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Akinesis and Plastral Scute Homologies in Sternotherus (Testudines: Kinosternidae)

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Shell kinesis—the presence of lines of flexion between bony elements of the chelonian shell—is widespread within the Order Testudines. The diversity of independent manifestations of kinesis among turtles was briefly reviewed by Pritchard (1993). Kinesis most often occurs in the form of transverse linkages across the plastron, notably in such unrelated genera as *Terrapene*, *Cuora*, *Pelusios*, and *Kinosternon*, but it also may occur in the bridge (*Rhinoclemmys*, *Platemys*), along the plastral midline (cheloniids, *Carettochelys*, *Pelusios gabonensis*, *Kinosternon scorpioides*), and in the carapace (*Kinixys*, *Dogania*). Inarticulate kinesis (without a specific hinge) also occurs in some juvenile tortoises (*Gopherus*, *Homopus*; Marolda, 2002).

True kinesis-the presence of defined hinging mechanisms, active or passive, between rigid shell elementsshould be distinguished from the general softness of the shell of many hatchling turtles, in which the ossification of the shell elements is incomplete. The thinness and frequent wide separation of these elements by fontanelles, which also occurs in adult turtles of a few species (Dermochelys coriacea, Malacochersus tornieri), gives rise to an overall flexibility that falls short of true kinesis. Typically, as bony elements thicken with overall growth and as their edges approach and finally achieve contact, a "decision" is made at both the developmental and evolutionary levels as to whether a given junction should proceed to become rigid by proliferation of progressively tighter sutural interdigitations (sometimes ultimately followed by overall ankylosis), or should maintain flexibility by such measures as blunting and ultimate loss of the interdigitations and development of a band of flexible, fibrous tissue between the adjacent bones, essentially a pseudarthrosis. An alternative form of kinesis occurs in the trionychid plastron, in which very coarse interdigitations develop, with rounded bone edges separated by connective tissue.

Generally, development of active kinesis (i.e., formation of kinetic structures that can be moved by voluntary muscular action of the turtle) is presumably under genetic control, and develops along with associated functional structures including new or modified muscles and ligaments. On the other hand, passive kinesis may have no such associated structures, and its development may rely more upon pressures exerted during respiratory, ovipositional, or other functions of the animals. Examples of passive kinesis include the overall distention of the plastron of cheloniids and carettochelyids during active respiration; or the depression of the posterior lobe of the plastron (e.g., Heosemys spinosa, Hieremys annandalei) or the entire plastron (Rhinoclemmys, Platemys) in adult females of certain species during oviposition of relatively enormous, hard-shelled eggs. Midline kinesis in certain species (Pelusios gabonensis, Kinosternon scorpioides) may also be passive but functionally linked to powerful, muscular elevation of a plastral lobe that is attached to the hyo-hypoplastral section of the plastron by means of a V-shaped rather than a straight, transverse hinge. In the case of *Pelusios gabonensis*, raising of the anterior plastral lobe forces a distension of the midline hyoplastral and hyoplastral sutures; in Kinosternon scorpioides, raising of the posterior plastral lobe forces each side of the lobe to be raised at a sharper angle laterally than medially, thus "wedging" these sections tightly against the inside of the posterolateral peripheral bones and marginal scutes.

Presumably, demands for kinesis that do not occur until the turtle has reached mature size (especially those associated with oviposition) have to be regulated by appropriate genetic programming, while those demands that may occur throughout life (in the course of respiration; defense/retraction, as in box turtles; or defense/threat, as in the kinosternids with reduced plastra) may, at least in part, develop in response to pressures placed, either regularly or episodically, upon the shell elements during ontogeny.

Shell Kinesis in the Kinosternidae. — In the four extant genera of mud and musk turtles of the family Kinosternidae, the carapacial structure remains relatively generalized, whereas the plastra display a suite of unusual or unique specializations. These plastral specializations include:

1) *Staurotypus*: cruciform plastron; four pairs of plastral scutes; narrow but rigid bridges; anterior passive plastral kinesis; retention of entoplastron; sutural connection between hyo- and hypoplastra.

 Claudius: cruciform plastron; four pairs of plastral scutes; very narrow, non-sutured bridges with considerable kinesis relative to carapace; no plastral kinesis; retention of entoplastron; complete fusion between hyo- and hypoplastra.

3) *Kinosternon* (most species): large, non-reduced plastron; five pairs of plastral scutes plus unpaired anterior element; relatively long, rigid bridges; two plastral hinges, allowing active elevation of anterior and posterior plastral lobes; loss of entoplastron; sutural connection between hyoand hypoplastra.

