

A PHYLOGENY AND CLASSIFICATION
OF THE HIGHER CATEGORIES
OF TURTLES

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ABSTRACT

Shared derived characters of the basicranium provide the basis for a new theory of relationships and a new classification of the major groups of living and extinct turtles. Post-Triassic turtles are characterized by a jaw-closing mechanism where the main adductor tendon rides over a trochlea, a condition unique among vertebrates. A study of the trochlear mechanism and associated basicranial adaptations for akinesis suggests

that the trochlea evolved independently in cryptodires and pleurodires. Cranial arteries and the canals and foramina associated with them provide characters used to develop hypotheses of relationship among the Cryptodira.

The taxon "Amphichelydia," characterized by primitive features and supposedly containing the ancestors of Recent turtles, is rejected and its members distributed to monophyletic taxa.

INTRODUCTION

Matthew (1924, p. 210) said: "I venture to remark that a more careful search for skulls of extinct chelonians, and less reliance upon the characters of the carapace and plastron might perhaps aid in clearing up the real affinities of both fossil and recent members of the order. A classification of mammals based primarily upon the number and relations of the ribs and taking no serious account of the skull would probably be as unsatisfactory as are the current classifications of fossil chelonians."

The purpose of the present paper is to take Matthew's advice and develop a hypothesis of relationships among the turtles using characters obtained, for the most part, from the skull. Cranial features of turtles have been infrequently used for phylogenetic purposes, yet the potential of the skull as a source of characters has been known for some time (e.g., Siebenrock, 1897). In addition, much of the known diversity of extinct turtles is represented by cranial material, and this adds an important perspective to studies of Recent forms.

I summarize here information from a larger, but as yet unpublished, work on turtle skull morphology (Gaffney, MS). More detailed descriptions and other figures will be found there. The terminology I use is from a figured glossary (Gaffney, 1972b).

Anatomical Abbreviations

Used in

Figures 2-5, 7, 9-19, 23

ang, angular	bo, basioccipital
art, articular	bs, basisphenoid

cor, coronoid
den, dentary
epi, epipterygoid
ex, exoccipital
fr, frontal
ju, jugal
mx, maxilla
na, nasal
op, opisthotic
pa, parietal
pal, palatine
pf, prefrontal

pm, premaxilla
po, postorbital
pr, prootic
pra, prearticular
pt, pterygoid
qj, quadratojugal
qu, quadrate
so, supraoccipital
sq, squamosal
sur, surangular
vo, vomer

Institutional Abbreviations

AMNH, Department of Vertebrate Paleontology, the American Museum of Natural History
 AMNH (H.), Department of Herpetology, the American Museum of Natural History
 MCZ, Museum of Comparative Zoology, Harvard University
 UT, Slide collection of Dr. Thomas Parsons, Department of Zoology, University of Toronto
 YPM, Yale Peabody Museum, Yale University

METHODOLOGY

Recent years have witnessed a renewed interest in self-examination by systematists. The primary concern in this endeavor involves the philosophic formulation of methodology for the purpose of increasing rigor and objectivity. The works of Popper (1968a, 1968b, 1972) have influenced some systematists (e.g., Ghiselin, 1969; Bock, 1973), and his characterization of science as a series of refutable but not confirmable hypotheses has considerable merit as a

basis for discussion. Any method of determining relationships (i.e., phylogeny reconstruction in the strict sense) should be expressed in the context of a testable hypothesis. Although there is no unanimity as to what particular method is most compatible with Popper's ideas, Hennig's phylogenetic systematics or cladism (1966) seems to me most fruitful. In any case it is important to explain the methods used in a study so that other workers will be able to test the hypotheses presented using different methods.

A number of reviews concern the use of shared derived characters in phylogeny reconstruction and provide extensive discussion: Hennig, 1966; Brundin, 1966, 1968; Schaeffer, Hecht, and Eldredge, 1972. Briefly, a cladistic phylogeny attempts to express the genealogic relations of taxa in the strict sense without indicating the degree of morphologic similarity or difference (except for shared derived characters that may be considered similarities). Relationship means relative recency of common ancestry, that is, two taxa are more closely related to each other than to a third taxon if the first two share an ancestor that the third does not. Recency of common ancestry is determined by shared derived characters, characters that are assumed to have evolved in the common ancestor of two taxa and to have been inherited by them. As with other methods of phylogeny reconstruction the identification of homologous characters and the recognition of parallelism is still a fundamental problem.

