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Emydid Shell Kinesis: Biomechanics and Evolution

DENNIS M. BRAMBLE

Mechanisms of shell closure in box turtles of the family Emydidae have been analyzed with respect to functional anatomy, evolution and phylogenetic significance. Structural requirements essential to the box turtle morphotype are: 1) plastral kinesis; 2) mechanisms for displacement (accommodation) of the limb girdles as the shell is closed; 3) additional space in the shell for displacement of the forelimbs; 4) musculature to effect shell closure. Girdle accommodation is structurally and evolutionarily the most "difficult" requirement; plastral kinesis is the least.

In typical box turtles of the subfamily Batagurinae, the anterior plastral lobe is elevated by the hypertrophied testoscapularis muscle. The scapulocarapacial articulation is modified to allow dislocation of the joint during shell closure. A portion of the main cervical retractor (M. retrahens capitis collique) raises the front end of the plastron in all hinged turtles of the subfamily Emydinae. In this group a unique, segmented scapula permits both effective accommodation of the girdle and a passive locking mechanism that stabilizes the girdle in locomotion. An enlarged M. testoiliacus is chiefly responsible for closure of the rear portion of the shell in box turtles of both subfamilies.

Excluding *Notochelys*, the box turtle specialization has arisen independently once each in the Batagurinae and Emydinae. Among batagurines, members of the *Cyclemys* Group (*Cyclemys, Pyxidea, Cuora*) share a common closing mechanism. This generic complex probably derives from a *Heosemys*-like ancestry, suggesting all four genera may be united in a *Heosemys* Complex. The batagurine, *Notochelys*, has evolved shell kinesis separately from the *Cyclemys* Group and is not closely related to members of this group.

A shared closing system and other morphological similarities warrant the inclusion of all hinged emydines (*Emys, Emydoidea, Terrapene*) in a single *Emys* Group. Within the group, *Emys* is most primitive with *Emydoidea* in most respects structurally and probably phyletically intermediate between it and *Terrapene*. *Emydoidea* is unrelated to *Deirochelys*, but is convergent with it in several features related to similar feeding systems. The *Emys* Group originates from a *Clemmys*-like ancestor and its members are joined with *Clemmys* in a distinct *Clemmys* Complex.

SINCE Triassic time the turtle shell has been remarkably conservative in structure and function. This fact itself attests to the overall success of the structure as an adaptive innovation. It is not until the Tertiary that there is definite evidence for any serious departure from the normal mode of shell organization and function. At this time several divergent families (Pelomedusidae, Trionychidae, Emydidae, Kinosternidae) independently evolved specializations of the plastron that permit one or both ends of the shell to be closed off in a manner not possible in other chelonians. Superficially, the "box turtle" adaptation appears relatively simple. The simplicity, however, is deceptive; in reality this form of adaptation demands morphological specializations so fundamental that its occurrence in turtles is understandably rare.

Casual reference to shell hinging is commonplace in the literature, but there are almost no studies dealing specifically with the problem of shell kinesis. Deraniyagala (1939) discussed movements of the plastron in the trionychid *Lissemys* and Hasan (1941) described the muscles moving it. Among the Emydidae, Legler (1960) has studied the ontogenetic events leading to the formation of plastral hinges in the genus *Terrapene*;

Richmond (1964) has provided similar data for the kinosternid, *Kinosternon*. The only attempt to survey the actual mechanical basis for shell closure in a wide variety of hinged chelonians was that of Shah (1960). Unfortunately, this study was of a superficial nature leading ultimately to misconceptions and erroneous conclusions.

The present paper is an outgrowth of efforts to investigate chelonian shell kinesis in a more analytical manner than heretofore attempted. The study has emphasized the identification of the morphological and biomechanical bases for shell kinesis, their expression in various turtle groups, and finally, their interpretation within a meaningful evolutionary framework. The closing mechanisms of all extant "box turtles" have been analyzed in this context, but the discussion here is confined to the family Emydidae. This is done because: 1) seven genera of emydids possess hinged plastra, a greater number than found in other families; 2) unlike other families, two distinct closing mechanisms have been evolved in emydids, thus offering the opportunity to examine convergent systems; 3) emydids provide the most dramatic evidence of the structural and functional difficulties that attend chelonian shell kinesis; 4) data from studies of shell kinesis have immediate bearing on several important questions of emydid phylogeny and systematics.

MATERIALS AND METHODS

The data presented in this study derive from several sources: 1) dissections of fresh and preserved turtles; 2) analysis of skeletal morphology; 3) behavioral observations on captive box turtles. Functional interpretations rest on a synthesis of information from all three sources. Stimulation of muscles in freshly killed animals representing several box turtle genera (*Cyclemys, Cuora, Terrapene*) provided an additional check on the functions of various muscles implicated in the closing mechanisms of the shell. For purposes of dissection fresh specimens were given preference over preserved ones since the relative rigidity of the tissues in the latter made accurate estimates of joint mobility and muscle action difficult. Of the seven genera of emydid box turtles investigated, fresh material was available for five (*Notochelys, Cyclemys, Cuora, Emydoidea, Terrapene*). Only preserved specimens of *Pyxidea* and *Emys* were examined. Behavioral data were obtained from specimens of *Notochelys, Cyclemys, Cuora, Emydoidea* and *Terrapene* maintained by Dr. J. M. Legler at the University of Utah.

The histological sections illustrated in Figs. 5 and 8 are from fresh material fixed in formalin, decalcified in Perenyi's solution, and stained with Lillie's modification of Masson's trichrome. Verhoeff's stain was used to demonstrate elastic fibers in the scapulo-carapacial joint capsule of *Cuora*.

The herpetological collection of the University of Utah (UU) was the principal source for dissected specimens and skeletal material. Other specimens were from the American Museum of Natural History (AMNH) and the collection of the author (DMB). Specimens dissected include: Batagurinae: *Cuora amboinensis*, UU 12130, 13348, 13602; *C. flavomarginata*, AMNH 50804; *Cyclemys dentata*, UU 11928–29, 13369; *Geoemyda spengleri*, AMNH 103733; *Heosemys grandis*, UU 11780, 13367, 13445; *H. spinosa*, UU 11782, 13603, 13604; *Notochelys platynota*, UU 11659, 13368, AMNH 95947; *Pyxidea mouhoti*, AMNH 28336; *Rhinoclemys funerea*, UU 11540; *R. areolata*, UU 6447, 6477. Emydinae: *Clemmys guttata*, UU 4328; *C. insculpta*, UU 4306; *C. marmorata*, UU 4313, DMB 540; *Deirochelys reticularia*, UU 4341, 4347; *Emydoidea blandingi*, UU 4317, 11857, 13109, 13110; *Emys orbicularis*, UU 10255–6; *Terrapene c. carolina*, UU 4262, 13319, 13320–1; *T. c. triunguis*, UU 12401, 13179, DMB 545; *T. coahuila*, UU 12552, 12556; *T. ornata*, UU 11635, 12874, 12899, DMB 544.

GENERAL CONSIDERATIONS

Appreciation of the evolutionary implications of a closable shell in turtles requires an awareness of the structural and functional problems that are inherent in this specialization. The more important of these are considered below.

Shell kinesis.—The development of movable joints between the bones of the shell is the most conspicuous specialization of box turtles, yet is the least difficult of the several problems faced by such turtles. Movable articulations are readily derived through relatively minor modifications of existing syndesmotic joints (i.e. sutures). Gradual suppression of the bony processes together with elaboration of the connective tissues normally associated with such joints is all that is