4) *Kinosternon (herrerai, angustipons, dunni, chimalhuaca)*: plastron reduced, but not fully cruciform; five pairs of plastral scutes plus unpaired anterior element; bridges narrow but rigid; posterior lobe essentially akinetic, anterior lobe with passive kinesis; loss of entoplastron; sutural connection between hyo- and hypoplastra.

5) Sternotherus: plastron reduced but not fully cruciform; bridges narrow and slightly kinetic; five pairs of plastral scutes with or without unpaired anterior element; loss of entoplastron; sutural connection between hyo- and hypoplastra; frequent proliferation of extensive cutaneous tissue along plastral seams, with corresponding reduction of keratinized scutes.

Scute Homologies Within the Kinosternidae. - While the carapaces of the extant kinosternid species are relatively uniform, the plastra vary to a much greater degree than within any other turtle family, in relative size (cruciform to extensive), kinesis (0, 1, or 2 transverse hinges), number of bony elements (7, 8, or 9), and number of scutes (8, 10, or 11). The challenge is thus to interpret plastral evolution and homologies within the Kinosternidae in ways that are commensurate with the overall assumption that the group is indeed monophyletic-or, if such efforts fail, to make proposals for subfamilies or even new families to include both the extant forms and the various fossil genera (e.g., Xenochelys, Baltemys; Hutchison, 1991). Kinesis is notoriously labile within the Testudines, and clearly develops easily under a variety of evolutionary pressures. However, variant numbers and arrangements of plastral scutes form rather rarely, these parts being generally very stable within a turtle family and indeed throughout the entire order, with the primary exceptions of some retention of inframarginals (Cheloniidae, Dermatemydidae) or appearance of supramarginals (Macroclemys), extra vertebral or costal scutes (Notochelys, Lepidochelys, Caretta) and sporadic development or retention of an intergular in certain forms (Cheloniidae, Pelomedusiae, Chelidae).

Hutchison and Bramble (1981) and Bramble et al. (1984) addressed this question in two extremely useful papers, and came to the conclusion that, apart from the presence of an intergular in Kinosternon and many Sternotherus, all kinosternids only had four pairs of actual plastral scutes. The ostensible presence of five pairs in Kinosternon and Sternotherus was an artifact, they argued, of the fact that the humeral scute in these genera was transversely divided by the anterior plastral hinge. Supporting this argument was the observation that the areolae, or remnants of the hatchling scutes, in the scutes immediately anterior and posterior to the anterior hinge remained juxtaposed throughout life (or at least as long as areolae are detectable), whereas the areolae of other adjacent pairs of plastral scutes become progressively separated by growth annuli with ontogeny. They also observed that this interpretation would make the plastra of Kinosternon and Sternotherus much more congruent with those of Staurotypus and Claudius.

Nevertheless, while genetic data or developmental studies would be instructive, actual demonstration that the humeral scute of *Kinosternon* and *Sternotherus* has been divided by the development of the anterior hinge, in the absence of fossils representing the crucial evolutionary stage, requires the examination of abnormal, i.e., akinetic, contemporary specimens, in that it would be hypothesized that the epi-hyoplastral suture would not correspond to a scute seam. Such anomalous specimens are unlikely to be found within *Kinosternon* (except possibly in the few smallplastroned species), because the anterior plastral lobe is subject to powerful, active kinesis in such turtles when adopting a protective stance. *Sternotherus*, with its smaller anterior plastral lobe subject only to passive kinesis, is a much more likely candidate.

Results. — A search through the *Sternotherus* collections of the Chelonian Research Institute (105 specimens, including 7 *S. carinatus*, 14 *S. depressus*, 41 *S. minor*, and 43 *S. odoratus*, revealed 3 akinetic specimens. They were:

PCHP 4147. *Sternotherus minor minor*, subadult (CL 85.5 mm). Empty shell only. Locality: junction of Wekiva and Little Wekiva River, Seminole County, Florida.

PCHP 5188. *Sternotherus odoratus*, adult male (CL 82 mm). Liquid-preserved. Locality: "Florida."

PCHP 6651. *Sternotherus odoratus*, adult female (CL 99 mm). Liquid-preserved. Locality: Reelfoot Lake, Tennessee.