COMPARISON OF THE HEAD IN LIVING CRYPTODIRES AND PLEURODIRES

The jaw mechanism. Schumacher (1954, 1955a, 1955b, 1956) has described the jaw musculature of turtles in an excellent series of monographs. He demonstrated that living turtles have a trochlear apparatus that is unique among vertebrate jaw-closing systems. Most tetrapods have the adductor jaw musculature arranged in a pinnate manner around one or more tendinous sheets (Lakjer, 1926; Edgeworth, 1935; Frazzetta, 1968). There is usually one pinnate tendon-muscle system that is the primary lower jaw adductor or at least the largest in the head, and it

has been termed the Bodenaponeurosis by Lakjer (1926) and the Adduktorenschne by Schumacher (1954) and others. In most tetrapods this main adductor tendon or Bodenaponeurosis attaches on or near the coronoid process (in mammals the coronoid process is essentially an ossified Bodenaponeurosis; see Frazzetta, 1968) and extends posterodorsally into the temporal region. The greater part of the adductor jaw muscle fibers extend from bones within the temporal region to attach onto the Bodenaponeurosis (Frazzetta, 1968, fig. 2). Contraction of these fibers pulls the Bodenaponeurosis or main adductor tendon posterodorsally into the skull and adducts the lower jaw. Recent turtles, as opposed to all other tetrapods, have a main adductor tendon that rides over a pulley or trochlea and changes its direction of movement within the skull (fig. 1). This tendon in turtles contains a cartilage, the cartilago transiliens of Schumacher (1956, figs. 3-5), which is developed where the tendon passes over the trochlea. The cartilago transiliens is roughly meniscus-shaped with the concavity fitting the trochlea.

This trochlear system seems to be related to the enlargement of the otic chamber in turtles that fills much of the area containing jaw musculature in other reptiles. This expanded otic region would interfere with the Bodenaponeurosis of a "typical" reptile if the trochlea were absent. The mechanism in turtles results in a reorientation of the main adductor musculature and has interesting consequences for the structure of the chelonian temporal region. Expansion of the muscle attachment area extends posteriorly in turtles, along an unusually well-developed sagittal crest and post-temporal fenestra, rather than posterodorsally, as in most tetrapods.

All living turtles possess this trochlear mechanism but a detailed examination of its morphology reveals that the trochlear apparatus is constructed differently in cryptodires and pleurodires (Schumacher, 1956). In cryptodires the cartilago transiliens is found in a true joint, with synovial cavity and underlying cartilage, that is formed on the anterodorsal margin of the otic chamber, the processus trochlearis oticum (figs. 1, 2). The processus (Gaffney, 1972b) is usually formed by the quadrate or prootic or both. In

