

Carapacial Pankinesis in the Malayan Softshell Turtle, *Dogania subplana*

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ABSTRACT. – Shell kinesis, usually by means of single or double transverse plastral hinges, but sometimes in other limited modes, occurs in most living turtle families. This paper reports a previously undescribed form of generalized carapacial kinesis occurring in fully mature specimens of the Malayan softshell turtle, *Dogania subplana*. Normal adult softshell turtles have carapacial sutural contacts that unite the bones tightly to form a completely rigid, shallowly convex disc. In adult *D. subplana* these sutural contacts break down into wide syndesmoses, with loss of sutural interdigitation and proliferation of fibrous tissue, resulting in loss of bony contact and generalized carapacial kinesis. Such flexibility is absent in juvenile and subadult specimens. *Dogania subplana* is a small, macrocephalic species, and the overall shell flexibility facilitates accommodation of the bulky head and neck when retraction is complete. Kinesis may also be an adaptation to the primary habitat of this species - rocky, upland, fast-running, shallow streams - where ability to take refuge under large, irregular boulders is advantageous.

Encasement of the chelonian body in rigid defensive armor provides an obvious contribution to protection from predators, but it also restricts movement and flexibility of the animal in ways that could easily become counterproductive. Throughout their phylogeny, turtles have evolved numerous responses to this dilemma, many of which have involved shell kinesis of one kind or another. Such kinesis is known in all living families of turtles except for the monotypic Dermatemydidae, and it takes many forms and has diverse functions.

Shell Kinesis in Chelonians

In the Cheloniidae, the carapace is rigid but the plastron has three longitudinal lines of flexion, one along each bridge and one along the midline, that, together with some kinesis between the epiplastra and the hyoplastra, permit a significant degree of in-and-out movement of the entire plastron that may be presumed to assist in rapid or deep respiration. In the monotypic Dermochelyidae, this flexibility is still more developed, the entoplastron being absent and the remaining plastral bones reduced to a large, open ring of splintlike rudiments (Deraniyagala, 1939).

In the Testudinidae, a unique posterior carapacial kinesis occurs in *Kinixys* (Loveridge and Williams, 1957), the anterior plastral lobe is kinetic in *Pyxis arachnoides*, except in the subspecies *P. a. brygooi* (Bour, 1978), and the posterior lobe has a limited degree of kinesis in several species of *Testudo*, especially in the adult females (Loveridge and Williams, 1957). In the related Bataguridae and Emydidae, a mid-plastral hinge, associated with reduction of the bridge to a purely fibrous union, occurs in many genera, including *Cuora*, *Cyclemys*, *Pyxidea*, and *Notochelys* among the batagurids, and in *Terrapene*, *Emys*, and *Emydoidea* among the emydids. Even among the batagurid genera, it appears that plastral hinging has developed independently more than once (Bramble, 1974), the hinge mechanism in *Notochelys*, for example, is fundamentally quite different from that in *Cuora* or *Cyclemys*. In addition, posterior lobe kinesis devel-

ops, presumably independently, in mature female *Heosemys spinosa*, *Melanochelys tricarinata*, and *Geoemyda silvatica* (Moll, 1985). In these forms, the hinge is in the same position as in *Cuora* and its allies (i.e., between the hyoplastra and hypoplastra), but the axillary buttresses and the anterior part of the bridge remain fully ossified, and the kinesis is restricted to the posterior part of the plastron.

Among the Kinosternidae, the numerous species of *Kinosternon* generally show kinetic anterior and (to a lesser degree) posterior plastral lobes, with a fixed midsection comprised of the hyo- and hypoplastra. In some forms (e.g., *Kinosternon scorpioides scorpioides*), the posterior hinge is medially angled rather than straight, and this may correspond to a slight degree of midline kinesis between the left and right hyo- and hypoplastra (Bramble and Legler, 1984). In *Staurotypus* and *Sternotherus*, only the anterior plastral lobe is kinetic, and this kinesis, rather than having a role in defense or reduction of evapotranspiration, as it probably does in *Kinosternon*, seems to function to facilitate the wide opening of the jaws in a threat posture when the head is retracted. Still another form of kinesis is present in the related *Claudius*. In this form, the entire plastron is reduced, the hyo- and hypoplastra are combined into a single pair of bones, and the bridges are long, extremely narrow, and are not sutured to the carapace bones. As in *Staurotypus*, this kinesis apparently also serves to facilitate wide gaping of the jaws when the head is retracted, but by a slight dorsoventral rocking of the entire plastron rather than by simple depression of the anterior lobe (Bramble and Legler, 1984).