In all three specimens, the plastra are akinetic and the entire area of each side of the plastron between the gular and the femoral scute is spanned by a very large anomalous scute (Fig. 1). In the *S. odoratus*, no growth annuli are evident on any of the plastral scutes, whereas in the *S. minor*, growth annuli are quite clear, and reveal a slight irregularity at the epi-hyoplastral boundary. Furthermore, traces of what appear to be partial seams are evident at the distal extremes of the epi-hyoplastral boundary, whereas the more medial parts show no sign of a seam.

In addition to these three preserved specimens, a live subadult male specimen (CL 63 mm) of *S. odoratus* (Fig. 2), recently captured in Wekiva Springs, Orange/Seminole county line, Florida, has a completely akinetic plastron. Nevertheless, a complete scute seam is evident along the epihyoplastral suture. The specimen is much younger than PCHP 5158 or 6651, with little development of cutaneous tissue along the seams, and with strong growth annuli.

The *Sternotherus* holdings of the Florida Museum of Natural History were also reviewed. Twenty-five specimens of *S. carinatus* from Arkansas uniformly showed very slight anterior kinesis but a well-defined seam was always present along this hinge line. The "hinge" itself was generally curved rather than rectilinear. No kinesis was detectable in two hatchling specimens, and the main point of plastral variation was in the inframarginal scute configurations. Among 80 specimens of *S. minor* from Columbia County, Florida, the hinge was uniformly present except for a single juvenile (UF/FSM 29384) in which the hinge was only weakly developed and the "anterior humerals" were separated.

One hundred specimens of *S. odoratus* from Wakulla County, Florida, were examined. In 10 of these, some deficiency in anterior kinesis was detected, and in 3 of these cases (UF/FSM 73777, male, CL 80 mm; UF/FSM 29297, female, CL 86 mm; UF/FSM 29778, male, CL 60 mm), the trans-humeral seam was present but incomplete, not meeting the edges of the anterior plastral lobe. These all appeared to be mature specimens.



Figure 1. (Left) Adult male *Sternotherus odoratus* (PCHP 5188), CL82 mm. (Middle) Subadult *Sternotherus minor minor* (PCHP 4147), CL 85.5 mm. (Right) Adult female *Sternotherus odoratus* (PCHP 6651), CL 99 mm. All three specimens have akinetic plastra and reduced plastral scute counts.

Discussion. — Examination of the above specimens of *S. odoratus* suggests that the turtles destined to be akinetic may have hatched with a seam or division in the scute covering the epi-hyoplastral suture. As the turtles grew, the anterior lobe remained immovable—an anomaly possibly deriving from some combination of relatively small head size and disinclination to adopt the "head retracted – gape/ threat" posture in these individuals. Behavioral factors could have resulted in there being little downward force to retard the development of a tightly sutured connection at this point. In that the growth of the scutes anterior to the epi-hyoplastral suture takes place in an anteromedial direction and that of the scutes posterior to the hinge in a posteromedial direction, no growth actually occurs along the epi-hyoplastral line itself,



Figure 2. Live subadult male *Sternotherus odoratus*, CL 63 mm. Specimen has akinetic plastron but normal plastral scute count.

and perhaps without the stimulus of a kinetic junction, progressive fusion of the scutes occurred. It is also possible that the akinetic plastron developed as a genetic anomaly without associated behavioral components.

As regards the hypothesis of Hutchison and Bramble (1981) concerning the nomenclature and homologies of plastral scutes in the Kinosternidae, we must first note there is a tendency for loss of the seam directly external to the epihyoplastral suture in specimens in which the underlying suture is akinetic. But the seam may have initially been present in the specimens examined, judging by its apparently progressive dissolution in the subadult akinetic specimens (although this cannot be certain), and may have been lost with growth in the same way that the seam between the anal scutes of Staurotypus and Claudius can be lost. In both cases, fusion occurs between scutes along whose mutual seam no growth annuli are deposited, i.e., a seam where no growth occurs, so steady proliferation of keratin from the secretory layer below, unaccompanied by progressive distancing of the scutes from each other with growth, leads to gradual loss of the seam. It would thus appear that, if scutes that may ultimately fuse must be considered single scutes (i.e., the nomenclature of Hutchison and Bramble), then the anal scutes of Staurotypus and Claudius should be considered as a single scute also. A more natural or phylogenetic nomenclature would emphasize the hatchling condition (i.e., seam possibly present even if no hinge ever develops) rather than the adult condition of seam elimination by scute fusion.