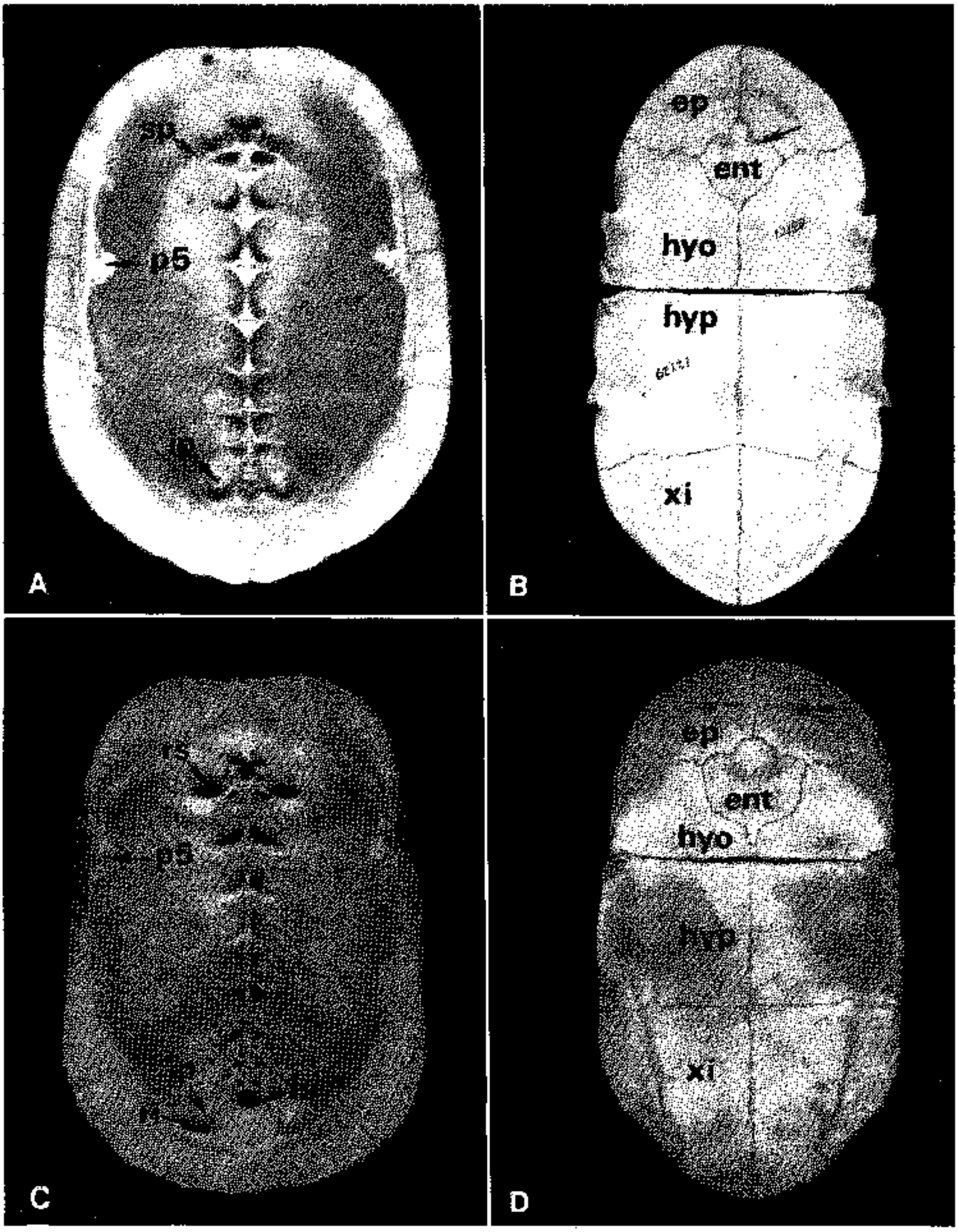


Fig. 1. Internal views of carapace and plastron of (A,B) *Cuora amboinensis* and (C,D) *Terrapene coahuila.* Abbreviations: ent, entoplastron; ep, epiplastron; fs, fossa for prezygapophysis of sacral vertebra 1; hyo, hyoplastron; hyp, hypoplastron; ip, ilial process; p5, pivot for plastral bones formed by peripheral bone 5; ri, ilial recess; rs, scapular recess; sp, scapular process; xi, xiphiplastron. Arrows in B and D indicate scar for attachment of acromion process of scapula and fossa for insertion of cervico-plastral ligament respectively. Plastral hinges are represented by transverse gaps between hyo- and hypoplastral bones.

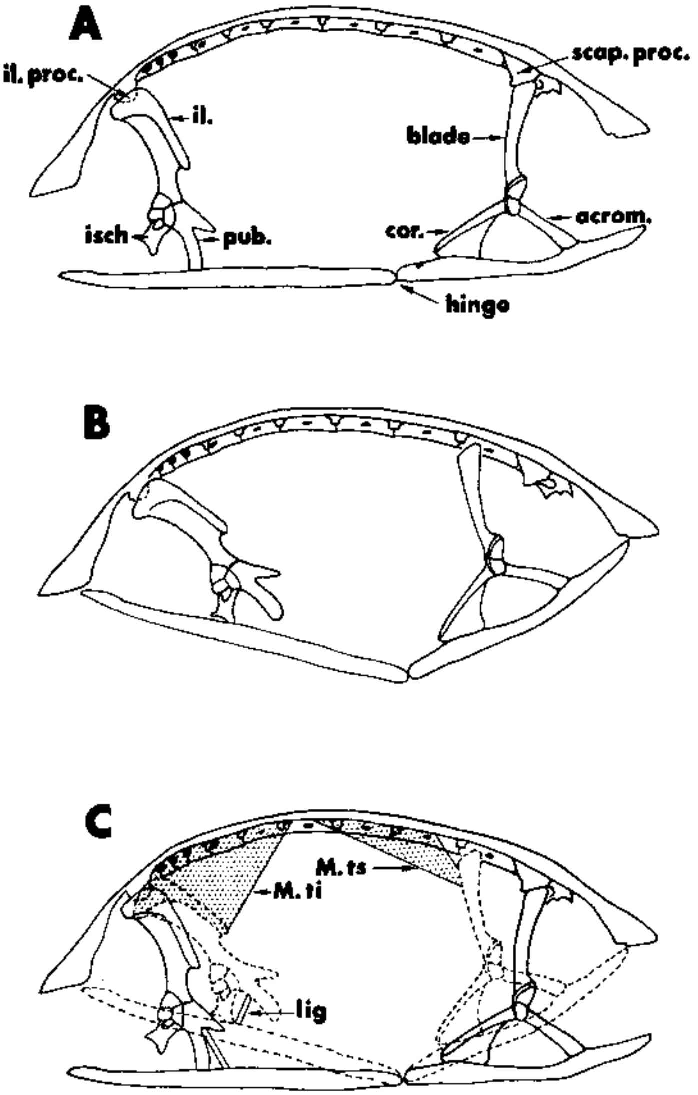


Fig. 2. Right longitudinal sections of shell of *Cuora* to illustrate its relationships to girdles with shell open (A) and closed (B). C is a composite to demonstrate girdle displacement and arrangement of the effector musculature (stippled). See text for discussion. Abbreviations: acrom., acromion process of scapula; blade, scapular blade; cor., coracoid; il., ilium; il. proc., ilial process; isch., ischium; lig., ligament joining pubis to plastron; M. ti, testoiliacus muscle; M. ts, testoscapularis muscle; pub., pubis; scap. proc., scapular process.

required to transform the akinetic union into a functional hinge. In emydid turtles this hinge is always formed along the transverse hyo-hypoplastral suture. A mobile hinge is invariably accompanied by the reduction or resorption of the axillary and inguinal buttresses of the plastron. In addition, there is necessarily a suppression of the sutural connection between the plastral bones and the adjacent peripheral bones of the carapace. The result is a plastron composed of movable anterior and posterior sections. The two lobes of the plastron pivot on bony processes that extend medially from the fifth and sometimes sixth peripheral bones (Fig. 1).

Girdle accommodation.—The limb girdles lie within the box-like shell, anchored by muscles and tough connective tissues (actual bony sutures in the case of the pleurodiran pelvis) to the internal surfaces of the carapace and plastron; they form noncompressible osseous struts. Approximation of plastron and carapace is therefore impossible without compensatory modification of the intervening girdles. Accommodation of the girdles is the most fundamental difficulty posed by shell kinesis.

Limb displacement.—In typical cryptodiran turtles with akinetic shells, complete retraction of the head, neck, and limbs leaves the antibrachia folded in front of or to either side of the head and exposed within the anterior aperture of the shell. Closure of the shell by elevation of the anterior plastral lobe requires further displacement of the forelimbs and the provision of a commensurate amount of space to accommodate them. No comparable problems arise with respect to the hind limbs since they can be withdrawn more or less completely even in turtles without closable shells.

Effector musculature.—The final requirement in the development of a closable shell is the possession of muscles to bring about closure. In emydid box turtles this requirement is met through the modification of existing musculature.

FUNCTIONAL ANATOMY OF SHELL KINESIS

Subfamily Batagurinae

With the exception of *Notochelys platynota*, all box turtles of the subfamily share a common closing mechanism. The mechanism is best developed in *Cuora* and for this reason its functional anatomy is described for this genus. Comments on the mechanism of *Notochelys* are deferred to a later section of this paper (see Phyletic Implications).

A longitudinal section of *Cuora* illustrating the relative positions of the limb girdles to the shell is shown in Fig. 2A. The enlarged distal end of the scapular blade articulates with the prominent scapular process of the carapace which is formed by the expanded distal end of dorsal rib 1. The articular surface of the process faces anteroventrally and somewhat laterally. It is covered by a smooth pad of hyaline cartilage which meets a similar pad over the end of the scapula. Sections of this articulation (Fig. 3) reveal that it is a true synovial joint enclosed by a tough joint capsule. This joint is much better developed in *Cuora* than in other emydids and differs further in that it contains a fibrocartilaginous meniscus that serves as a cushion between the scapula and carapace. Ventrally, the acromion process of the scapula has a firm ligamentous union with the entoplastron.

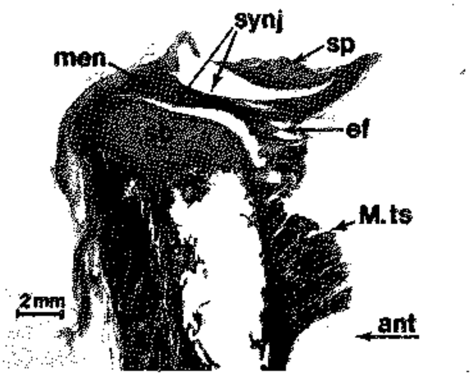


Fig. 3. Longitudinal section of scapulo-carapacial articulation of *Cuora amboinensis* (UU 12130) to show complex structure of the joint. Abbreviations: ef, region of joint capsule rich in elastic fibers that facilitate stretching during shell closure; M. ts, testoscapularis; men, meniscus; sb, scapular blade; sp, articular pad of scapular process of carapace; synj, synovial joints.

The pelvis joins the carapace by articulation with a ball-like ilial process (Fig. 1A) composed chiefly of the last (10th) dorsal rib. The dorsal surface of the first sacral rib and the adjacent portions of the ilial crest produce a socket in which the process is seated. The ilio-carapacial articulation of *Cuora*, then, consists of a ball and socket joint that is unique among turtles. With the shell open, the lateral extensions or pectineal processes (Zug, 1971) of the pubes rest on the visceral surface of the plastron; the ischia do not contact the plastron.

During shell closure, accommodation of the shoulder girdle requires actual dislocation of the scapulo-carapacial joint (Fig. 2B). Posterior displacement of the scapular blade allows elevation of the plastron and, in addition, makes room for the forelimbs within the anterior portion of the shell. Displacement of the scapula necessarily demands stretching of the capsule surrounding the scapulo-carapacial joint. An abundance of elastic fibers in the posterior wall of the capsule serves to facilitate this action. Fibers of this type appear to be rare or absent in the joint capsules of other chelonians.