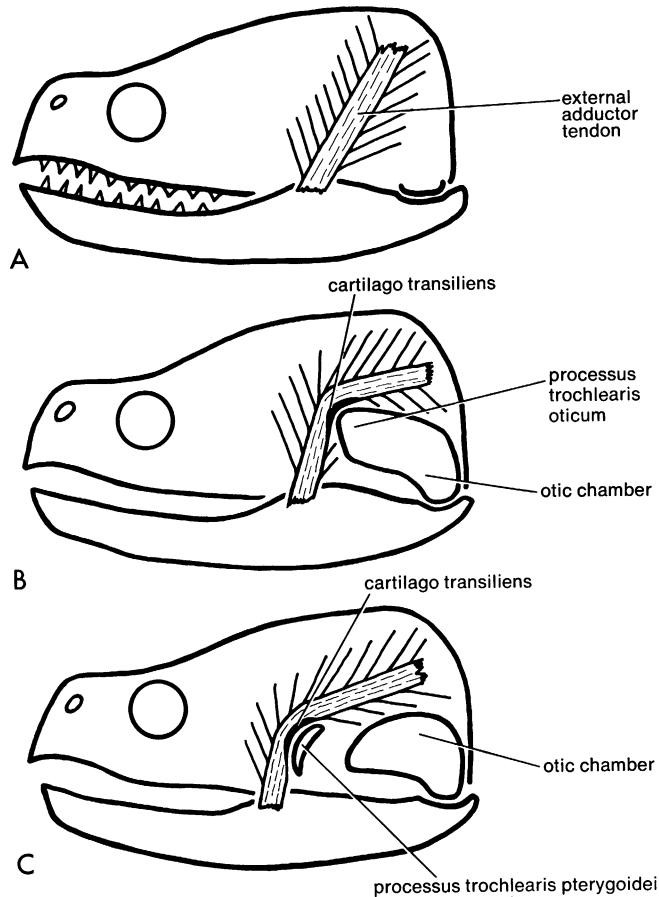


FIG. 1. A comparison of the external adductor tendon in nonchelonian reptiles (A), cryptodiran turtles (B), and pleurodiran turtles (C). Size and shape of structures are indicated diagrammatically.

pleurodires a different bony element, a postero-lateral process of the pterygoid, the processus trochlearis pterygoidei (*ibid.*) bears the cartilago transiliens of the main adductor tendon or Bodenaponeurosis (figs. 1, 3). Although the trochlea consists of a true joint with synovial capsule in cryptodires, it is morphologically very different in pleurodires. The cartilago transiliens has the same shape, but instead of a synovial capsule the "joint" is formed by an infolding of the mucous membrane of the mouth (the ductus angularis oris of Schwartz, 1934, fig. 9) in pleurodires (fig. 13). Also, the position of the

trochlea differs with respect to the *M. adductor mandibulae internus* musculature as indicated by Schumacher (see especially 1954, pls. 11 and 12). In pleurodires the trochlea is anterior to this musculature, whereas in cryptodires the trochlea is posterior to it.

These features, summarized below, strongly suggest that the trochlear apparatus of cryptodires, as a trochlear mechanism, is not homologous to that of pleurodires.

1. The bony elements supporting the trochlea are nonhomologous, i.e., the pterygoid in pleurodires and the quadrate-prootic in cryptodires.

