Restoration of Epidermal Scute Patterns During Regeneration of the Chelonian Carapace

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ABSTRACT. – Adult individuals of many chelonian populations may experience damage to their carapace which can regenerate. In terrestrial chelonians, extensive damage and regeneration of the carapace occur relatively frequently as a result of fire. In contrast to box turtles (genus *Terrapene*) of the family Emydidae, several tortoise species of the family Testudinidae (suborder Cryptodira) and *Pelusios subniger* (Pelomedusidae, suborder Pleurodira) are shown to have the capability of restoring normal scute patterns during carapace regeneration if the underlying bone plates have not been totally destroyed. If bone plates have been totally destroyed, the typical scute patterns derive from the dermal bone plates, the regeneration of which is in turn influenced by the axial skeleton. This regenerative capability seems to be a primitive feature of chelonians. Differences between chelonian groups in the capability of restoring the scute pattern during regeneration may be related to their relative degree of evolutionary specialization.

KEY WORDS. – Reptilia; Testudines; Testudinidae; Emydidae; Pelomedusidae; morphology; osteology; carapace regeneration; wound healing; epidermal scute pattern formation

The known history of chelonians began in the Triassic with the genus Proganochelys, which already had typical turtle morphology consisting of a bony shell with epidermal external scutes, and composed of a dorsal carapace and a ventral plastron. With the exception of the highly aquatic Trionychidae, Carettochelyidae, and Dermochelyidae, all extant chelonian families retain the typical chelonian shell of dermal bone plates sutured together and covered by a mosaic of epidermal scutes. During ontogeny the development of the scutes precedes that of the bones by a considerable span of time (Ewert, 1985). The morphogenetic control that determines the bone and scute patterns is unquestionably complex. It is generally assumed that the non-congruous mosaic patterns of the scutes and bones are independently controlled and that the forces that determine the differentiation of the overall shell mosaic are functional only during the period of ontogeny when the epidermal and mesenchymal components of the shell are ordinarily formed (Zangerl, 1969).

Probably due to their shell, which has changed little over 200 million years, chelonians represent the most successfully persistent tetrapod group through geological times. The rigid, box-like armor also makes individual chelonians good survivors. All chelonians appear to be potentially longlived, with many reaching and some surpassing the life span of humans.

Few attempts have been made to gain insights into the morphogenesis of scute patterns by studying patterns of regeneration of the adult turtle shell following serious injuries. Gadow (1886) provided the most comprehensive description of extensive regeneration of the chelonian carapace, studying captive *Testudo graeca* which had sustained serious transport injuries: "the epidermal scutes fell off, followed, after some three to ten months, by the thick

osseous plates, which were completely atrophied and then raised above the old surface, until the greater portion of the old carapax was bodily lifted up and was kept in connexion with the animal merely by the overlapping margins of some of the neighbouring uninjured scutes. Underneath this old armour, and separated from it by a space partly filled with decaying matter, comes a layer of new tortoise-shell. This layer is of typical structure, and even contains the usual patches of black and yellow pigment. In bad cases the whole renewed area is covered with a mass of horny large tubercles without any regular arrangements..." (Gadow, 1886:220). He did not specify whether or not scute seams were ever reconstituted in their typical mosaic pattern in Testudo graeca and it is open for interpretation what he meant by "typical structure." A century later, in their review of regeneration in reptiles, Bellairs and Bryant (1985:383) interpreted Gadow's results as follows: "...eventually formed a new atypical horny scute; beneath this, a new layer of bone developed."

Several cases of extensive carapace regeneration have also been reported for North American box turtles of the genus *Terrapene* (Smith, 1958; Legler, 1960; Rose, 1986). All these authors concluded that the corneous epidermal covering of the regenerated shell showed no evidence of seams and that the typical scute mosaic was not reconstituted. It is a general assumption that, after large-scale loss of the integument, post-traumatic wound healing in reptiles (and birds and mammals) leads to scar tissue which differs macro- and microscopically from the original structure (Bellairs and Bryant, 1985; Maderson, 1985).