In the Chelydridae and Platysternidae, the plastron is reduced and unhinged, but the presence of fibrous rather than bony connections along the bridges and the plastral midline facilitates a degree of plastral bulging when the large head is rapidly retracted.

Shell kinesis is also manifested in certain representatives of the two sideneck families. In the Pelomedusidae, the genus *Pelusios* is characterized by a (usually) well-developed plastral hinge that permits the elevation of the anterior plastral lobe (Loveridge, 1941; Bramble and Hutchison,

1981), although in the form *Pelusios broadleyi* (Bour, 1986) the hinge is absent or non-functional. Among the Chelidae, actual hinging of carapace or plastron is not known, but in certain small forms that produce large eggs (e.g., *Platemys platycephala*), oviposition is facilitated by the fibrous bridge and by the "cushioned", fibrous attachments of the ilia to the visceral surface of the carapace.

In the monotypic Carettochelyidae, there may be slight kinesis in life between the peripheral bones and the pleurals - even in large specimens, these juxtaposed series of bones do not become sutured to each other. Extensive plastral kinesis is present in *Carettochelys*, the attachment of the anterior plastral lobe being quite flexible, and the fibrous connections along each bridge and along the plastral midline facilitating a degree of overall kinesis closely paralleling that of the cheloniids.

Shell Kinesis in Trionychids

In the softshells of the family Trionychidae, generalized plastral kinesis is facilitated by the absence of scutes and a typically reduced network of bones. Even in such well-ossified turtles as old specimens of *Apalone ferox*, in which the fontanelles close throughout the entire central and posterior parts of the plastron, plastral midline and bridge kinesis remains, and the anterior lobe remains scantily ossified and highly flexible.

Normally the bony carapace of mature trionychids is a rigid, shallowly convex disc from which the peripheral rib-tips penetrate a variable distance into the highly flexible leathery margins of the carapace. In a few forms (e.g., *Cycloderma frenatum*), the pleural bones may overgrow these rib-tips, which are then only visible on the ventral aspect of the carapace. In *Lissemys*, not only may the pleural bones extend beyond the rib-tips, but there is a series of isolated bones analogous to the peripherals of hard-shelled turtles, embedded in the leathery shell margin but not sutured to each other.

Deformation of the trionychid carapace by stress may be countered by elimination of one or two of the posteriormost neural bones and formation of a strong median suture between the often enlarged posteriormost pleurals. Minor deviations from true rigidity exist - the wide nuchal bone, for example, is often attached by a flexible, fibrous connection to the first pleural bones in juvenile and subadult trionychids, with extensive fontanelles along the junction. The purpose of this paper is to report on the ontogenetic development of extraordinary and unique kinesis throughout the entire carapace in mature specimens of the Asiatic trionychid *Dogania subplana*.

Habitat and Morphology of *Dogania*

The primary literature on *Dogania subplana* remains decidedly scant despite the relative abundance of the species in upland (and some lowland) areas of Thailand, Malaysia, Burma, and Indonesia, and despite having been described

nearly two centuries ago (Geoffroy Saint-Hilaire, 1809). Smith (1931) and van Dijk (1992) have alluded to the habitat of the species (rocky, shallow, relatively fast-flowing streams in upland areas), whereas Barbour (1912) found *Dogania* to be about as common as *Amyda cartilaginea* in sluggish or stagnant waters on Java. Nutaphand (1979) reported some minor geographic variation in *D. subplana* within Thailand. Apart from these, most published mentions of *Dogania* have been mere inclusions in global or regional lists of turtle species, digests or synopses of previous published information, or comments of a purely morphological nature.