It is probably more instructive to contemplate the growth and fusion patterns of scutes under different scenarios rather than to become preoccupied with questions of scute nomenclature. Homologies between bones, whether the topic be the transmutation of the bones near the jaw articulation in reptiles into the middle ear bones of mammals, or the interpretation of hind limb remnants in pythons or forelimb remnants in elephant birds, can be very instructive. But in such cases the assumption is made, even when intermediate forms are unavailable, that there has been evolutionary continuity and progressive, imperceptible re-shaping that links corresponding bony elements in highly divergent vertebrate lineages.

Such an assumption may not be valid for turtle scutes, in which major saltations, or evolutionary jumps from one configuration to another, can occur without intermediate stages. A turtle with five vertebral scutes may be the parent of one with six, and in the absence of intermediate conditions or even knowledge of any genetic component to the change, it may not be meaningful to assign a homology or a number to the new element.

In some cases, allusion to related species may be enlightening. For example, in the chelid snakeneck turtle Hydromedusa tectifera, an unusual, wide scute is located behind the anteriormost marginals. Is this a widened nuchal scute recessed from the carapace margin, or is it an interposed additional vertebral? On the face of it the question is unanswerable. However, examination of the congener Hydromedusa maximiliani may provide insight. In this species, the additional scute is much narrower than in H. tectifera, and thus suggests that it may have expanded from a small scute (i.e., a nuchal) in the latter rather than appeared as a fully-developed addition to the vertebral series. Furthermore, in H. maximiliani, examination of the bony structure of the anterior of the carapace reveals that the nuchal bone is also recessed behind the anterior peripherals (Wood and Moody, 1976), a unique condition that suggests strongly that superficial elements (i.e., the nuchal scute, originally forming part of the shell margin) may also have been recessed by overgrowth and median conjunction of the anterior peripheral and marginal elements.

But more often, scute homologies will remain obscure. A scute is just a scale that happens to be located on a rigid substratum and thus occupies an area not subject to flexion. In general, scales will be small when they cover flexible structures (e.g., eyelids), medium when they cover stiffer but still flexible components (e.g., the leading and trailing edges of the flippers of marine turtles), and larger still (shell scutes) when they cover completely rigid structures. Evolutionarily, they can clearly respond rapidly to mechanical demands.

Why the shell of hard-shelled turtle species has not become armored with a single continuous scute in the course of evolution, like the crown of the head of *Platysternon*, may relate to favorable, strengthening interaction or alternation of a scute mosaic with sutural lines between underlying bones. In some turtle genera (*Batagur*, *Callagur*, *Dermatemys*), the scute seams disappear with age, leaving a shell with a continuous superficial layer of keratin. However, in these forms, the scute layer is paper-thin, and shell strength derives from the very massive, often highly buttressed bony structure rather than from a complex architecture based upon superimposed mosaics of scutes and bones, with strength deriving from a specific relationship between the two. These genera are also noteworthy for showing complete ankylosis of shell bones in old adults; so that the fused condition of both scutes and bones of the shell is only reached after growth has ceased. It may well be that, in a young, actively growing turtle, it is essential to have distinct scutes because it is only at the borders of such scutes that growth can occur. Growth in a turtle with a single, continuous carapacial scute would be constrained to occur only around the periphery, and would not only involve an unrealistic degree of "sliding" of scute over bone as bones grew in the central part of the shell, but during active growth, the peripheral parts of the shell would be protected only by an extensive and dangerously thin layer of newly-deposited keratin.

Certain turtle groups, including the Trionychidae, Carettochelyidae, and Dermochelyidae, have for diverse reasons eliminated the shell scutes and replaced them with a continuous skin-like epidermis. The survival of these groups to the present time indicates that, whatever the function of rigid scutes may be, it is not a condition for which there are no substitutes or alternatives, or which cannot be sacrificed when there is an ecological or physiological need for vascular superficial shell tissues or shell flexibility.

In general, as components of a turtle shell undergo allometric expansion, the scutes respond accordingly. Tortoises with wide shells (*Gopherus polyphemus, Manouria impressa*) have wide nuchal scutes, for example, and pleurodires invariably show an intergular scute as a component of the overall expansion of the anterior part of the plastron (required to protect the side-retracting neck). When the needed anterior plastral expansion is especially great (e.g., in the snake-necked or big-headed forms; *Chelodina, Hydromedusa, Pseudemydura*, etc.), the intergular expands correspondingly. But whether there is any homology between the intergular of a pleurodire, a cheloniid, a dermatemyid, or a kinosternid is not a useful question.

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