During a field study in Yugoslavia near Budva (Montenegro) in May 1976 I found a female *Testudo hermanni* with about one quarter of her carapace covered with white bony plates which were about to be shed; a further one half of her carapace was regenerated, with the dead bony plates recently shed (Fig. 1). When I lifted the dead bony plates off the shell in the area of the third and fourth vertebral scutes I found underneath a new, thin epidermal scute layer, with the seams of the vertebral scutes clearly visible as thin, pale lines (Fig. 2). This finding did not support the accepted wisdom regarding carapace regeneration and I began to document all subsequently discovered cases of carapace regeneration. In this paper I summarize and discuss my observations of carapace regeneration in various chelonian species in regard to the occurrence of epidermal scute seams.

MATERIALS AND METHODS

During studies of wild populations of tortoises and turtles in Europe and Madagascar over the last 20 years I documented photographically free-living adult individuals with carapace damages in various stages of repair and regeneration. In addition I photographed tortoises and turtles with major carapace regeneration in zoos and private collections. Major regeneration (affecting more than five vertebral or costal shields) was observed in adults of the following species: Testudinidae - Testudo hermanni (n = 37), Testudo graeca (n = 3), Testudo marginata (n = 2), Geochelone radiata (n = 3), Kinixys belliana (n = 1), Pyxis arachnoides (n = 2); Emydidae – Terrapene ornata (n = 3); and Pelomedusidae – Pelusios subniger (n = 1). Most specimens were released at the point of capture or remained in captivity. A few dry shell specimens of carapace regeneration are in my private collection. In this paper I present photographs of selected specimens to demonstrate different degrees in the reconstitution of scute seams in cases of carapace regeneration.

RESULTS AND DISCUSSION

Populations of terrestrial chelonians sometimes show a high prevalence of shell damage. Apart from mechanical damage, e.g., by hoofed animals, predators, machinery, or cars, a frequent cause is fire. For example, a severe summer fire in the habitat of Testudo hermanni in northern Greece caused an estimated 40% population reduction, with juveniles showing the highest mortality, while large adults survived best; many of those remained in shallow depressions (pallets) and were scarred when the fire swept through rapidly, showing burn damage to the rear of the carapace (Stubbs et al., 1985). Such burns may destroy virtually the whole epidermal scute layer of the carapace and affect and expose most of the carapacial bone plates without killing the animal, as demonstrated for Testudo hermanni by Schweiger (1989). Many terrestrial chelonians in Mediterranean and savanna climates may experience fires during their lifetimes. The need for shell regeneration may be common in terrestrial species and must serve as a selective factor of some importance in evolution. In contrast to most mechanical injuries, fire damage often affects relatively large areas of the carapace, but the depth of tissue damage may be

limited depending on the intensity and duration of fire exposure.

A morphological and histological description of the regeneration process of the carapace of *Testudo graeca* was given by Gadow (1886) and seems to apply to chelonians generally: from the margin of the wound the Malpighian cell layer (horn-producing stratum germinativum) grows below the dead exposed bone and forms a new scute layer, allowing the necrotic bone to slough off (Figs. 3, 4). The subcutaneous connective tissue thickens and proceeds towards the center of the damaged area (Fig. 5). These regenerative processes of the chelonian shell closely follow the model of "wound rejection reaction" for integumentary wound healing in reptiles (Maderson, 1985).

My examination of carapace regeneration in Testudinidae revealed that tissue damage after extensive



Figure 1. Wild adult female *Testudo hermanni* near Budva, Montenegro, May 1976. Regenerating carapace, presumably after fire damage.



Figure 2. Detail of third and fourth vertebral scutes of specimen in Fig. 1 after removal of the necrotic bone plates. Arrow indicates thin, pale scute seams in thin epidermal scute layer.



Figure 3. Wild adult female *Testudo hermanni* near Budva, Montenegro, June 1977. Regenerating carapace, presumably after fire damage.

destruction of the shell surface is often rather superficial and may not totally destroy the bony plates. The bony plates of the adult chelonian shell have a spongy middle region (medulla) surrounded on both sides by zones of compact lamellar bone (cortex). Many non-lethal fire injuries (which may cover most of the carapace) may only destroy the epidermal scute layer and the thin outer layer of the mesenchymal bone plates, the superficial lamellar zone. In this situation the Malphigian layer does not grow under the bony plates (as described by Gadow, 1886), but rather grows under the injured portion of the bone along the spongy middle region of the plates and forms a new scute layer. In these cases the inner compact zone of the bone plates forms the nucleus for regeneration of the new bony shell.