The species has several noteworthy characteristics. It is a small species in a family of generally large turtles. The maximum carapace length is uncertain and is confused by some authors who were unclear whether they were referring to the length of the bony disc or of the entire leathery "shell." Authors from Boulenger (1889) to Meylan (1987) have suggested a maximum length for *D. subplana* of 25 cm, although Meylan examined none with a bony disc longer than 17.7 cm, the figure of 25 cm being estimated from the reported dimensions of a misidentified skull illustrated by Dalrymple (1977). Perhaps the species occasionally reaches a disc length of 25 cm [Moll and Khan (1990) report that the "shell" length, presumably including the leathery rim, is "usually less than 30 cm"]. But 18 cm is a more typical adult bony disc length, and I doubt the accuracy of Nutaphand's statement that *Dogania* may reach 35 cm in length and 15 kg in weight. Even if the former were a total "stretch" length (including head and neck), the alleged weight seems to be exaggerated by a factor approaching tenfold.

Dogania is markedly macrocephalic. The skull becomes very wide in certain individuals, and the total skull length is well over half the bony carapace length in mature specimens. The carapace is very flat and includes eight fully developed pairs of pleural bones and, usually, eight discrete neural elements (nine neurals in Meylan's terminology, on the assumption that neurals 1 and 2 are fused into a single element). The hyo- and hypoplastra do not fuse, and plastral callosities are scarcely detectable; but when they can be detected, there are four (Meylan, 1987), although Gray (1873) reported only two "sternal tubercles," very indistinctly indicated and narrow, in a large adult.

An almost unique feature of *Dogania* is the presence of a series of neural bones that completely separate all of the pleural pairs. Among trionychids this feature is otherwise known only as a minority (41%) condition in *Apalone mutica* (Webb, 1962), and in some specimens of *Amyda cartilaginea* (3 out of 22 examined by van Dijk (1992), but with a possibility noted that the two smallest individuals may have been misidentified *Dogania*). Another noteworthy feature is the posterior displacement of the orbits: The snout is long, and the postorbital bar so reduced that its width is only about 10% of the orbital diameter ("one ninth" according to Meylan, 1987).

Whether these latter two features justify generic distinction of *subplana* has been debated. The species was originally included within the widespread *Trionyx* (Geoffroy

Saint-Hilaire, 1809) and was elevated to generic rank (*Dogania*) by Gray (1855). Boulenger (1889), Loveridge and Williams (1957), Meylan (1984), and Iverson (1986) declined to recognize Gray's action. On the other hand, authors ranging from De Rooij (1915) and Smith (1931) to Wermuth and Mertens (1961) and Iverson (1992) recognized *Dogania* as valid. Siebenrock (1902) did not accept *Dogania*, but later he did (Siebenrock, 1907, 1909). None of these authors have alluded to the unique carapacial kinesis of adult *Dogania*.

Carapacial Kinesis in *Dogania*

I first detected the condition of carapacial kinesis when thawing a frozen specimen of *Dogania subplana* that had been donated to my personal collection. The entire carapace, although well ossified, was flexible, with kinesis occurring between all contiguous pairs of bones. The condition appeared to be non-pathological, in that the turtle had been recently wild-caught in Penang, Malaysia, and had died during shipment to the United States. Quantification of this flexibility is difficult, in that it would presumably be affected considerably by the overall muscle tone of the animal, and thus quite different in live specimens, in freshly dead (or freshly thawed) material, or in formalin-fixed specimens. Nevertheless, other species of trionychid turtles typically have completely rigid bony carapaces as adults, the rigidity being imparted not only by closely and sometimes extremely complexly interdigitating sutures between adjacent bones, but also by the broad, strong rib heads that provide inner buttressing between the neural and the pleural bones. Furthermore, the slightly to markedly convex (rather than flat) bony carapace of most trionychids precludes kinesis even if there was potential flexion between adjacent bones. But even such very flat forms as *Pelochelys* and *Chitra* have thick, well sutured carapace bones in adults, with little or no kinesis possible.

This specimen and two other adults (PCHP 2918, 2919, 3368; Figs. 1-3) were skeletonized and the shell structure examined. The variation between the specimens was considerable despite their similar size, and the ontogenetic characters thought to define relative maturity or age (macrocephaly, degree of extension of the rib-tips beyond the bony disc, extent of closure of the suprascapular fontanelle) were curiously inconsistent. However, it was clear from examination of this small series of three adults that the carapace showed progressive kinesis with maturity, manifesting itself initially by the replacement of the normally interdigitating sutures between adjoining bones by smooth edges, and with subsequent reduction of the characteristically sculptured surfaces of the neural and pleural bones so that these surfaces were separated by soft tissue. In four juvenile skeletons examined (PCHP 1791, 2752, 2922, 1923, all less than 8.5 cm in bony disc length), normal carapacial suturing was present.