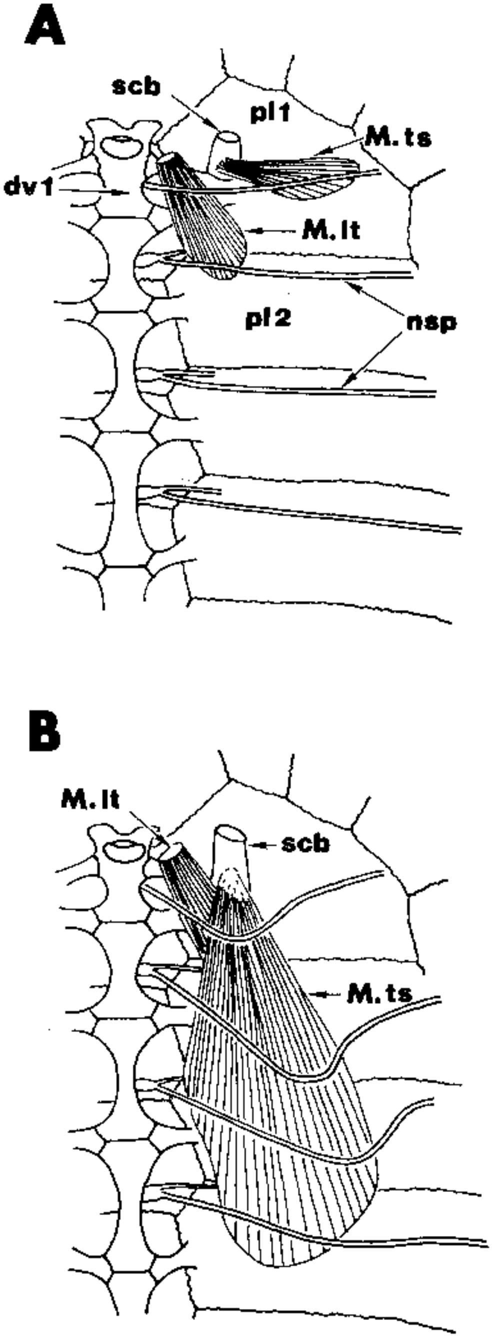


Fig. 4. Internal views of left anterior quadrant of carapaces of A) an akinetic batagurine (*Heosemys*) and B) an advanced batagurine box turtle (*Cuora*). Note that in B hypertrophied testoscapularis muscle has partly covered longissimus thoracis and displaced spinal nerves rearward. The longissimus thoracis and scapular blade have been cut. Abbreviations: dv 1, dorsal vertebra 1; M. lt, longissimus thoracis muscle; nsp, ventral rami of spinal nerves; pl 1, pl 2, pleural bones 1 and 2; scb, scapular blade.

Closure of the rear portion of the shell depends on the forward and upward rotation of the pelvis toward the carapace (Fig. 2B). Rotation is about the ilio-carapacial articulation.

Actual girdle displacement commensurate with plastral elevation is shown in Figure 2C. Also indicated are the basic relationships of the effector musculature. The testoscapularis muscle elevates the anterior half of the plastron. This is normally a small muscle in turtles, originating from the undersurface of the first pleural and sometimes adjacent peripheral bones and inserting near the upper end of the scapular blade (Fig. 4A). The muscle has been implicated in respiratory movements of the pectoral girdle in *Chelydra* (Gaunt and Gans, 1969) and this may be its principal function in most chelonians. In *Cuora* (and to a lesser extent, *Cyclemys* and *Pyxidea*), however, the testoscapularis is hypertrophied and its origin has shifted rearward to the proximal ends of pleural bones 2–4 (Fig. 4B). The new orientation permits the muscle to exert a strong posterodorsal pull on the distal end of the scapula. Since the scapula is firmly connected to the plastron and braced posteriorly by the coracoid, the entire bone acts as a lever to enhance the mechanical advantage of the testoscapularis. As a result, *Cuora* is able to close the front of the shell with considerable force.

The posterior lobe of the plastron is indirectly elevated by the M. testoiliacus. This muscle is more massively developed in *Cuora* than in typical emydids (Zug, 1971). The muscle takes its origin from the internal surfaces of pleural bones 6–8 and inserts on a pronounced crest along the anterior and dorsal margins of the ilium. Contraction of the testoiliacus draws the pelvis forward and upward on its articulations with the carapace. The pull of the muscle is transferred to the plastron by a pair of strong ligaments that run from the base of the pectineal processes of the pubes to the neighboring surfaces of the xiphiplastra (Fig. 2C).

The articulation between the shoulder girdle and the carapace functions to reduce the possibility of dislocation and thereby to increase stability during locomotion. As

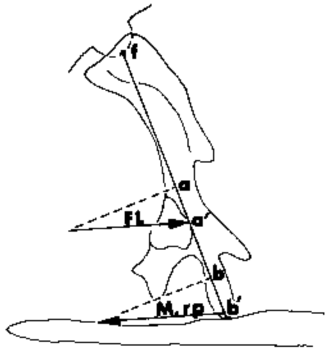


Fig. 5. Right laterval view of pelvis of *Cuora* to show mechanical advantage of stabilizing musculature (M. retrahens pelvium). The structural axis (line f-b') of pelvis constitutes a third class lever with fulcrum (f) located at ilio-carapacial articulation. The force of retrahens pelvium (M. rp) acts on system at a point (b') more distant to fulcrum than opposing force (FL) of hind limb acting at acetabulum (a'). Both actual (f-b') and effective (f-b) lever arms of muscle therefore exceed those (f-a', f-a) of hind limb.

was noted earlier, the distal end of the scapular blade in *Cuora* is expanded anteromedially to form a blunt projection. When the joint is articulated, the articular facet of the scapula abuts on the inclined face of the scapular process of the shell and the intervening meniscus of the joint capsule. At the same time the anteromedial projection of the scapula rests in a pocket of connective tissue overlying the muscles lateral to the cervico-dorsal articulation.

Due to its inclination the scapular process effectively checks forces transmitted upward along the scapula from the forelimb that would otherwise tend to drive the scapula posteriorly from its articulation. The process acts as an inclined plane to redirect such forces in an anteromedial direction. This action, in turn, functions to seat the anteromedial process of the scapula more firmly in its recess where it is buttressed by the first dorsal vertebra and associated soft tissues. The angle of insertion of the testoscapularis causes it to rotate the scapula slightly outward in addition to drawing it posteriorly. The rotation releases the distal projection of the blade from its recess and directs it anteriorly where it cannot impede the movement of the blade past the scapular process.

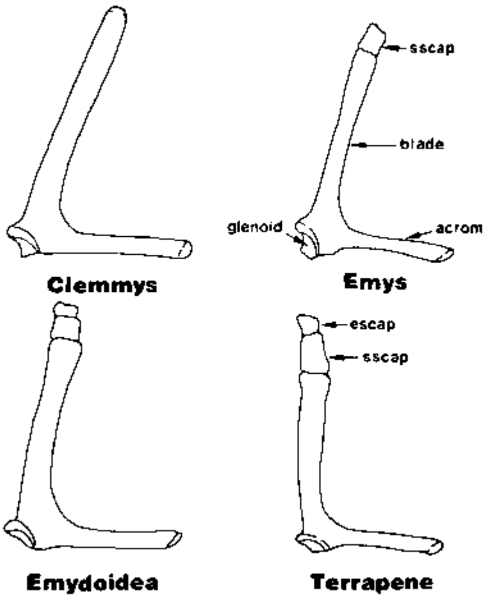


Fig. 6. Anterior views of the right scapulae of genera of *Clemmys* Complex. Abbreviations: escap, episcapula; sscap, suprascapula; other abbreviations as in Fig. 2.

Unlike the pectoral girdle, which is held in place largely by passive means, the pelvic girdle is stabilized by muscular effort during locomotion. The M. retrahens pelvium originates from a shallow fossa on the posterodorsal side of the xiphiplastron and passes anteriorly to insert on the posterodistal end of the pectinal process of the pubis (Fig. 5). The muscle is relatively larger in *Cuora* than in nonhinged batagurine turtles. As the retrahens pelvium (posterior slip of M. rectus abdominis of Zug, 1971) forces the pelvis posteriorly about its hinge with the carapace, the processes of the pubes push the xiphiplastra downward, thus opening the rear of the shell. Once open, active contraction of this muscle continues to anchor the girdle in place; to a lesser extent the M. attrahens pelvium may aid in this. Mechanically, the pelvis, the pull of the retrahens pelvium, and the resistance force of the hind limb constitute a third class lever system (Fig. 5). Since the point at which the retrahens pelvium applies its force to the system is nearly twice as distant from the fulcrum (ilio-carapacial joint) as the point of resistance (acetabulum), the considerable mechanical advantage of the muscle is obvious. It is chiefly for this reason that the muscle is able to maintain the posi-

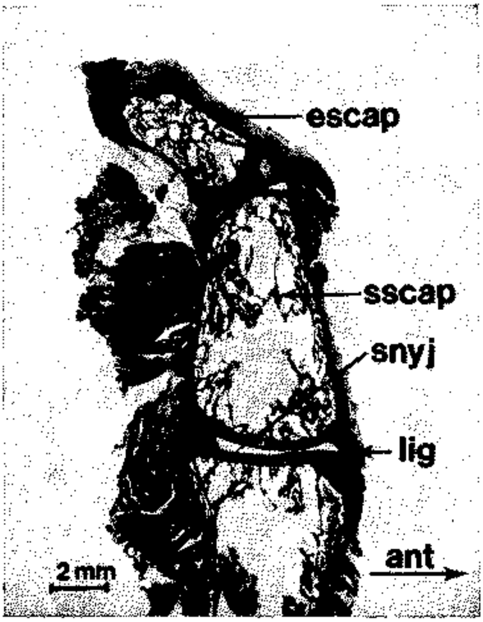


Fig. 7. Longitudinal section of the scapular suspensorium of *Terrapene carolina* (UU 13320). Abbreviations: escap, episcapula; lig, ligament; sscap, suprascapula; synj, synovial joint.

tion of the pelvis even in the face of strong propulsive efforts by the hind limbs.

Subfamily Emydinae

Among the emydines, the genera *Emys*, *Emydoidea* and *Terrapene* all possess a closable anterior plastron and, additionally, the posterior region of the plastron exhibits varying degrees of kinesis. All three genera share a common closing mechanism more complex than that of *Cuora*. The following discussion deals primarily with the most advanced state of this mechanism as present in *Terrapene*; important differences in *Emys* and *Emydoidea* are noted.