The chelonian bony shell is a composite of superficial dermal bones fused with an internal endochondral axial skeleton. The carapace is formed from dermal costal bones with fused ribs, dermal neural bones with fused thoracic vertebrae, and purely dermal marginal bones. If a superficially damaged regenerated carapace is viewed from the internal surface, the regular pattern of the bony plates remains visible (though not necessarily perfect) and the fusions of the vertebral column and rib processes remain intact (Fig. 6). This process has also been described in detail for a box turtle (Rose, 1986).

In cases of superficial destruction of the outer layers of the carapace, tortoises (Testudinidae) are often able to reconstruct the typical mosaic pattern of the epidermal scutes. Figures 1, 3, and 4 show animals that regenerated virtually their entire carapace, much of it with the typical scute pattern. Although the typical scute pattern is reconstituted, there are also often additional small scutes and tubercles along the seams of the typical pattern. The seams defining the anterior four vertebral scutes are generally much more clearly developed than those of the posterior and lateral portions of the carapace, i.e., the fifth vertebral, costal, and marginal scutes (Fig. 7). Elements of the axial skeleton exert a morphogenetic influence upon the pattern of the dermal bone plates during regeneration of the box turtle shell (Smith, 1958; Rose, 1986). The present findings demonstrate that the axial skeleton may even provide morphoge-



Figure 4. Adult male *Testudo hermanni* near Budva, Montenegro, August 1980. Regenerating carapace, presumably after fire damage.



Figure 5. Detail of empty shell of specimen in Fig. 4 from the inside, right pleural bone area, regenerating bone growth extending towards the center of damage where the bone plates were totally destroyed.



Figure 6. Detail of empty shell of specimen in Fig. 4 from the inside, left pleural and central neural bone area with vertebral column. The inner compact zone of the bone plates remained viable and formed the nucleus for regeneration of the new shell.

netic control by mesenchymal induction of the epidermal scutes, presumably indirectly via the dermal bone plates. In the lateral areas of the carapace where the axial skeleton is relatively distant, the shape of the regenerated scutes and seams is more variable and shows more deviations from the typical pattern than in the central vertebral region close to the axial skeleton.



Figure 7. Near total regeneration of carapace of adult female *Testudo graeca*, left and right sides. Pet trade specimen, origin unknown.

An alternative explanation to mesenchymal induction of the epidermal scute pattern would be that during regeneration the existing seams at the margins of intact scutes are simply extended towards the center of damage to reconstitute the pattern. This probably occurs with small injuries which do not cover entire scutes. However, when larger areas of the carapace are deeply destroyed the typical scute pattern cannot be restored by simply extending existing seams (Figs. 8, 9). Although some new seams have been formed in such cases, the tortoises were not able to restore the typical pattern of vertebral and costal scutes (the specimen in Fig. 8 may actually have had much of the vertebral column damaged, but, when found, was capable of coordinated locomotion). The forces that determine the differentiation of the typical epidermal scute pattern during carapace regeneration seem to depend on the condition and the mode of regeneration of the dermal bones which, themselves, are influenced by the axial skeleton.

Why should tortoises reconstruct scute patterns during shell regeneration? In animals, generally, there seems to be a central relationship between repair, longevity, and reproduction. The disposable soma theory predicts that longerlived species should have better somatic repair (Kirkwood, 1981). Chelonians as iteroparous organisms spread their reproductive effort over most of their adult lifespan. Reptiles, in general, keep growing throughout much of their life, although growth slows once individuals reach sexual maturity and may become very slow or ceases in old age. Theoretically the shell of chelonians keeps growing throughout their life, although some authors suggest that, in certain species, growth may become negligible in adult or old individuals (Andrews, 1982). A box-like armor sets relatively rigid limits on the quantities of food, water, air, energy stores, waste products and, in the case of females, eggs that the body can accommodate. Reproductive traits in several chelonian species indicate that large (and often old) females have higher reproductive success and better quality offspring than smaller females (Congdon and Gibbons, 1990). This suggests that, in evolutionary terms, continued growth well into adulthood may be an important trait for chelonians. Since natural selection operates through differences in reproductive fitness, any repair mechanisms should evolve to maximize future reproductive success of the individual. For many chelonians this may include the potential for further shell growth after carapace regeneration, which may require reconstituted scute seams.