The connective surfaces between the carapace bones of the adult *Dogania* may be described as syndesmoses rather

than as sutures. In a sense, there is a gradation rather than a sharp step between a suture and a syndesmosis, in that in both cases there is fibrous tissue between the adjoining bony surfaces, the difference being primarily one of thickness of this tissue and the presence or absence of interdigitating bony spicules. However, the normal ontogenetic progression in a turtle is one of progressive firming up of the sutural connections in the carapace. These connections in the juvenile may involve thin bones with relatively simple interdigitations, and thus they may show some resulting capacity for passive deformation. With growth, the sutures become immovable as the bones thicken, the interdigitations become more complex, and the intervening fibrous tissue diminishes, or even disappears completely in those forms (e.g., *Terrapene carolina*, *Dermatemys mawii*, *Cuora galbinifrons*, extinct Subrecent *Cylindraspis peltastes*, and others), in which the shell becomes completely ankylosed with maturity. However, this process proceeds in a reverse direction at specific bony junctions in those forms in which shell kinesis develops ontogenetically, with simplification of the interdigitations and proliferation of fibrous tissue. This process apparently occurs, uniquely, at all of the bony connections in the carapace of *Dogania subplana*.

Specimen Descriptions

Characteristics of the three adults examined were as follows:



Figure 1. Bony carapace and skull of adult *Dogania subplana* (PCHP 2918; max. disc length 16.5 cm).

PCHP 2918 (max. bony disc length 16.5 cm) showed the following features (Fig. 1): eight pairs of pleurals, pleurals II distally slightly wider than I or III to V; eight discrete neural elements, the first four hexagons with the short sides posteriorly, the fifth and sixth each pentagonal and asymmetrical, the seventh roughly triangular, the eighth small and pentagonal, with a vacuity separating most of the midline between pleurals VIII. Suprascapular fontanelle extensive. Sutures between the carapacial elements only slightly reduced, with the bony carapace able to be reassembled with no separation between the sculptured surfaces of the various bones. Lateral projection of the rib tips beyond the margin of the bony disc considerable (over 1 cm in all cases; over 2 cm at pleural VIII). Callosity on the nuchal bone covering the middle 85% of the posterior half of the bone. A callosity present on each xiphiplastron and on each hyo-hyoplastral unit. Macrocephaly moderate - skull width 5.6 cm; basicranial length 7.5 cm; total skull length 9.6 cm. Atlas unfused - four discrete elements present.

PCHP 2919 (max. bony disc length 17.5 cm) showed the following features (Fig. 2): eight pairs of pleurals, pleurals II being distally much wider than pleurals I or III to V; eight neural bones, with the sculptured surfaces all