A uniquely specialized scapula is central to the closing mechanism of emydine box turtles (Fig. 6). In typical emydines such as *Clemmys*, and in the majority of other chelonians as well, the scapula is little more than a rod-like process extending dorsally from the glenoid region. In *Emys* there is an additional bone, the suprascapula, attached to the distal end of the scapular blade; *Emydoidea* and *Terrapene* have still another element, the episcapula, joined distally to the suprascapula. All three elements (scapula, suprascapula, and episcapula) meet one another in true synovial joints (Fig. 7). Serial sections of the scapulae of late embryonic *Terrapene* reveal that the two distal elements arise from secondary subdivision of the cartilaginous scapular blade. Thus the scapula of these box turtles is, in contrast to other turtles and vertebrates in general, segmental. Both the supra- and episcapular bones are conspicuous in good skeletal preparations of adult emydine box turtles; it is surprising that they have almost completely escaped the attention of morphologists. Bojanus (1821) clearly illustrated and labeled the suprascapula of *Emys orbicularis*. Some of these illustrations have had wide circulation in later works (e.g. Romer, 1956; Fig. 215), but to my knowledge there has been no published mention of these bones subsequent to Bojanus. White (1929), in an unpublished masters thesis, recorded the bones in both *Emydoidea* and *Terrapene* and applied to them the terminology utilized here. Following the author's own discovery of the bones, White's thesis was brought to his attention by Dr. J. M. Legler, who had earlier noted their occurrence in *Terrapene*.

With the shell open the shoulder girdle of *Terrapene* has the relationships shown in Fig. 8A. The acromion process is ligamentously attached to the entoplastron but the connection is much weaker than in *Cuora*. Dorsally there is merely a ligamentous connection between the episcapula (suprascapula in *Emys*) and the first dorsal rib rather than a synovial joint. The combined episcapula and suprascapula, or *scapular suspensorium*, folds inward against the first dorsal vertebra and associated musculature. In this position the suspensorium constitutes a "locking mechanism," the details of which are discussed later.

The ilium of *Terrapene* articulates with an ilial process (Fig. 1C) supplied largely by the 10th dorsal rib as in *Cuora*. The articulation is primarily between the process and an extensive facet developed on the dorsal surface of the first sacral rib. This rib is particularly massive in *Terrapene* and appears to be partly ankylosed with the ilium in some adult specimens. The ilial process and the sacral rib together comprise what is best described as a roller bearing joint, with the rib moving on the flattened process of the carapace. The pelvis contacts the plastron much as in *Cuora* with the only important difference being that in *Terrapene* the keeled ischial symphysis rests on

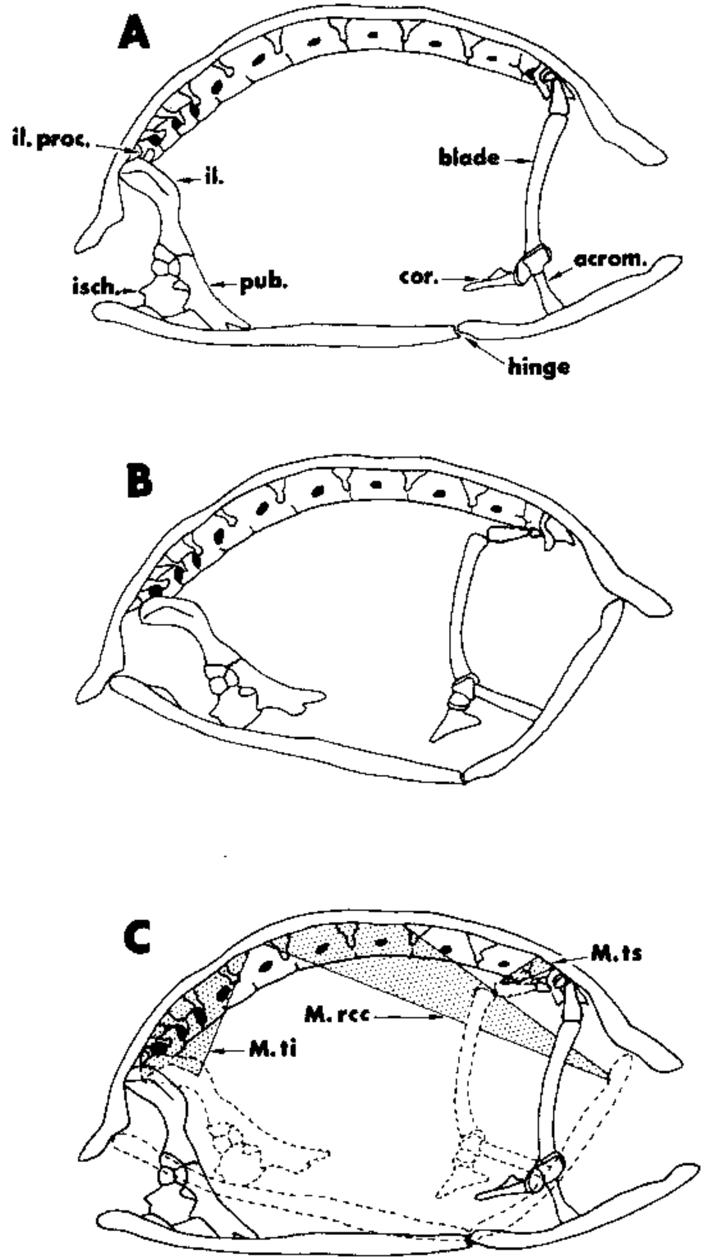


Fig. 8. Right longitudinal sections of shell of *Terrapene* to illustrate its relationships to girdles with shell open (A) and closed (B). C is a composite to illustrate girdle displacement and arrangement of effector musculature (stippled). See text and Figs. 9, 10 and 11 for details. Abbreviations: M. rcc, retrahens capitis collique muscle; other designations as in Fig. 2.

a ridge formed along the interxiphiplastral suture.

In elevation of the anterior portion of the plastron, girdle accommodation is effected by an "unfolding" of the scapular suspensorium (Fig. 8B). The process involves hyperextension of the joints between the various segments as well as posterior rotation of the episcapula at its hinged connection with the shell. The scapulo-carapacial articulation is thus functionally disengaged, but without actual loss of contact between the girdle and the carapace as is required in *Cuora*.

The mechanical basis for the locking mechanism of the scapular suspensorium is illustrated in Fig. 9. The suspensorium folds in against the first dorsal vertebra (Fig. 9A). In this position all joints of the suspensorium are in a maximum state of flexion. Forces (F1) from the forelimb, whether originating from static postural resistance or actual propulsive efforts, are transmitted along the scapular blade to the suspensorium. Due to the relative angles of the several segments and the overall alignment of their articulations, it is clear that such forces can act only to increase *flexion* of the joints involved. Force reaching the scapulo-suprascapular joint can be resolved into medial (horizontal) and dorsal (vertical) vector components (Fig. 9A). The former component is resisted by the buttressing action (Rv) of the dorsal vertebra and associated soft tissues. The dorsal component is, for the most part, redirected (F2) through the suprascapula to its articulation with the episcapula where it is opposed by the resistance (Rc) of the shell. Any lateral component translated to the episcapula (F3) is likely to be small since most of the original force will have been effectively dissipated at this point. Stress at the scapulo-carapacial articulation is therefore expected to be minimal. In most adult *Terrapene* the supra-episcapular articulation is seated in a well-formed recess in the first pleural plate, a fact that contributes to the stability of the suspensorium.

Additional stability derives from the nature of the soft tissues associated with the suspensorium (Fig. 7). The anterior surfaces of the joints are covered by exceptionally strong ligaments that function to resist tensile stresses resulting from hyperflexion of the suspensorium while it is under load. The posterior surfaces of the joints, in contrast, are spanned by a very thin, elastic tissue that facilitates hyperextension.

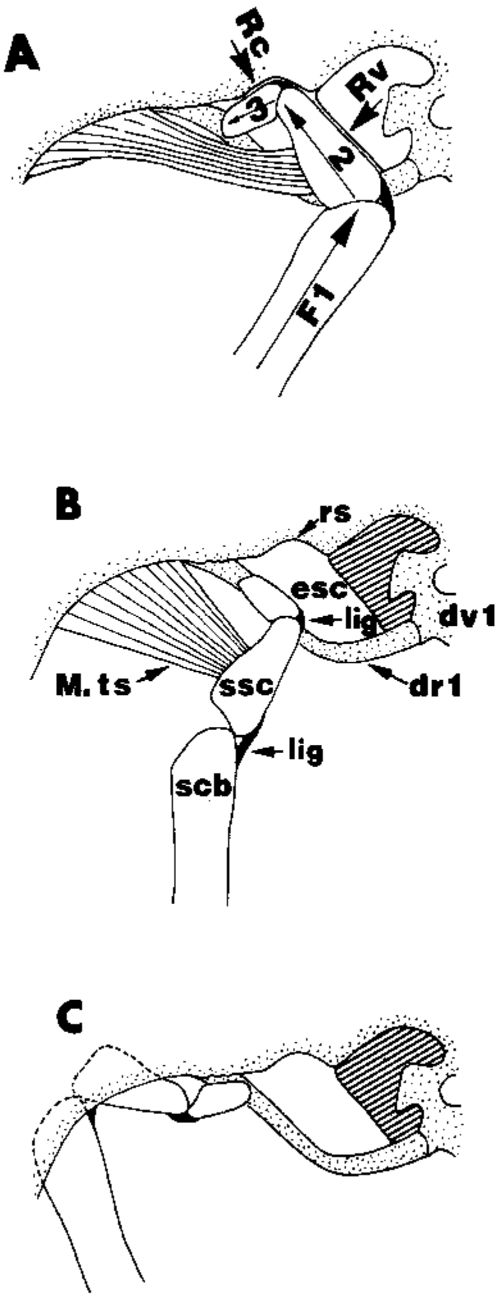
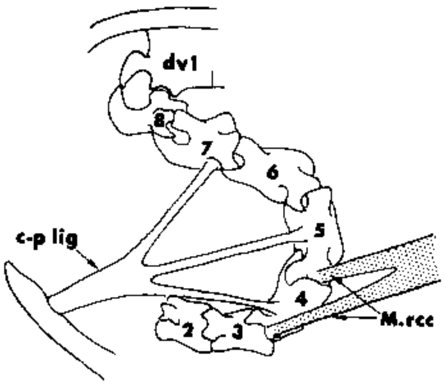


Fig. 9. Cross sections of right scapulo-carapacial articulation of *Terrapene* to demonstrate relationships of scapular suspensorium when (A) "locked" (shell open), (B) partially disengaged (shell closing), and (C) completely disengaged (shell closed). See text (p. 716) for discussion. Abbreviations: dr 1, dorsal rib 1; dv 1, dorsal vertebra 1; esc, episcapula; F 1, 2, 3, force transmitted from forelimb to suspensorium; F2 and F3 represent fractions of original force (F1) redirected through suprascapula and episcapula respectively; lig, ligament; M. ts, testoscapularis muscle; Rc, resistance force of carapace; Rv, resistance force of dorsal vertebra 1 and associated musculature (hatched); rs, scapular recess; scb, scapular blade; ssc, suprascapula.