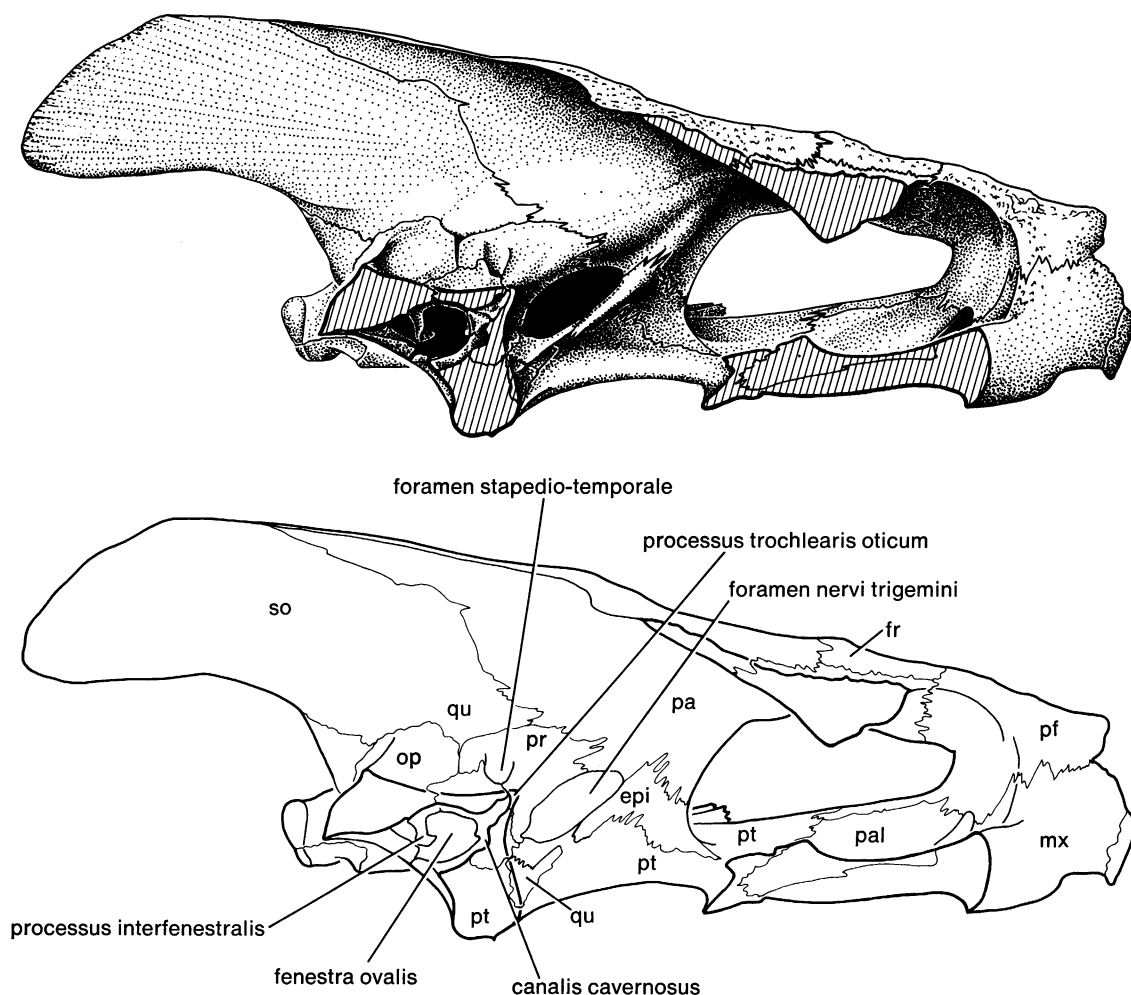


FIG. 2. *Chelydra serpentina*, AMNH (H.) 9249. Lateral view of a cryptodire skull with a parasagittal section on right side removed to show ethmoid region and processus trochlearis oticum. Hatching indicates cut surfaces; compare with figure 3 (see also Gaffney, 1972b, figs. 5, 6).

2. The morphology of the joint capsules are nonhomologous, i.e., a synovial joint in cryptodires and folded oral mucosa in pleurodires.

3. The trochlea is in a different morphologic position with respect to the M. adductor mandibulae internus jaw musculature.

At the present time I contend that neither jaw mechanism type is primitive with respect to the other but that both are derived and, therefore, are important characters for demonstrating the strictly monophyletic nature of the Cryptodira and Pleurodira (as here conceived).

The palatoquadrate region. Cryptodires and pleurodires have distinct differences in the relative proportions and positions of the bones making up the basicranium. Pleurodires have a medial process of the quadrate that forms the main brace to the braincase, whereas in cryptodires the pterygoid extends posteriorly to form the brace between braincase and quadrate (figs. 10, 11, 18, 19). The cavum acustico-jugulare is covered ventrally (in part) by this posterior extension of the pterygoid in cryptodires but in pleurodires this area is not floored by the pterygoid. These