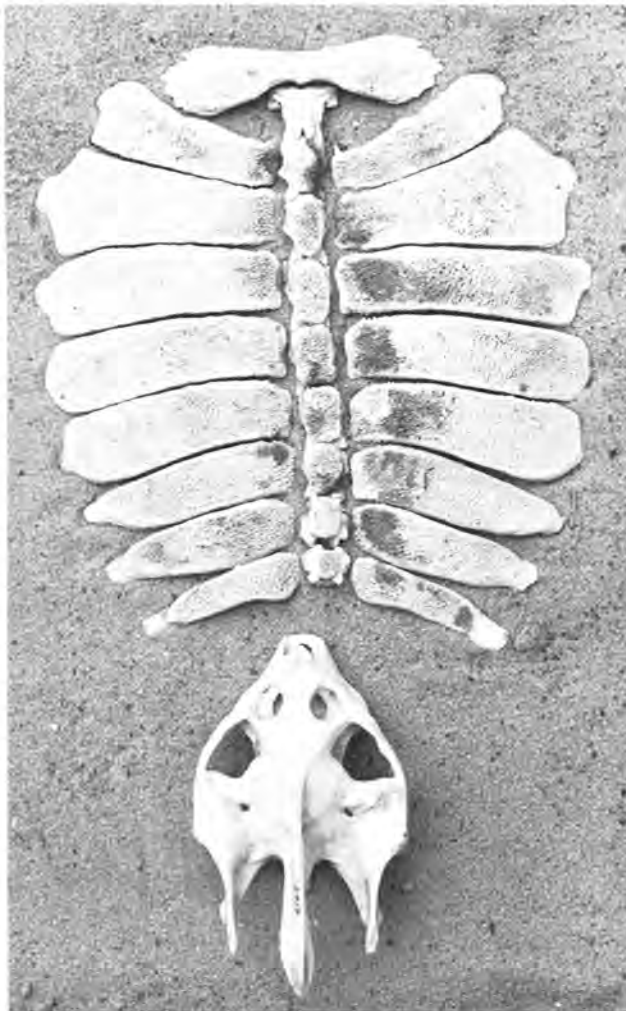


Figure 2. Bony carapace and skull of adult *Dogania subplana* (PCHP 2919; max. disc length 17.5 cm).

roughly oval in shape, except for the fourth which was roughly rectangular. Pleurals VIII narrow and posterolaterally directed, separated medially by neural VIII and a short posterior vacuity. Suprascapular fontanelle moderately extensive. No interdigitating sutures between any bony elements, and (in life) considerable soft tissue between the neural and pleural series and around the individual neural bones. Lateral projection of rib tips beyond the distal ends of the pleural bones very limited; typically 3-4 mm. Callosity on nuchal bone continuous over about 95% of posterior half of the bone. Callosities evident on each xiphiplastron and on each hyo-hyoplastral unit. Macrocephaly considerable - skull width 6.3 cm; basicranial length 7.6 cm; total length 10.6 cm. Atlas bones fused into a single element.

PCHP 3368 (max. bony disc length 17.1 cm) showed the following features (Fig. 3): eight pairs of pleurals (plus a single rudimentary pleural bone and rib, probably a unilateral atavism corresponding to the normally lost ribs associated with the first dorsal vertebra [Kordikova (1990) reported the presence of a pair of such additional pleurals at the front of the series in a specimen of *Pelodiscus sinensis* (PCHP 2771)]; pleurals II wider distally than pleurals III to V, much wider (ca. 3x) than pleurals I. Nine discrete neural elements, the callosity very reduced on the first, larger but irregular to oval on each of the remainder of the series. Two small neurals, no vacuity, separating pleurals VIII. Suprascapular fontanelle extensive. Sutures between pleural bones almost completely lost, extensive soft tissue (in life) separating sculptured areas of pleurals and neurals and around individual neurals. Lateral projection of the rib ends beyond the margin of the bony disc small: 5-7 mm. Callosity on nuchal bone divided into a single, well isolated small patch on each side. No plastral callosities evident. Macrocephaly

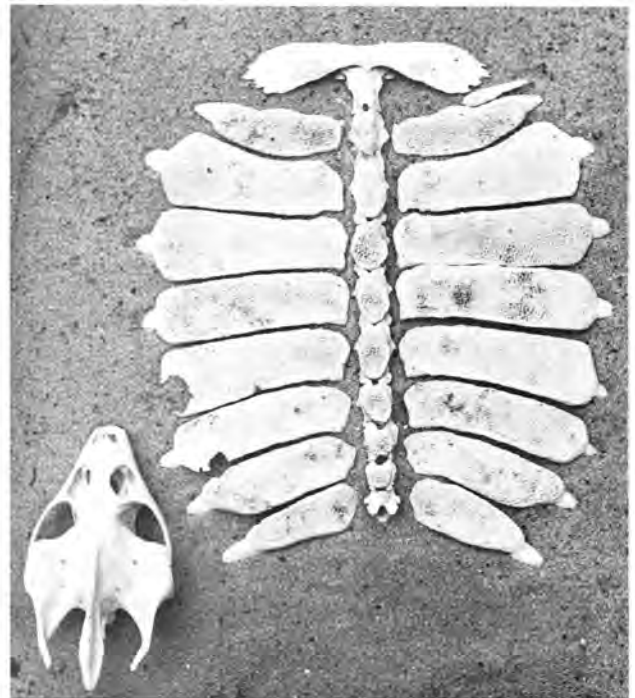


Figure 3. Bony carapace and skull of adult *Dogania subplana* (PCHP 3368; max. disc length 17.1 cm).

minimal - head width 5.1 cm; basicranial length 7.4 cm; maximum length 9.2 cm. Atlas unfused - four discrete elements.