When the chelonian shell increases in size the epidermal scutes grow along their margins creating concentric growth lines. Growth of individual scutes typically is not the same in all directions and, depending on the scute and species, may be extremely asymmetrical (Zangerl, 1969). The subdivision of the epidermal surface cover of the shell into a mosaic of scutes certainly facilitates its proper growth



Figure 8. Wild adult male *Testudo hermanni* near Budva, Montenegro, June 1981.



Figure 9. Wild adult male *Testudo hermanni* near Budva, Montenegro, October 1978.



Figure 10. Adult male *Testudo marginata* from Greece, August 1986. Specimen had been in captivity for ten years following collection with regenerated carapace.

according to its species-specific shape. For tortoises it may be an advantage to maintain the ability to grow after a regeneration event, in particular in species occupying habitats where individuals may experience several fire events during their lifetime. Figure 10 shows a tortoise which grew significantly after the carapace had regenerated, as evidenced by the new concentric growth rings at the scute margins.

I examined three specimens of the box turtle Terrapene ornata (Emydidae) with old, extensive carapace regeneration. All their regenerated shell portions entirely lacked scute seams (Fig. 11). This finding supports the views of other authors (Smith, 1958; Legler, 1960; Zangerl, 1969; Rose, 1986) that box turtles are not able to restore the typical scute pattern during regeneration of the carapace. Although I do not know the extent or depths of the original damage in the specimens I examined, the detailed description of the regeneration of a box turtle shell by Rose (1986) indicates that a tortoise with similar damage to its shell would have restored at least some of its scute seams. Box turtles of the primarily aquatic family Emydidae developed terrestrial living habits independently from the true land tortoises (Testudinidae). This may suggest that the ability to reconstitute the typical scute pattern is an adaptation for the terrestrial existence of the advanced Testudinidae that the less progressive box turtles did not acquire.

However, my discovery of a case of extensive carapace regeneration with near perfect reconstruction of the epidermal scute pattern in a more primitive pleurodire turtle, *Pelusios subniger* (Fig. 12), does not support this theory. Pleurodire and cryptodire chelonians represent separate lineages since early stages of turtle evolution (Gaffney et al., 1987). Although *Pelusios* is aquatic, this genus has, at least in Madagascar, extensive periods of terrestrial dormancy; during the dry season *Pelusios* frequently aestivates under leaf litter or in dense vegetation (reed tussocks) where they may be exposed to bush fires (Kuchling, 1993). Carapace damage due to fire may also occur in other semi-aquatic species that aestivate or hibernate terrestrially.

It has been suggested that the most primitive chelonians, the Triassic Proganochelyidae, were most probably marsh dwellers and that the fully aquatic preference of many modern turtles is a secondary adaptation. Truly terrestrial chelonians first appeared in the Upper Cretaceous in different ancient families - the assumed terrestrial lifestyle is postulated on several morphological parallels to modern terrestrial forms. The terrestrial tortoises of the family Testudinidae did not appear in the fossil record until the mid-Eocene and reached their greatest abundance and diversity in the Pliocene. Tortoises (Testudinidae) evolved from primitive Emydidae, and the emydid turtles have also subsequently given rise to several other terrestrial lines, e.g., the box turtles of the genus Terrapene (Pritchard, 1979). The regenerative capacity to restore normal scute patterns may be a primitive feature of chelonians which may have been lost by adult box turtles which have reached a relatively high degree of evolutionary specialization.

From the perspective of natural selection, repair is only beneficial to the extent that it improves the individual's future reproductive output and fitness, which also depends on the rate of mortality through causes other than senescence. *Terrapene ornata*, for example, has a predilection for dung insects and for moving along ungulate pathways which exposes it to the risk of being trampled and damaged by



Figure 11. Adult male *Terrapene ornata* with the upper portion of its carapace regenerated without scute seams. Pet trade specimen, origin unknown.



