ernst et al., 1973; Gibbons, 1983; Frazer et al., 1991a
- *Kinosternon baurii*
  - Iverson, 1979b
- *Kinosternon creaseri*
  - Iverson, 1988a
- *Kinosternon scorpioides*
  - Pritchard and Trebbau, 1984
- *Kinosternon alamosae*
  - Iverson, 1989a
- *Kinosternon flavescens*
  - Mahmoud, 1969 (10); Iverson 1989b (10); Mahmoud, 1967; Long, 1986; Iverson, 1991
- *Kinosternon sonoriense*
  - Hulse, 1976 (9-11); Hulse, 1982 (5); van Loben Sels et al., 1997 (9)
- *Kinosternon hirtipes*
  - Iverson, 1981; Iverson et al., 1991
- *Kinosternon chimalhuaca*
  - Berry et al., 1997

EMYDIDAE
- *Chinemys reevesii*
  - Liu and Hu, 1940 (ca. 5)
- *Mauremys japonica*
  - Yabe, 1989 (15); Yabe, 1992
- *Mauremys leprosa*
  - Meek, 1987 (13); Keller, 1997 (8); Perez et al., 1979
- *Melanochelys tricarinata*
  - Mitchell and Rhodin, 1996
- *Melanochelys trijuga*
  - Mitchell and Rhodin, 1996
- *Rhinoclemmys punctularia*
  - Pritchard and Trebbau, 1984
- *Clemmys guttata*
  - Ernst, 1975 (14, ♂; 18, ♀); Ernst, 1970; Graham, 1970; Graham, 1995; Ernst and Zug, 1994; Perillo, 1997
- *Clemmys muhlenbergii*
  - Ernst, 1977 (13); Lovich et al., 1998
- *Clemmys insculpta*
  - Harding and Bloomer, 1979 (15); Farrell and Graham, 1991 (20); Ross et al., 1991 (19); Brooks et al., 1992 (29); Garber, 1989; Lovich et al., 1990; Ernst et al., 1994; Harding, 1997; Daigle, 1997
- *Clemmys marmorata*
  - Storer, 1930 (12); Bury and Germano, 1998 (12-14, [16])
- *Emys orbicularis*
  - Sergeev, 1937 (12)
- *Emydoidea blandingii*
  - Graham and Doyle, 1977 (15); Ross, 1989 (18); Congdon and van Loben Sels, 1991; Congdon and van Loben Sels, 1993 (19); Rowe, 1992 (14, [19]); Graham and Doyle, 1978; Gibbons, 1987; Congdon et al., 1993; Herman et al., 1994; Harding, 1997
- *Terrapene carolina*
  - Nichols, 1939 (15); Stickel, 1978 (18-20); Schwartz et al.,1984 (9); Stickel and Bunck, 1989 (13); Ewing, 1939; Minton, 1972; Harding, 1997; Pilgrim et al., 1997
- *Terrapene ornata*
  - Legler, 1960 (12-13); Blair, 1976; Doroff and Keith, 1990
- *Chrysemys picta*
  - Sexton, 1959 (8); Ernst, 1971a; Ernst, 1971b (4); Quinn and Christiansen, 1972 (10); Ernst and Ernst, 1973 (5); Wilbur, 1975 (9); Tucker, 1978 (5-6); Iverson, 1982 (7); MacCulloch and Secoy, 1983 (7-11); Mitchell, 1988 (7); Frazer et al., 1991b (7); Congdon et al., 1992 (6-9); Frazer et al., 1993 (5); Lindeman, 1996 (7); Rowe, 1997 (8); Agassiz, 1857; Cagle, 1954a; Gibbons, 1967; Gibbons, 1968b; Gibbons, 1968c; Christiansen and Moll, 1973; Moll, 1973; Bayless, 1975; Hart, 1982; Mitchell, 1985a; Mitchell, 1985b; Balcombe and Licht, 1987; Gibbons, 1987; Ernst and McDonald, 1989; Rickard et al., 1989; Ross, 1989; Zweifel, 1989; Iverson and Smith, 1993; St. Clair et al., 1994; Lindeman, 1997
- *Trachemys scripta*
  - Cagle, 1948a (4-5); Tucker et al., 1995a; Tucker et al., 1995b (6); Cagle, 1946; Cagle, 1950; Webb, 1961; Gibbons, 1970; Moll and Legler, 1971; Gibbons et al., 1981; Gibbons, 1987; Frazer et al., 1990; Gibbons and Lovich, 1990; Dunham and Gibbons, 1990; Gibbons and Greene, 1990; Mitchell and Pague, 1990; Tucker and Moll, 1997
- *Pseudemys concinna*
  - Jackson and Walker, 1997
- *Pseudemys floridana*
  - Gibbons and Coker, 1977 (7?); Gibbons, 1987
- *Pseudemys rubriventris*
  - Graham, 1971 (10); Graham, 1969
- *Deirochelys reticularia*
  - Gibbons, 1969 (6); Gibbons, 1987; Buhlman, 1995
- *Graptemys geographica*
  - Iverson, 1988b (9-10); Gordon and MacCulloch, 1980; Vogt, 1980; Graham, 1989
- *Graptemys barbouri*
  - Cagle, 1952a
- *Graptemys ernsti*
  - Cagle, 1952a; Shealy, 1976
- *Graptemys gibbonsi*
  - Cagle, 1952a
- *Graptemys pseudogeographica*
  - Vogt, 1980 (6, ♂; 12, ♀)
- *Graptemys ouachitensis*
  - Vogt, 1980 (6, ♂; 12, ♀); Moll, 1976 (6); Cagle, 1953; Webb, 1961
- *Graptemys oculifera*
  - Kofron, 1991 (6); Jones and Hartfield, 1995 (5-6); Cagle, 1953
- *Graptemys flavimaculata*
  - Cagle, 1954b
- *Graptemys nigrinoda*
  - Lahanas, 1982
- *Malaclemys terrapin*
  - Cagle, 1952b (6-7); Seigel, 1984 (7); Coker, 1906