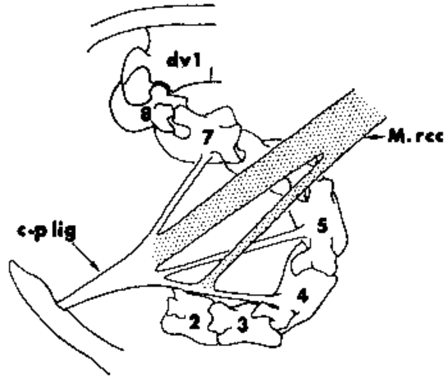
The effectiveness of the shoulder locking mechanism in *Terrapene* is considerable. This fact is dramatically demonstrated in box turtles struck by automobiles while attempting to cross roadways. Postmortem examination of *T. ornata* and *T. carolina* from roadways in eastern Kansas revealed that when the turtles were run over while the shoulder was in the locked position, the plastron was forced upward with sufficient strength to break the blade of the scapula cleanly in several places. Despite this stress, the suspensorium remained locked and undamaged.

In addition to stability, the suspensorium must also assure the movements of the girdle necessary for locomotion. Walker (1971) has shown that the scapula normally swings through a considerable arc during terrestrial locomotion in *Chrysemys*. Comparable motion probably accompanies locomotion in most nonhinged chelonians. The required axial rotation of the pectoral girdle is accomplished in *Terrapene* by pivotal movements of the scapula on the suprascapula and on its ligamentous attachment with the entoplastron. There appears to be little axial rotation possible at the supra-episcapular junction.

In sharp contrast to *Cuora*, the anterior plastron of all emydine box turtles is raised by a portion of the main cervical retractor (M. retrahens capitis collique) (Fig. 8C). The manner in which the retractor exerts its force on the plastron is illustrated in Fig. 10. In *Emys* and *Emydoidea* the muscle sends slips to cervical vertebrae 4 and 5, although poorly developed slips are occasionally inserted on the more posterior cervicals. The pull of the cervical retractor is relayed to the plastron by a cervico-plastral ligament. The ligament arises as separate slips from several cervicals, typically 4, 5 and 7, which then coalesce before joining the epiplastron just medial to the dorsal termination of the seam bewteen the gular and humeral scales (Fig. 1D). A more advanced version of the same system occurs in *Terrapene*. Here the retractor muscle has, to varying degrees, shifted its insertion from the cervicals to the cervico-plastral ligament. In so doing the muscle is able to effect a more direct pull on the plastron. The mass and consequently the strength of that portion of the M. retrahens capitis collique associated with shell closure increases progressively from *Emys* through *Emydoidea* to *Terrapene*.



Emys, Emydoidea



Terrapene

Fig. 10. Left lateral views of cervical column and adjacent portions of shell in emydine box turtles to illustrate manner in which a complex cervico-plastral linkage translates pull of cervical retractor muscle to plastron. Abbreviations: c-p lig, cervico-plastral ligament; dv 1, dorsal vertebra 1; M. rcc, retrahens capitis collique; 2–8, cervical vertebrae.

The M. testoscapularis of *Terrapene* is slightly larger, but otherwise comparable to that of nonhinged emydids in its development. It nevertheless has a crucial role in the mechanism of shell closure (Fig. 9A,B). The muscle takes its origin lateral and slightly posterior to the scapulo-carapacial articulation; its insertion is on the posterior surface of the suprascapula (as in *Emys* and *Emydoidea*). Contraction of the testoscapularis draws the suspensorium posterolaterally, thereby "unlocking" it. This is a necessary prerequisite to shell closure. Activation of the testoscapularis presumably occurs slightly

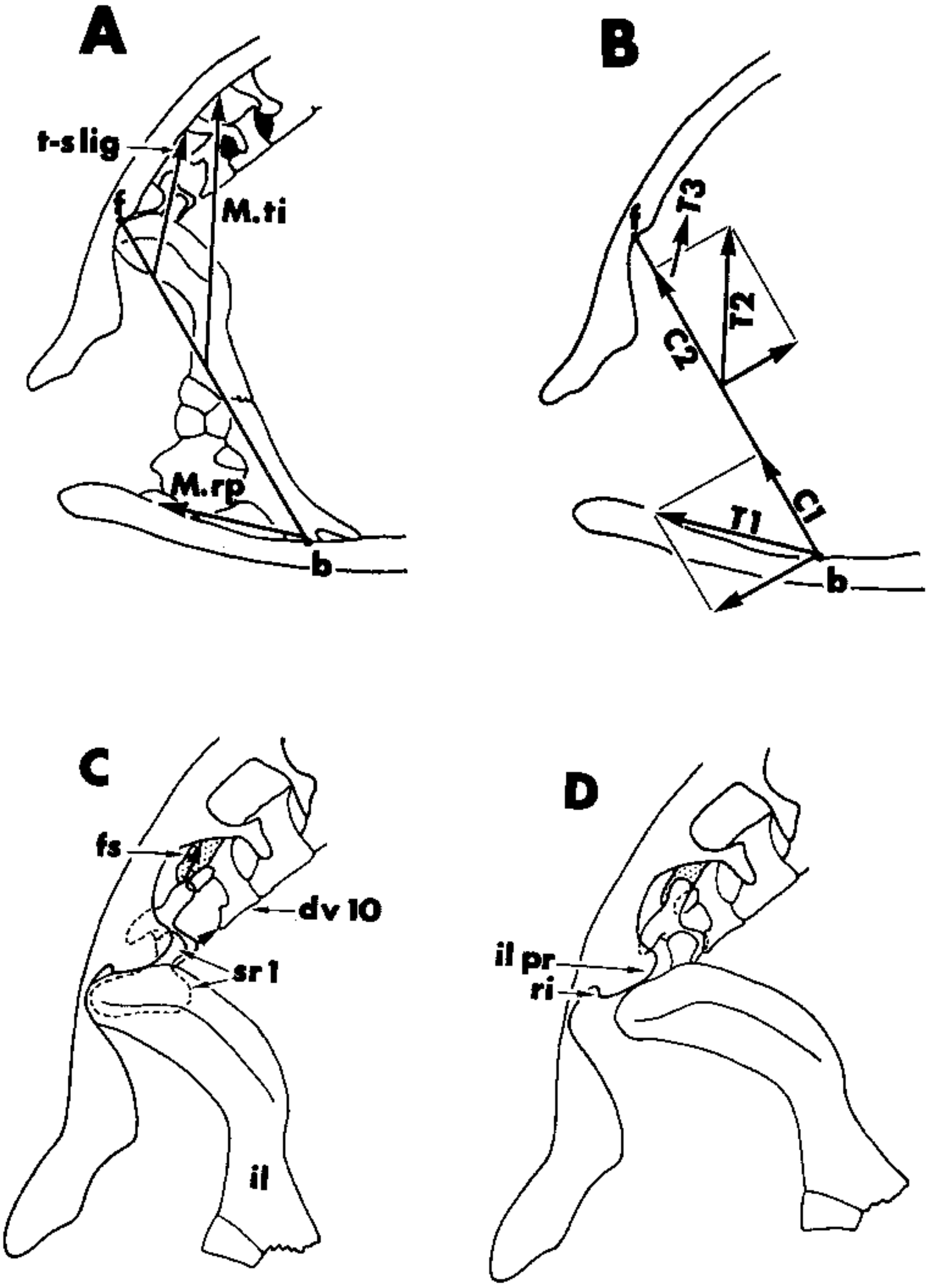


Fig. 11. Right lateral views demonstrating stabilizing and closing mechanics of pelvic girdle in *Terrapene*. A and B, pelvis in "open" position showing the major tensile forces acting on the structural axis (line f-b) of girdle. Sources of tension are: retrahens pelvium muscle (M. rp; T1), testo-iliacus muscle (M. ts; T2), and the elastic testo-sacral ligament joining first sacral and last dorsal vertebra and carapace (t-s lig; T3). B, resolution of vector components of forces T1 and T2; note that each has a significant compressive component (C1, C2) driving pelvis upward against carapace. C and D illustrate relationships of ilium (il), ilial process (il pr) and ilial recess (ri) of carapace, and the sacro-dorsal articulation with shell open (C) and closed (D). Notice that in C the sacro-dorsal

in advance of or synchronously with the M. retrahens capitis collique.

The mechanism for elevation of the posterior region of the plastron is basically similar to that employed by *Cuora,* but with a few important differences. An enlarged M. testoiliacus also draws the pelvis forward and upward in *Terrapene,* but there is no special ligament joining the pelvis and plastron. The pull of the testoiliacus is transferred to the shell by virtue of a strong muscular connection between the ventral bones of the girdle and the adjacent portions of the xiphiplastra. A further difference is that during closure the ilium (actually sacral rib 1) slides anteriorly over the ilial process (Fig. 11C,D). When the shell is open the pelvic girdle is stabilized in large part by its relationships to the shell. The posterior crest of the ilium is seated in a pronounced depression or ilial recess developed on the underside of pleural bone 8; in front of this it is buttressed by the ilial process. Ventrally, a tripod of support is provided by the contact of the pubic processes in front and the ischial symphysis behind with the xiphiplastra. This position is maintained largely by the effort of the M. retrahens pelvium muscles which originate and insert as in *Cuora.* The muscles are, however, much more extensively developed in *Terrapene,* a fact reflected by the size of the fossae on the xiphiplastra for their origin and the expanded pectineal processes of the pubes for their insertion.