The persistent, wide suprascapular fontanelle was observed in all ten specimens examined by Meylan (1987). It apparently makes possible considerable independent movement of the nuchal bone. Vertical rolling or tilting of the nuchal occurs as the head is retracted. In addition, the fibrous contacts with the first pleurals facilitate some lateral sliding along these planes when the pleural bones are folded-down, as the carapace is thrust into an arched or distended configuration.

Functional Interpretation

The generalized shell kinesis of *Dogania subplana* is functionally paralleled, to a degree, by the crevice-dwelling terrestrial testudinid *Malacochersus tornieri*. It seems highly probable that the flexible shell has a similar function in the two genera, namely to allow the animal to insert itself deep into crevices and under boulders that present irregular and unyielding surfaces to the animal. Such crevices are submerged in the case of *Dogania* and terrestrial in the case of *Malacochersus*. Nevertheless, the shell modifications permitting the flexibility are completely different in the two genera. In *Malacochersus*, the shell margin is rigid and fairly well ossified, and the flexibility derives from a huge median plastral fontanelle and reduction of the neural and pleural bones to a membrane-thin, extensively fenestrated bony carapace overlain by flexible horny scutes (Procter, 1922). In *Dogania*, the carapacial mosaic is complete, but the elimination of the normally rigid bony sutures allows a comparable degree of accommodation to the irregularities of the rocky retreat. Such accommodation may be further facilitated by the absence (or great reduction) of median processes on the hypoplastra (Siebenrock, 1902), a feature that results in a wide mid-plastral fontanelle. In addition, the enormous head and long neck of adult *Dogania*, when retracted, can be contained only within the corselet of the animal if the latter is significantly distensible. This distention of both carapace and plastron is obvious when one holds a live *Dogania* in the hand and the animal rapidly extends and retracts its head and neck.

Comparative Morphology

No other turtle is known in which the entire shell achieves plankinesis by elimination of all of the sutures between the bony elements of the carapace. Even in *Dermochelys*, in which the shell bones are extraordinarily reduced, the carapace (although not the plastron) achieves substantial rigidity by means of the complex overlay of ribs, mosaic bones, and the thick layer of underlying fibrous tissue. However, examination of the bony shells of a series of the batagurid *Rhinochelymys punctularia* suggests that a comparable condition may manifest itself in this species and its congeners, although only in the posterior part of the shell

and to a much more limited degree. In large adult females of these species, the sutural connections between many of the posterior peripheral bones may break down and become smooth and invaded by fibrous material, as may the bridge, the connection between the posterior buttress and the inside of the carapace, and the sutures between the hypoplastra and the xiphoplastra. These modifications seem to be an adaptation to allow the passage of extraordinarily large, hard-shelled eggs by turtles of rather moderate size. Additionally, these species inhabit environments with a suite of potential predators that may preclude compromising the armor by development of a permanently wide posterior shell opening. The testudinid *Chersina angulata*, which also has a very narrow posterior plastral opening but lays large, single eggs, demonstrates similar kinesis between the posterior peripherals and plastral bones during oviposition.

It is conceivable too that extensive kinesis between the plastral bones was present in the Mascarene tortoise *Cylindraspis indica*. This species was first described (as "Tortue des Indes") by Perrault (1676), and the description included a statement that the plastral elements were attached together by strong, hard ligaments, which nevertheless allowed some freedom of movement: "*attachés ensemble par des ligamens forts et durs, mais qui laissent néanmoins la liberté à quelque mouvement*" in Perrault's French text; "*Scutum sterno ope durorum fortiumque ligamentorum jungitur, ut tamen aliqua mobilitatis libertas supersit*" in the Latin rendition by Schoepff (1794). But this observation cannot be confirmed, as the species became extinct around 1735 (Bour, 1984).

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