TESTUDINIDAE
- *Acinixys planicauda*
  - Kuchling and Bloxan, 1988 (20)
- *Chersina angulata*
  - Branch, 1984 (20)
- *Geochelone pardalis*
  - Lambert, 1995 (20-25, [28])
- *Geochelone sulcata*
  - Lambert, 1993 (20-24)
- *Geochelone gigantea*
  - Gaymer, 1968 (25); Grubb, 1971 (20-30); Bourn and Coe, 1978 (20-25); Swingland and Coe, 1979; Gibson and Hamilton, 1984; Swingland et al., 1989
- *Geochelone carbonaria*
  - Pritchard and Trebbau, 1984 (20-26)
- *Geochelone vicina*
  - Townsend, 1931; Townsend, 1937
- *Testudo graeca*
  - Castanet and Cheylan, 1979 (17-18); Lambert, 1982 (19, [35]); Stubbs et al., 1984 (< 20); Benedetti, 1926; Braza et al., 1981; Hailey, 1988; Inozemtsev and Pereshkolnik, 1994; Bayley and Highfield, 1996
- *Testudo hermanni*
  - Castanet and Cheylan, 1979 (17-18); Stubbs et al., 1984 (< 20); Meek, 1985; Meek, 1989 (19); Stubbs et al., 1985 (15); Hailey, 1988 (8); Hailey, 1990 (16); Hailey and Loumbourdis, 1990
- *Gopherus agassizii*
  - Germano 1994 (24); Germano and Joyner, 1988; Germano, 1988; Germano, 1992; Germano, 1998
- *Gopherus berlandieri*
  - Auffenberg and Weaver, 1969 (18); Germano, 1994 (24); Judd and Rose, 1983
- *Gopherus polyphemus*
  - Landers et al., 1982 (20-30?); Germano, 1994 (24); Mushinsky et al., 1994 (23); Spearman, 1969; Aresco and Guyer, in press
- *Gopherus flavomarginatus*
  - Germano, 1994 (25)
- *Malacochersus tornieri*
  - Moll and Klemens, 1996 (15-18)

species. Also, many scientists that have worked for decades on chelonians find the technique useful.

Evidence of Annual Deposition of Scute Rings

Major reviews that have supported the use of scute annuli to determine age in chelonians include Zangerl (1969), Gibbons (1976, 1987), Graham (1979), Castanet (1988), and Zug (1991). Coker (1906) was the earliest worker who gave data in support of the annual deposition of scute rings reporting that two *Malaclemys terrapin* added 2 annuli after 2 years. In *Geochelone vicina*, Townsend (1931) found that two known-age captive tortoises (12 and 15 yrs) had 12 and 15 scute annuli. Ewing (1939) did not show specific data confirming annual deposition of rings in *Terrapene carolina*, but he made plaster casts of shells and recaught turtles several years later. He indicated that scute rings are formed annually and that care is needed to distinguish pseudoannual (false) rings when making age estimates.