Beyond the anchoring effect of the retrahens pelvium, tensile forces from at least two additional sources help fix the position of the pelvis. As the girdle rotates into the "open" position, the M. testoiliacus is noticeably stretched and is therefore one such source of tension. If a certain level of tonus were maintained, this muscle would provide an even greater tensile force. Stretched elastic tissue joining the sacrum and carapace (see below) is the other source of tension. Both of these tensile forces along with that provided by the retrahens pelvium act on the structural axis of the pelvis as indicated in Figure 11A. Resolution of the forces into vector components shows that each has a significant vertical or compressive component directed upward along the axis of the girdle (Fig. 11B). The cumulative compressive force is essential to keeping the ilia well seated in their carapacial recesses.

The pelvic girdle effectively opposes upward forces from the hind limb in the manner outlined for *Cuora.* Pelvic resistance in *Terrapene* is actually more effective due to the fact that such forces tend, in part, to press the ilia more firmly into the carapace. More importantly, as long as the ilia are so positioned they resist the rotation necessary for elevation of the plastron (Fig. 11C). By sliding forward on the ilial processes the posterior extensions of the ilial crests are withdrawn from the carapacial recesses; this movement must therefore be regarded as a release mechanism preparatory to rotation of the girdle. Certain modifications of the sacral region appear to relate directly to this mechanism.

The articulation between the last dorsal (10th) and the first sacral vertebra in *Terrapene* is unlike that of all other emydids including *Emys* and *Emydoidea.* There is no formed central articulation; the opposed central surfaces are joined by a tough elastic ligament. The postzygapophyses of the dorsal vertebra are close together, frequently fused, and their articular facets are vertically oriented. These are received in a slot-like space between the attenuated prezygapophyses of the sacral vertebra. Additionally, there is a deep sacral fossa (Fig. 1C) in the carapace on either side of the dorsal vertebra for reception of the corresponding prezygapophysis of the sacrum. The modifications just outlined permit the sacral vertebra to "telescope" on the dorsal vertebra, thereby allowing the ilia to move anteriorly in the unlocking sequence (Fig. 11D). The carapacial pits also contain a tough elastic tissue firmly attached to the carapace and the sacral vertebra. When the pelvis is in the open position these ligaments are stretched and under tension. With the cessation of contraction of the retrahens pelvium the ligaments automatically help release the ilia from the shell, thus facilitating the closing mechanism. This appears to be an important function of the "spring-loaded" sacrum of *Terrapene.*

articulation is well separated, stretching ligaments (heavy arrows) uniting it; in D ilium is sliding forward and rotating on ilial process as sacro-dorsal articulation "telescopes." See text for discussion. Other abbreviations: fs, sacral fossa (stippled); sr 1, sacral rib 1.

EVOLUTION OF EMYDID SHELL KINESIS

The only prior effort to investigate the mechanics of emydid shell closure was that of Shah (1960); his study suffers from superficiality, descriptive errors, and a failure to perceive the fundamental mechanisms of shell kinesis. The specialized scapula, the cervico-plastral ligament and the role of the cervical retractor muscle in the closing mechanism of emydines were not mentioned. Shah was seemingly unaware of the importance of the M. testoscapularis in Asiatic box turtles.

Shah stated that the clavicular division of the M. deltoideus and the M. pectoralis were chiefly responsible for elevation of the anterior region of the plastron in all emydid box turtles. The present study indicates that neither muscle contributes in any significant way to shell closure. The main function of the clavicular deltoid is, as in other turtles, that of rotating the shoulder girdle and humerus anteriorly. The pectoralis acts primarily to retract the humerus. Both the origin and insertion of the clavicular deltoid lie in front of the hyo-hypoplastral hinge. Consequently, the muscle does not act across the hinge and hence cannot induce motion at the joint. This portion of the deltoideus may actually help open the front of the shell. The pectoral muscle does span the plastral hinge but its insertion is on the humerus, not the plastron. It imparts motion at the the shoulder and brings about some outward rotation of the pectoral girdle, but does not produce elevation of the plastral lobe. Shah further suggested that forward rotation of the shoulder girdle aided plastral elevation when, in fact, backward rotation of the girdle accompanies raising of the plastron; in any event, axial rotation of the girdle contributes little or nothing to closure of the shell in emydids.

One fact that emerges strongly from this study is the overriding importance of girdle accommodation in chelonian shell kinesis. Due to the more intimate relationship between girdle and shell, accommodation appears to be a more serious problem with respect to the pectoral than pelvic girdle. Forelimb displacement is also a contributing factor. It is in the shoulder region, then, that the most profound modifications are to be expected in hinged chelonians. Accommodation has taken two separate paths in the Emydidae. The system employed by the batagurines (e.g. *Cuora*) is the simpler, although it has involved considerable modification of the musculature and capsule surrounding the scapulo-carapacial articulation. The system utilized by the emydines, requiring a jointed scapula and special linkage between the neck and plastron, appears to have been the more "difficult" to evolve. However, reorganization of the associated musculature has been less demanding here than in the batagurines.

It is interesting that in the least specialized batagurine box turtles (e.g. *Cyclemys*) a functional plastral hinge appears only in adult specimens. Even so, the testoscapularis muscle is fully modified in akinetic juveniles. Plastral kinesis is, therefore, maturational while the development of the musculature is not. The significance, if any, of this incongruity is not clear. It might suggest that specialization of the muscles preceded the attainment of a movable plastron in those turtles ancestral to the Asiatic box turtles. If this has been the case, the factors initiating muscular specialization are even less apparent.

The three extant genera of emydine box turtles clearly possess the same fundamental mechanism for closing the shell. Moreover, there is a logical progression in the organization and function of the mechanism from the primitive condition of *Emys* through *Emydoidea* to the advanced condition of *Terrapene*. It is doubtful that the relatively unspecialized scapular suspensorium of *Emys* forms an effective locking mechanism, although this could not be determined with certainty on the preserved materials utilized in this study. Girdle accommodation is likely to be the sole function of the suprascapula in *Emys*. With the addition of the episcapula a locking mechanism with the functional properties illustrated in Figure 9 becomes possible. *Emydoidea* has such a mechanism, but it is both less developed and less efficient than that of *Terrapene*. The special suspensorium of *Emydoidea* and *Terrapene* provides for girdle stability in locomotion as well as for accommodation during closure of the shell.

There is an approximate correlation between the relative development (length) of the suspensorium and scapular blade and the degree of plastral elevation required for shell closure. The shell of *Emys* is relatively depressed and the plastron must be raised only slightly (ca. 12°) to contact the carapace;

here the suspensorium is only about 15% of the length of the scapula. *Terrapene* has a relatively high domed shell and a plastral arc of up to 50° is necessary to bring about full closure; the suspensorium may be up to 35% of the length of the scapular blade. *Emydoidea*, again, is intermediate (ca. 20–25°; 20%). A gradual increase in shell height is likely to have been a prime factor in the appearance of the new segment (episcapula) in the suspensorium shared by *Emydoidea* and *Terrapene* since this ultimately demands greater girdle accommodation. A two-part suspensorium provides for greater flexibility and ease of accommodation than would a single long suprascapula.

There is also a very evident structural trend from *Emys* to *Terrapene* in specializations associated with the mechanism for closing the rear of the shell. Though the inguinal buttresses are reduced and the hypoplastral-peripheral sutures are suppressed, there is very little real kinesis associated with the posterior plastral lobe of *Emys*. The same region of the shell is truly kinetic in *Emydoidea*, although not nearly so mobile as that of *Terrapene*. Related to the development of a closable posterior lobe, one sees in *Emydoidea* incipient modifications of the pelvis and musculature that are clearly in the direction of those characteristic of *Terrapene* (Zug, 1971). No comparable specializations exist in *Emys*.

The selective advantages of a closable shell are certainly central to any overall understanding of the evolutionary significance of the box turtle morphotype, but no concise answer to this question is presently possible. One prevalent theory on this issue, that closable turtle shells are basically a terrestrial adaptation, appears to be without foundation. This idea has most often been voiced by those engaged in studies of the genus *Terrapene* (e.g. Legler, 1960; Milstead, 1969). The fact nevertheless remains that *Terrapene* is the exception rather than the rule; all other modern chelonians with closable shells (*Lissemys*, *Pelusios*, *Kinosternon*, *Emys*, *Emydoidea*, *Cyclemys*, *Cuora*) are predominantly or exclusively aquatic. Zug has recently suggested (1971) that most or all emydid box turtles may stem from terrestrial or semi-terrestrial ancestors, but there is no direct evidence for this. At least in the case of emydines, available morphological evidence I shall present later would seem to indicate exactly the reverse. It therefore seems reasonable to postulate that the closable shell originates in turtles as an aquatic adaptation.

The origin of shell kinesis within aquatic rather than terrestrial species is entirely consistent with the functional implications of this specialization. Again the issue is girdle accommodation, especially at the shoulder. For land locomotion a stable scapulo-carapacial articulation is of paramount importance since the girdles and limbs must support considerable body weight. Because girdle accommodation in hinged turtles normally demands sacrifice of stability at this articulation, such a specialization becomes a distinct liability in terrestrial forms. It is for this reason that a fully kinetic anterior plastron appears never to have arisen directly in a terrestrial chelonian. [*Pyxis* of Madagascar may be the exception. An anterior hinge, apparently involving the entoplastron is reported in adult specimens (Siebenrock, 1906).] In contrast, the stability of the pelvis seems to be far less critical. Some movement of the pelvis is possible in most land dwelling turtles even in the absence of plastral kinesis. A movable posterior plastral lobe has probably evolved directly in several land tortoises (e.g. *Testudo graeca*, *hermanni*, *kleinmanni*).