Figure 12. Adult male *Pelusios subniger*, Zoo Tsimbazaza, Antananarivo, Madagascar, November 1986. Upper and posterior part of the shell regenerated with scute seams, presumably after fire damage. Origin Madagascar, locality unknown.

hoofed animals. Most adults of wild populations were found to have one or more mechanical injuries on the carapace, probably caused by hoofed stock, that had healed or were undergoing repair (Legler, 1960). Individuals of the genus Terrapene frequently trade increased strength of the bony shell against the potential for future growth relatively early during adulthood through ankylosis, the complete ossification of shell sutures and fusion of bone plates (Pritchard, 1979). In box turtles in general, as well as in those individuals which regenerate their carapace, heavy ossification and strength of the shell may be critical for survival. Regaining shell strength after damage may be more important for reproductive fitness than the regeneration of scute seams and the potential for further growth. A further correlation between shell ankylosis, cessation of shell growth, and the loss of scute boundaries is offered by old individuals of the largebodied, highly aquatic turtles Batagur baska and Kachuga kachuga (Bataguridae) in which the loss of bone sutures as well as scute seams is a normal event. The shells of old individuals are covered with a continuous horn layer that, presumably, has no further growth capacity (Pritchard, 1979; P.C.H. Pritchard, pers. comm.). In Terrapene this trait may be partially developed, with frequent complete ankylosis of bone plates in adults, but loss of scute seams only in damaged, regenerated individuals.

Older individuals of any species show reduced regenerative abilities (Goss, 1969) and larger individuals are less likely to regenerate successfully than smaller individuals (Reichman, 1984). The present study does not provide data on the influence of age on regenerative capacity as regenerations were only observed in adult chelonians. A loss of scute seams during regeneration and, presumably, cessation of further shell growth may not significantly reduce the reproductive fitness of adult box turtles, but in small, juvenile box turtles, the resumption of growth after carapace regeneration should be of selective advantage. I hypothesize that young, growing box turtles should still have the capacity to restore at least some scute seams during carapace regeneration, but this remains to be investigated. Due to their longevity, delayed maturity, range of adult sizes, diversity of life styles, and long evolutionary history, chelonians offer excellent models to study costs and benefits of somatic repair and to test evolutionary theories.

Also of interest is the ability of different chelonian species to reconstitute the typical color pattern of the scutes during regeneration. This capability apparently occurs independently of the ability to restore the scute pattern. In the species that I examined, all shell regenerations of *Testudo marginata*, *Geochelone radiata*, and *Pyxis arachnoides* were uniformly yellow without dark markings, at least in the absence of significant shell growth occurring after the regeneration event. In one specimen of *T. marginata* that had grown after the regeneration event the typical black pigmentation of the scutes eventually partially reappeared along the new growth rings (Fig. 10). In contrast, all shell regenerations of the species *Testudo hermanni*, *T. graeca*, *Kinixys belliana*, *Terrapene ornata*, and *Pelusios subniger* exhib-

ited, at least to some degree, the species-specific pigmentation and color patterns.

The regenerative capability of the chelonian integument is not restricted to the shell; regeneration — as opposed to simple wound healing — of other integumentary appendages may also occur. Davenport (1995) reported that, following amputation of the tail spur of an adult male *T. hermanni* including 2 mm of the flexor caudae lateralis muscle, the spur regenerated. After 12 years it measured 8 mm in length and had regained the pattern, coloration, and shape typical for the species. The regenerative capability of adult chelonians, therefore, is comparable in complexity to that of lizards that regenerate their tails (Bellairs and Bryant, 1985) or to the specialized skin regeneration in the gecko *Geckolepis* which regenerates its typical epidermis without scarring from totipotent reserve cells or neoblasts arising from the deep connective tissue (Schubert et al., 1990).

These observations of epidermal scute regeneration after fire damage in chelonians of three different families invite speculation about the validity of the claim by various indigenous hawksbill turtle hunters that *Eretmochelys imbricata*, if its scutes are removed by roasting the live animal over a fire, is able, when released back into the sea, to regenerate a set of new scutes. In this respect it is also interesting to note that occasional hawksbill turtles are found that do not show the normal color pattern, but have scutes that are nearly entirely yellow (C.J. Limpus, *pers. comm.*). The Japanese tortoiseshell market prices these yellow hawksbill scutes particularly high. Maybe some of these rare and highly sought-after yellow individuals are survivors of live roastings.

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