Numerous other studies since the 1930s have shown that growth rings on scutes match age in young turtles. The validity of scute rings being deposited annually has been shown in *Chelodina rugosa* and *Elseya dentata* (Kennett, 1996), *Pseudemydura umbrina* (Burbidge, 1981), *Phrynopes rufipes* (Magnusson et al., 1997), *Chelydra serpentina* (Galbraith and Brooks, 1987; Congdon et al., 1994; Brooks et al., 1997), *Kinosternon sonoriense* (van Loben Sels et al., 1997), *Chrysemys picta* (Cagle, 1946; Sexton, 1959; Zweifel, 1989; Congdon et al., 1992; Rowe, 1997), *Trachemys scripta* (Gibbons, 1970), *Graptemys ernsti* (Shealy, 1976), *Clemmys guttata* (Ernst, 1975), *C. insculpta* (Harding and Bloomer, 1979; Lovich et al., 1990; Ernst et al., 1994), *C. marmorata* (Bury and Germano, 1998), *Emydoidea blandingii* (Congdon and van Loben Sels, 1991), *Terrapene carolina* (Stickel and Bunck, 1989), *T. ornata* (Legler, 1960; Schwartz et al., 1984), *Geochelone gigantea* (Grubb, 1971; Bourn and Coe, 1978), *Testudo graeca* (Benedetti, 1926; Castanet and Cheylan, 1979), *T. hermanni* (Stubbs et al., 1985; Castanet and Cheylan, 1979), *Gopherus polyphemus* (Mushinsky et al., 1994; Aresco and Guyer, in press), and *G. agassizii* (Germano, 1988, 1998). For all these studies, annuli can be used to determine age only up to the time when linear growth slows to a low rate, which is generally at or just after the onset of sexual maturity (Bury, 1979).

It is important to determine the maximum number of scute annuli that are countable so that age estimates are reliable. There is a maximum number (or range) of scute growth rings that are useful for determining age (Table 1). Past this number of rings, even if very narrow rings can be counted, the periodicity of deposition has not been determined. Maximum numbers of countable scute annuli generally are 5–14 for freshwater species and 15–29 for tortoises (Fig. 1). The greatest number of scute annuli regularly counted for any species is 36–45 in *Macroclemys temminckii* (Table 1). In both studies, the number of growth rings on scutes were determined on dead animals after lifting the scute off the shell, soaking the scute in water, and back-

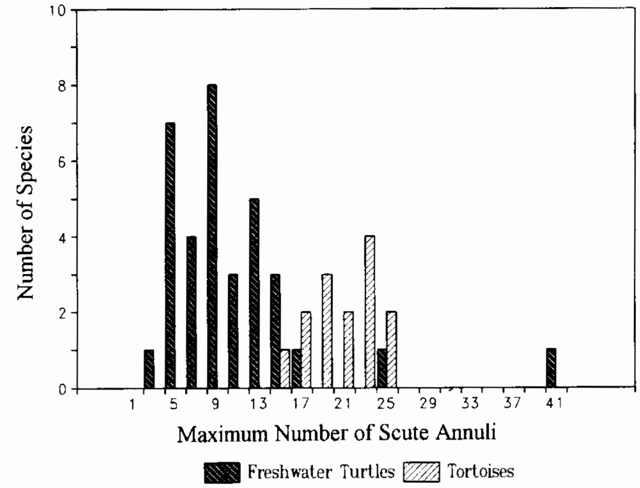

Figure 1. Distribution of maximum number of scute rings among freshwater turtles and tortoises.

lighting the scute. This differs from traditional methods of counting annuli on live turtles, but we do not know if this difference accounts for the unusually high numbers of annuli on *Macroclemys* compared to other species. This is also one of the largest turtles and they frequent quiet waters with muddy substrata, which may reduce wear.

There is a weak relationship between maximum carapace length (CL) of a species and maximum number of countable scute layers ($R^2 = 0.37$, $n = 45$), but the relationship is due mainly to the large number of layers found by Dobie (1971) and Tucker and Sloan (1997) on *Macroclemys temminckii* (Fig. 2). Otherwise there is much scatter between size and scute layers for freshwater turtles, and essentially a flat line for tortoises (Fig. 2). This indicates that size is not a reliable estimator of age in turtles and tortoises. Irrespective of size, species appear to have a set number of annuli that are deposited during juvenile growth.