Very different conditions surround the development of plastral kinesis in aquatic turtles. Here much of the body weight and hence the stress on the girdles is taken up by the buoyancy of the medium. Moreover, aquatic box turtles are known to have densities only slightly exceeding the specific gravity of water (Williams and Han, 1964; Zug, 1971). Most aquatic box turtles tend to be bottom-walkers rather than true swimmers (Zug, 1971). Zug has interpreted this as possibly indicative of terrestrial ancestry, but it seems more probable that bottom-walking is a secondary mode of locomotion imposed by the limitations of the specialized shell. In any case, minimal structural loading of the pectoral girdle in aquatic chelonians seems certainly to have facilitated accommodation and hence plastral kinesis.

The foregoing brings into sharper focus an apparent evolutionary paradox in turtles. Chelonian terrestrialism is invariably accompanied by specializations aimed at protecting those soft parts (esp. the extremities) not directly shielded by the shell. Such specializations usually take the form of increased keratinization of the epidermis and frequently extensive dermal ossification. The development of a closable shell would seem a more direct and effective method of coping with this problem but, for reasons just discussed, this line of adaptation has not been accessible to terrestrial forms. On the other hand, the possession of a closable shell by an aquatic turtle might be regarded as a significant prospective adaptation to land life, thereby giving it a competitive advantage in this direction over species possessing hingeless shells. Yet the record indicates that precisely the opposite prevails; land tortoises have arisen, perhaps several times (Bramble, 1971), from akinetic emydids. Excluding *Terrapene*, the strongest trends toward terrestrialism among living emydids are found in hingeless genera (e.g. some *Clemmys*, *Rhinoclemys*, *Melanochelys*, *Geoemyda*).

The above points strongly to the conclusion that while a closable shell in aquatic turtles may itself represent an important "preadaptation" for terrestrial existence, affiliated modifications of the shoulder girdle normally preclude this possibility. In this context the uniqueness of *Terrapene* is more evident. By perfecting a scapular suspensorium that combines excellent stabilization and accommodation capabilities, *Terrapene* has overcome the paradox that confronts other box turtles. This, no doubt, contributes in large measure to the remarkable success of the genus in terrestrial environments.

PHYLETIC IMPLICATIONS

My original intent was to avoid, so far as practical, any confrontation with the complex taxonomic and nomenclatorial problems that pervade the Emydidae. This has not been possible. Data pertaining to the shell closing mechanisms of various emydids bring new evidence to several important questions of emydid systematics and phylogeny.

The striking superficial resemblance between the Asiatic (*Cuora*) and the North American box turtles (*Terrapene*) has frequently lead to speculation that an actual relationship exists between the two. Williams (in Loveridge and Williams, 1957) recognized two distinct lineages, a unicarinate and tricarinate, among the existing emydids. According to Williams' scheme (Loveridge and Williams, 1957; Fig. 2) *Emys*, *Terrapene* and *Cuora* are all members of the tricarinate lineage and derived ultimately from the genus *Clemmys*; *Emys* directly, *Terrapene* and *Cuora* by way of *Geoemyda* with *Cyclemys* being transitional between *Geoemyda* and *Cuora*. *Emydoidea*, in contrast, is placed in the unicarinate assemblage, far removed from all other emydid box turtles. McDowell (1964) has subsequently reorganized the Emydidae chiefly on the basis of cranial morphology. His study led to the formal establishment of the subfamilial categories Batagurinae and Emydinae. *Cuora* and the other Asiatic emydids together with maining New World emydids comprised the the single New World genus *Rhinoclemys* were allocated to the Batagurinae, while *Emys*, *Emydoidea*, *Terrapene* and the re- Emydinae. Despite their many differences, the schemes of Williams and McDowell find agreement on two points: 1) the independent evolution of hinged plastra in several emydid turtles; 2) the denial of any close relationship between *Emydoidea* and either *Emys* or *Terrapene*.

Williams' proposed phylogeny provides for the appearance of the box turtle specialization on at least four separate occasions in emydid history (*Emys*; *Terrapene*; *Cyclemys-Cuora*; *Emydoidea*). McDowell's calls for the same event on possibly three occasions in the subfamily Emydinae and an unspecified number of times in the Batagurinae. Agreement between the two schemes is actually on a point of inference, since neither presents direct evidence to substantiate the independent development of closing mechanisms. Excluding the problematic genus *Notochelys*, the present investigation plainly demonstrates that closable shells have otherwise arisen only twice in the Emydidae. Separate solutions to the difficulties posed by this specialization have been reached once each in the emydine and batagurine complexes.

McDowell's (1964) partitioning of the Batagurinae places hinged species in four distinct genera (*Cuora*, *Cyclemys*, *Notochelys*, *Geoemyda*). Both *Notochelys* and *Cyclemys* are monotypic; in each plastral kinesis is evident only in mature individuals following resportion of the plastral buttresses. Significant movement is restricted to the anterior region of the plastron in these taxa and is much more limited than that seen in *Cuora*. Immature *Cuora* exhibit considerable kinesis of both plastral lobes. As defined by McDowell, *Geoemyda* contains three species, two of which (*flavomarginata*, *mouhoti*) show well developed plastral hinging and a third (*spengleri*) in which the plastron is

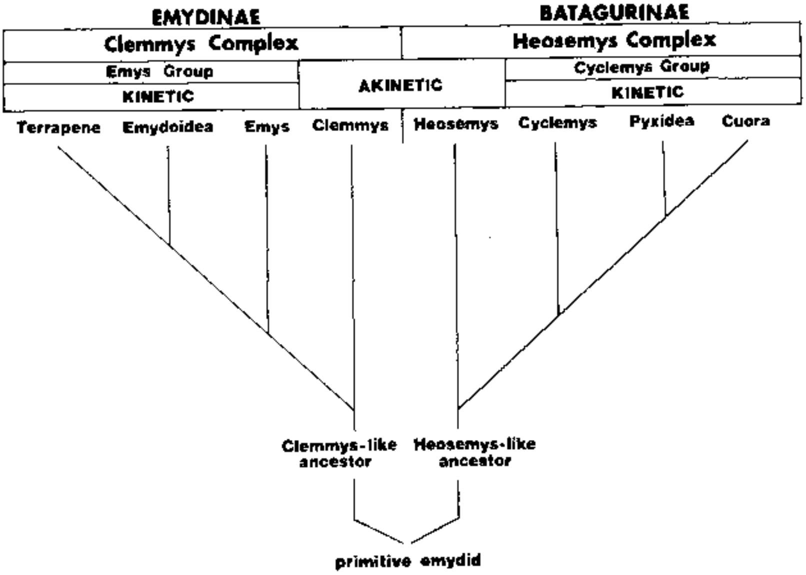


Fig. 12. Schematic representation of the probable phyletic relationships among emydid box turtles.

akinetic. The closing mechanism of *G. flavomarginata* is identical to that of typical *Cuora* (e.g. *amboinensis*); I see no compelling reason for not returning the species to *Cuora*, a position accorded *flavomarginata* by most authors prior to McDowell.

Geoemyda mouhoti is likewise similar to *Cuora* in the anterior closing mechanism, although to judge from the single specimen examined, enlargement of the testoscapularis muscle has not progressed as far as in the latter. Unlike *Cuora*, relatively little kinesis is evident in the posterior lobe of the plastron. In this and other important respects (see Smith and James, 1958) this species differs enough from *Cuora* to probably warrant its allocation to a separate genus, *Pyxidea* (Gray, 1863; Smith and James, 1958; Taylor, 1970). *Geoemyda spengleri*, it seems, is the only legitimate representative of McDowell's *Geoemyda*; fortunately, it is the type species (Gray, 1834). The plastral buttresses are well formed in *G. spengleri* and prevent any visible plastral kinesis. Since McDowell (1964) viewed *Geoemyda* as a derivative of *Cuora* he was forced to postulate paedomorphosis to account for the absence of shell mobility in *Geoemyda spengleri*. This hypothesis may now be safely discarded. There is absolutely no evidence from the shoulder apparatus of *G. spengleri*, including the relationships of the testoscapularis, to suggest that it has ever been modified from the condition of akinetic batagurines. *Geoemyda* (*sensu stricto*) appears not to be closely related to the hinged batagurines.

The *Geoemyda* Complex was erected (McDowell, 1964) to house *Geoemyda*, the hinged batagurines, and an additional suite of akinetic genera (*Rhinoclemys*, *Melanochelys*, *Sacalia*, *Mauremys*, *Heosemys*). At best, intergeneric relationships within the complex are obscure. However, *Cyclemys*, *Pyxidea* and *Cuora* share an identical mechanism for closing the anterior end of the shell. The mechanism incorporates a number of morphological specializations that are unlikely to have been independently derived. These and additional shared morphological features indicate that the genera comprise a closely related phyletic assemblage, here termed the *Cyclemys* Group. *Cyclemys* is clearly the most primitive of the three hinged genera, with *Pyxidea* in most respects structurally intermediate between it and the more derived *Cuora*.

The origin of the *Cyclemys* Group is most probably in some primitive form of *Heosemys*, a genus which McDowell (1964: 272) regarded as "isolated" and "without clear affinity to any other particular genus of the *Geoemyda* Complex." On overall shell morphology, including the distinctive radiate pattern of the plastral scales, *Heosemys grandis* is barely distinguishable from *Cyclemys dentata*. So far as known adult *Heosemys* never develop a functional hinge but otherwise the plastral buttresses are nearly as reduced as those of *Cyclemys* and the bones of the plastron are equally thin and flexible. The testoscapularis is slightly better developed in *Heosemys* than in some other akinetic batagurines (e.g. *Rhinoclemys*, *Geoemyda*) and there is a hint of incipient posterior displacement in some specimens. It is entirely possible that more clear cut evidence of muscular specialization is to be found in one or more of the species of *Heosemys* not examined in this study (i.e. *H. depressa*, *leytensis*, *silvatica*). As a step toward further clarification of batagurine relationships, *Heosemys*, *Cyclemys*, *Pyxidea* and *Cuora* are here removed to a separate *Heosemys* Complex. Relationships within the complex are indicated in Fig. 12.