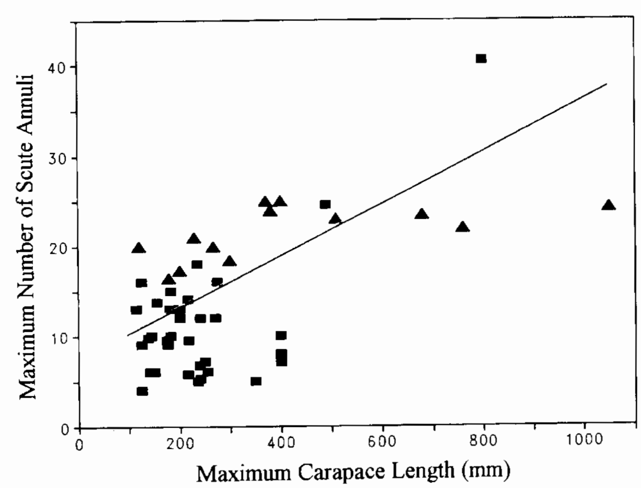

Figure 2. Relationship of the maximum number of scute layers (from Table 1) to maximum carapace length for freshwater turtles and tortoises of the world. Maximum carapace lengths were taken from Ernst et al. (1994) and Ernst and Barbour (1989). Squares = freshwater turtles, triangles = tortoises ($R^2 = 0.37$, $n = 44$).

Alternative Views

The validity of using scute annuli to determine age has been questioned recently for all turtles (Cox et al., 1991; Kennett, 1996; Brooks et al., 1997) and specifically for *Chelodina longicollis* (Stott, 1988), *Gopherus agassizii* (Tracy and Tracy, 1995), *Chelydra serpentina* and *Chrysemys picta* (Brooks et al., 1997), and *Clemmys guttata* (Litzgus and Brooks, 1998). Both Cox et al. (1991) and Kennett (1996) cited papers on *Sternotherus m. minor* by Tinkle (1958) and Iverson (1978) and a paper on *Chelydra serpentina* by Galbraith and Brooks (1987) as evidence of lack of reliability of scute annuli to determine age in most turtle species. Contrary to the statement of unreliability, Galbraith and Brooks (1987) specifically showed that the number of scute annuli matched age in young *C. serpentina*, but they warned that annual formation of rings should be checked in each species. In contrast, some *Sternotherus m. minor* apparently did not show distinct annuli (Tinkle, 1958; Iverson, 1978), but in these studies the species occurred in year-round equitable habitats (springs and nearby streams), which are unusual in temperate latitudes. It is erroneous, however, to generalize the possible unreliability of scute annuli to determine age in a few populations of a few species to most other turtle species, especially species in temperate latitudes. In fact, both Tinkle (1958) and Iverson (1978) used annuli to determine age of a portion of the population of *S. m. minor*, and Iverson has successfully used the technique subsequently on many other species (Table 1). Further, although Kennett (1996) questioned the reliability of scute annuli to determine age of turtles, he found that they were reliable for determining age of young individuals of two species he studied in Australia (Table 1).

Stott (1988) showed that one *Chelodina longicollis* marked in January 1980 had produced 6 scute rings when recaptured in late November 1983. He concluded that scute rings were not produced annually in this species. However, he only reported ring formation on the small nuchal and first marginal scutes as opposed to the larger scutes, such as costals or abdominals, where rings are easier to count. Also, non-annual production of scute rings in this one individual does not preclude annual deposition in other individuals in this or other populations.

For *Gopherus agassizii*, Tracy and Tracy (1995) studied laboratory-reared tortoises fed a high protein diet and kept continually active. This artificial environmental regime led to the formation of multiple growth rings in a year. The authors concluded that single scute rings were not produced annually and, therefore, scute rings could not be used to determine age of young desert tortoises (Tracy and Tracy, 1995). These conditions bear no resemblance to natural environmental conditions that produce annual deposition of scute rings in *Gopherus agassizii* (Germano, 1988) and, therefore, invalidates their experiment as a test of this method (Germano, 1998).

Studies by Brooks et al. (1997) on *Chelydra serpentina* and *Chrysemys picta* and by Litzgus and Brooks (1998) on *Clemmys guttata* were done on populations in Ontario at the northern limit of the range of these species. Both studies reported that scute annuli cannot be used to determine age because there was a non-significant relationship between number of scute rings added and time elapsed. They found that in some individuals for which scute annuli had not worn off, the number of rings added were less than annual or, in some cases, actually less than originally counted.

Similar problems in methodology are apparent in both papers. Brooks et al. (1997) showed that juvenile *C. serpentina* and *C. picta* have a one-to-one relationship between the number of scute annuli and age. However, because the relationship does not hold throughout life, they dismissed the use of annuli at any age. They also showed that *C. serpentina* with 22–23 rings do not add additional rings after 10 yrs. This is to be expected for adults that are growing linearly at a slow rate. Data in their paper support the use of scute annuli as an accurate indicator of age in young turtles. For *Clemmys gutatta*, Litzgus and Brooks (1998) admitted that their use of different field assistants during the study probably led to misreadings of the number of scute rings or possibly the coded identifications of individuals. This is the likely explanation for the apparent loss of scute rings exclusive of wear. The number of scute rings can only decrease in subsequent years by wear or by absorption; the authors discounted the first explanation and no one has ever reported the absorption of scute rings. As with the study by Brooks et al. (1997), Litzgus and Brooks (1998) attempted to use scute rings to estimate age of all turtles for which all or some annuli were still visible. However, there is a maximum number of scute rings that can be counted with the unaided eye (Table 1). The authors did not indicate how old the turtles were at the start of the study. Ernst (1975) showed that production of visible scute annuli in *C. guttata* ceased by 14 yrs in males and 18 yrs in females. Litzgus and Brooks (1998) had 64.3% (27 individuals) of their sample with $\geq$ 15 scute rings and 47.6% (20 turtles) with $\geq$ 19 rings. When rings become too small to be counted, it is a misuse of the method to try to use scute layers to determine age of individuals. Although the number of scute rings produced may be slightly less than age as the turtle approaches the time it ceases production of visible rings altogether (Germano, 1988, 1998; Galbraith and Brooks, 1989), it is a fairly accurate method of determining age as long as counts are made carefully and estimates are not made on individuals past the time rings are being produced annually.

There are a few instances where the number of scute rings do not seem to be formed annually, primarily among species in tropical areas. Species where annuli were not found to correspond with chronological age include *Batagur baska* (Moll, 1980) and some populations of *Malacochersus tornieri* (Moll and Klemens, 1996). Such instances underscore the need for testing the assumption that annuli match chronological age for each species, and, in some cases, for each population.

However, even in tropical areas, scute annuli appear to form in some species. In Venezuela, scute annuli are distinct in *Kinosternon s. scorpioides*, *Geochelone carbonaria*, and *G. denticulata*, and are apparent on at least some individuals of *Podocnemis expansa*, *Chelus fimbriatus*, and *Rhinoclemmys diademata* (Pritchard and Trebbau, 1984). *Trachemys scripta* in Panama may form more than one growth layer in a year, but the pattern of scute shedding allowed for determining age of young turtles up to 9 yrs of age using scute annuli (Moll and Legler, 1971). Recaptures of marked *T. scripta* from Costa Rica ($n = 12$) confirmed that major annuli were formed annually for this population as well (J. Tucker, *pers. comm.*). *Phrynops rufipes* in central Amazonia, Brazil, appear to deposit annual scute layers, at least for a short period of time (Magnusson et al., 1997). Scute annuli are apparent in *Melanochelys* species in tropical Nepal (Mitchell and Rhodin, 1996), in *Chelodina rugosa* and *Elseya dentata* in northern Australia (Kennett, 1996), and in *Chelodina mccordi* on Roti in Indonesia (Rhodin, 1994). All of these cyclical tropical growth patterns probably represent differential growth related to distinct wet and dry periods.

Relatively unusual environmental conditions can also affect deposition of scute annuli. In the temperate species *Pseudemydura umbrina* and *Gopherus agassizii*, unusually low rainfall years can lead to the lack of an annulus being deposited (Burbidge, 1981; Germano and Fritts, 1994). Although there are a few exceptions, environmental conditions for most species or in most years seem to cause the development of annual rings during early life.

Conclusions and Guidelines

With few exceptions, counting scute annuli is a reliable method of estimating ages of chelonians and can be used to determine the age of individuals often to or near the age of maturity (Table 1). The method involves counting growth annuli found on either the plastron or the carapace as described by Carr (1952), Sexton (1959), Legler (1960), Zangerl (1969), Moll and Legler (1971), Bourn and Coe (1978), Graham (1979), and Zug (1991). Scute lamellae are laid down as a series of underlying plates that are extremely thin under previous years' layers but expand on the outer edge to form a thickened ring. These annual rings can be recognized by the deep indentation they leave in the epidermal layer of the scute and because they form a complete annulus around the scute. Indentations should be visible at least on three sides.