Adult *Notochelys* exhibit a hyo-hypoplastral hinge similar to *Cyclemys*. The extent to which *Notochelys* is capable of lifting the anterior region of the plastron is unknown to me; presumably some limited movement is possible. While the specimens examined in this investigation did not reveal the precise closing mechanism of *Notochelys*, they demonstrated conclusively that it is not that of the *Cyclemys* Group. Plastral kinesis in *Notochelys* has apparently arisen apart from that of the other hinged Asiatic emydids; from this and other evidence *Notochelys* is not closely related to them. Nor does the genus seem to bear any special relationship to *Heosemys*. For the moment at least, the evolutionary position of *Notochelys* remains quite unclear. In details of forearm scutellation *Notochelys* is similar to *Siebenrockiella* and unlike all other members of the *Geoemyda* Complex (McDowell, 1964).

A more urgent matter is the phyletic position of the North American semi-box turtle *Emydoidea*. Until the paper by Loveridge and Williams (1957) this turtle was widely regarded as a congener of Old World *Emys*. Evidence for the relationship rested principally on undoubted resemblances in shell coloration and plastral hinging. Nevertheless, Williams (in Loveridge and Williams, 1957) presented a forceful case for a relationship between *Emydoidea* and *Deirochelys*. Although *Deirochelys* possesses no plastral hinge and on many points of shell morphology closely approaches certain members of the genus *Chrysemys* (McDowell, 1964), it does, as Williams noted, share with *Emydoidea* a number of specializations of the skull, cervical vertebrae and neck musculature. On these grounds Williams suggested that *Emydoidea* was a derivative of *Deirochelys* and only convergent with *Emys*. This view has been widely adopted by later workers (Tinkle, 1962; McDowell, 1964; Zug, 1966; Pritchard, 1967; Milstead, 1969; Ernst and Barbour, 1972), some of whom (Tinkle, 1962; Zug, 1966) have presented additional evidence in support of it. McDowell (1964: 275) found no "significant cranial differences between *Deirochelys* and *Emydoidea*" and accordingly placed both genera in a *Deirochelys* Complex within the Emydinae. At the same time he recognized a close relationship between *Clemmys*, *Emys* and *Terrapene* for which he proposed the *Emys* Complex.

The current study, nevertheless, offers convincing evidence that *Emydoidea* is indeed a close phyletic associate of *Emys* and *Terrapene*. A multiple origin for the complex closing mechanism held in common by these box turtles appears extremely remote. Moreover, a detailed evaluation of the relationships of *Emys*, *Emydoidea* and *Terrapene* has revealed a large suite of morphological characters that link these genera to one another and to *Clemmys* (Table 1). The same characters distinguish them from *Deirochelys* and members of McDowell's *Chrysemys* Complex to which *Deirochelys* surely belongs. These differences far outweigh the few similarities shared by *Emydoidea* and *Deirochelys* that are undoubtedly the result of convergent feeding systems.

That *Emydoidea* is a close ally of *Emys* and *Terrapene* and in many ways structurally intermediate between the two, has obvious implications concerning the origin of *Terrapene*. The mistaken belief that *Emydoidea* was related to *Deirochelys* has systematically excluded it from the possible ancestry of *Terrapene*. As previously noted, McDowell (1964) advocated a relationship among the genera *Clemmys*, *Emys* and *Terrapene* primarily on the basis of shared cranial characters. Within this *Emys* Complex McDowell believed that certain skull features precluded *Emys* from the direct ancestry of *Terrapene* and that the latter must therefore have arisen directly from *Clemmys*. Milstead (1969) has since shown that some of these same cranial characters are quite variable and has hy-

TABLE 1. DISTRIBUTION OF CHARACTER STATES AMONG GENERA OF THE CLEMMYS (*Clemmys, Emys, Emydoidea, Terrapene*) AND CHRYSEMYS (*Chrysemys, Deirochelys*) COMPLEXES.

	Clem.	*Emys*	*Emyd.*	*Terr.*	*Chrys.*	*Deir.*
1. Orbito-nasal foramen small	+	+	+	+	–	–
2. Caroticopharyngeal for. enlarged	+	∓	+	+	–	–
3. Interorbital width narrow; orbits widely exposed dorsally	–	–	–	–	∓	+
4. Interorbital region coarsely sculptured	+	+	+	+	–	–
5. Postorbital bar relatively wide	+	+	+	+	–	–
6. Jugal contacts palatine	–	–	–	–	+	+
7. Masticatory surfaces of jaws narrow, unridged*	+	+	+	+	–	+
8. Skull noticeably elongated*	–	–	+	–	–	+
9. Cervical column very long*	–	–	+	–	–	+
10. Cervical extensor muscles hypertrophied*	–	–	+	–	–	+
11. Scapular suspensorium	–	+	+	+	–	–
12. Cervico-plastral ligament	–	+	+	+	–	–
13. Metischial processes of pelvis prominent, rounded	–	–	–	–	+	+
14. Plastron hinged; ligamentously attached to carapace	–	+	+	+	–	–
15. Humero-pectoral sulcus crossing entoplastron	+	+	+	+	–	–
16. Surface of carapace with vermiculate sculpture	–	–	–	–	∓	+
17. Dorsal ribs elongated, bowed ventrally*	–	–	+	–	–	+
18. Suprapygal bones reduced to 1	∓	∓	+	+	–	–
19. Coloration of carapace light and dark mottled	+	+	+	∓	–	–
20. Musk glands	+	+	+	+	–	–

* Characters functionally related and indicative of convergent feeding systems in *Emydoidea* and *Deirochelys*.

pothesized a common ancestry for *Emys* and *Terrapene*. The common ancestor, according to Milstead, would have its roots in the genus *Clemmys* but be distinct from it.

Fig. 12 depicts the phyletic relationships of *Terrapene* as I now conceive them. There is agreement with earlier views (e.g. Loveridge and Williams, 1957; McDowell, 1964; Milstead, 1969) in that *Emys* certainly has *Clemmys* as its source. However, the *Clemmys* Complex is used in preference to McDowell's *Emys* Complex to connote the generic assemblage originating in *Clemmys*. Accordingly, the *Emys* Group is proposed for the three derived hinged genera, of which *Emys* is the most primitive.

No *Clemmys* is known to possess a plastral hinge and in all cases the scapula is of the normal emydid type. However, regular reduction of the plastral buttresses in *Clemmys marmorata* is not without significance, since this itself is an important prerequisite to plastral kinesis. *Emydoidea*, in turn, must stem from an ancestral form that on overall organization would be regarded as *Emys*. On present distribution and several points of morphology (mostly minor; see McDowell, 1964; Milstead, 1969) Recent *Emys* is not an acceptable ancestor for *Emydoidea*. The entire *Clemmys* Complex as conceived herein would appear to have had its origin and most of its history within North America. *Emys orbicularis*, with a present range that includes western Europe, North Africa and adjacent portions of Asia, is the only representative of the complex known outside of North America. *Emys* has presumably reached its current range from the New

World, but the time and route of dispersal are not yet known.

Aside from the objections raised by Recent *Emys*, all available evidence points to the origin of *Emydoidea* from a primitive *Emys* in North America. In all probability it is in such an early form of *Emydoidea* that *Terrapene* has its beginnings. Modern *Emydoidea* is the end product of evolution that has emphasized feeding specializations of the skull, neck and related musculature. It is both reasonable and necessary to expect that ancestral *Emydoidea* was much less extreme in these specializations. Such a hypothetical turtle, otherwise not materially different from *E. blandingii*, would provide a very adequate ancestral radical for *Terrapene*.

The projected origin of *Terrapene* from *Emydoidea* demands a reappraisal of current thinking on evolutionary patterns within *Terrapene* itself. Milstead's work in particular (Milstead, 1967, 1969; Milstead and Tinkle, 1967) shows that the history of *Terrapene* is complex and that important aspects of it remain unresolved. No effort is made here to examine *Terrapene* relationships in detail; I wish only to make a few comments that seem applicable. Milstead (1969) has endeavored to place all extant and valid fossil species in one or the other of two distinct lineages (Carolina and Ornata Groups) within *Terrapene*. Recent *T. carolina major* and related fossil forms are generally acknowledged as primitive for terrestrial *Terrapene* but serious differences of opinion surround modern *T. coahuila* from northern Mexico. Several skeletal features together with its aquatic habits have lead some workers (Auffenberg, 1958; Legler, 1960; Webb et al., 1963) to the opinion that *T. coahuila* is the most primitive of the living species. Milstead (1960, 1967, 1969), nevertheless has advanced the argument that *Terrapene coahuila* has a terrestrial ancestry in extinct *T. carolina putnami*. In the view of Milstead and some others (e.g. Brown, 1971), *T. coahuila* is secondarily aquatic and therefore not truly primitive.

The fact still remains, however, that *Terrapene coahuila* approaches *Emydoidea* more closely in overall shell morphology than do any of the terrestrial species including *T. carolina major*. In limb morphology *T. coahuila* departs noticeably from other modern *Terrapene* and again in the direction of *Emydoidea*. Perhaps most significant is the fact that *T. coahuila* is intermediate between *Emydoidea* and terrestrial *Terrapene* in neck length and the relative development of the cervical extensor muscles, the same characters that have played such an important role in separating *Emydoidea* from *Emys* and terrestrial *Terrapene*. Thus despite arguments to the contrary there is now good reason to regard *T. coahuila* as the plesiomorphic facies of the genus. If correct, this interpretation has considerable meaning for future evolutionary and biogeographic studies of *Terrapene*.

It is unfortunate that the existing fossil record offers little insight into evolutionary relationships among the emydine box turtles. Fossil *Emys* is presently known only from Europe where the only certain records are of Pleistocene age (Loveridge and Williams, 1957). On the other hand, the earliest *Emydoidea* is from the Late Pliocene (Blancan) of Kansas (Taylor, 1943). Preston and McCoy (1971) have suggested that this as well as additional Pleistocene material is referable to Recent *E. blandingii*. The oldest recognized *Terrapene* remains come from still earlier Middle Pliocene (Hemphillian) deposits also in Kansas (Hay, 1908; Milstead, 1967). Hopefully, more enlightening fossil material will soon be forthcoming. When available, this material will provide a crucial and needed test for the phyletic inferences drawn from this study.

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