The best and least worn scutes should be used to determine age and this varies from species to species and from individual to individual. Annuli on the plastron may be more distinct in some species, such as *Gopherus polyphemus* and *Clemmys marmorata*, and resist wear longer than annuli on the carapace. In contrast, annuli on the plastron of *G. agassizii* often are worn faster than on the carapace.

Although we believe that counts of scute annuli provide a reliable estimate of age of most younger chelonians, there are several drawbacks to this technique that must be recognized when determining age. There may be temporary cessation of growth during the growing season of an individual and non-annual or false rings can sometimes form. These must be recognized when making counts. Generally, false rings can be distinguished from annual rings because they form shallower indentations on the epidermal surface (Legler, 1960). However, in some instances false rings may be almost as deep as annual rings. False rings do not form completely around the scute but may form a deep ridge on the lateral (carapace) or medial (plastron) aspect of the scute (Legler, 1960; Landers et al., 1982). There is no substitute for experience in distinguishing rings on turtle shells. Errors can be reduced by inspecting several scutes and comparing numbers obtained among scutes.

Another limitation of the technique is that counting rings is useful only to determine age of younger turtles. Most young turtles deposit relatively large annuli for several years when they are growing rapidly. When linear growth slows, usually at or near sexual maturity, turtles no longer deposit rings large enough to be detected (Cagle, 1946; Legler, 1960; Table 1). Although very small rings at the edges of scutes may be visible under magnification, no one has yet shown these to be produced annually (Germano, 1992), and we recommend that only rings that can be counted without magnification be used to determine age. The appearance of the edges of scutes (Germano, 1992) is the criterion for determining whether the individual is the same age as the number of growth rings counted on the scute or is older than that count. The individual is the same age (± 1-2 yrs) if the last scute ring is flat and smooth or if the lateral (carapace) or medial (plastron) edge of the scute is not beveled. If the total number of annuli is greater than the maximum number reported for that species (Table 1), then caution needs to be used in the interpretation of the data. If scute annuli are still being formed, the ring closest to the seam is usually soft and can easily be indented using a pointed object. Especially in turtles with dark shells, new scute growth is often visible as a lighter colored area around the scute. If very thin rings are visible near the seam, particularly if beveling is evident, and the last countable layer is hard, then the turtle is likely older than the countable number of growth rings.

Besides the ability to determine the age of many individuals in a population by counting scute annuli, this technique also means that growth of a large segment of a population can be modeled with only one handling of individuals. However, accurately counting annuli is relatively time consuming and can slow down field work. If the goal of the study is to maximize captures, the time needed to determine age of all individuals may be prohibitive. However, we believe that the advantages of determining age of individuals outweighs the time spent in most instances. Further, capture rates of some species, such as tortoises, are generally low so it is time well spent to maximize data obtained for captures.

One method that can accelerate data acquisition in the field is to make a cast (negative) of one or several scutes using dental alginate material followed by making a positive impression using dental plaster in the laboratory (Ewing, 1939; Galbraith and Brooks, 1987). We have found that these casting materials are readily available from most dental supply houses. Besides decreasing the time necessary to gather age data in the field, a permanent record of growth is obtained. This can be quite useful when an individual is recaptured in later years. Although any scute can be cast, we have found that the second costal or the abdominal are usually the best to cast because of the relatively straight annuli formed. When we make casts, initial age determination is made in the field using a variety of scutes, but casts allow us to make final determinations of age and record growth data in the laboratory. We have used this method successfully in the field on *Gopherus agassizii*, *G. berlandieri*, *G. flavomarginatus*, *Clemmys marmorata*, and *Emydoidea blandingii*. This technique greatly decreased time spent in the field determining age and measuring growth annuli and reduced error under field conditions.

No technique is without error. We recognize that counting scute annuli does not work in all instances, and we agree with Galbraith and Brooks (1987) and Litzgus and Brooks (1998) that counts need to be validated as an estimate of age in turtles. We note, however, that this technique has been shown to estimate age reliably in a variety of species. Ultimately, any technique is only as good as those who apply it. We believe that with care, and following the assumptions of the technique, most researchers can use counts of scute annuli to determine the age structure of a large segment of a population. Unfortunately, no non-invasive method is available to determine the age of turtles past the maximum number of countable scute annuli, except to recapture and re-examine turtles of known age.

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