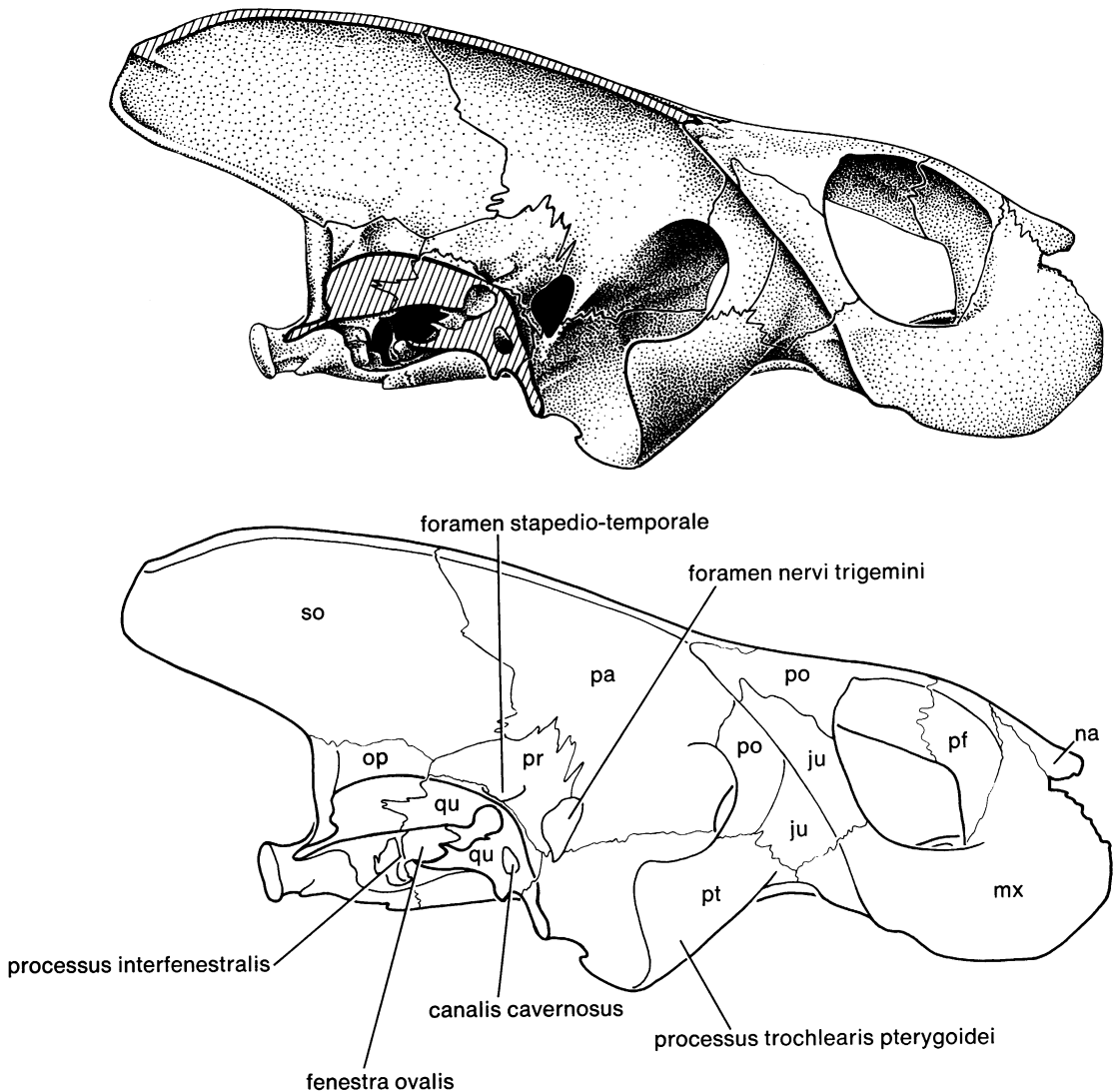


FIG. 3. *Emydura* sp., AMNH (H.) 72418. Lateral view of a pleurodire skull with a parasagittal section on right side removed to show ethmoid region and processus trochlearis pterygoidei. Latter structure projects lateral to the plane of the section. Hatching indicates cut surfaces. Compare with figure 2.

differences are related to a more general condition which involves the morphology of the palatoquadrate, neurocranium, and the intervening area, the cranioquadrate space.

The cranioquadrate passage or space, the elements of the palatoquadrate, and the primary neurocranium are described and discussed by Goodrich (1930, see especially figs. 339, 493)

and DeBeer (1937). A relatively generalized condition of this area can be seen in primitive reptiles, such as *Captorhinus* (Romer, 1956, fig. 36). In these forms, the palatoquadrate is articulated to the braincase solely by means of the basiptyergoid articulation, and the skull is usually considered to be kinetic (Goodrich, 1930; Bock, 1964). In Recent turtles, the basiptyergoid

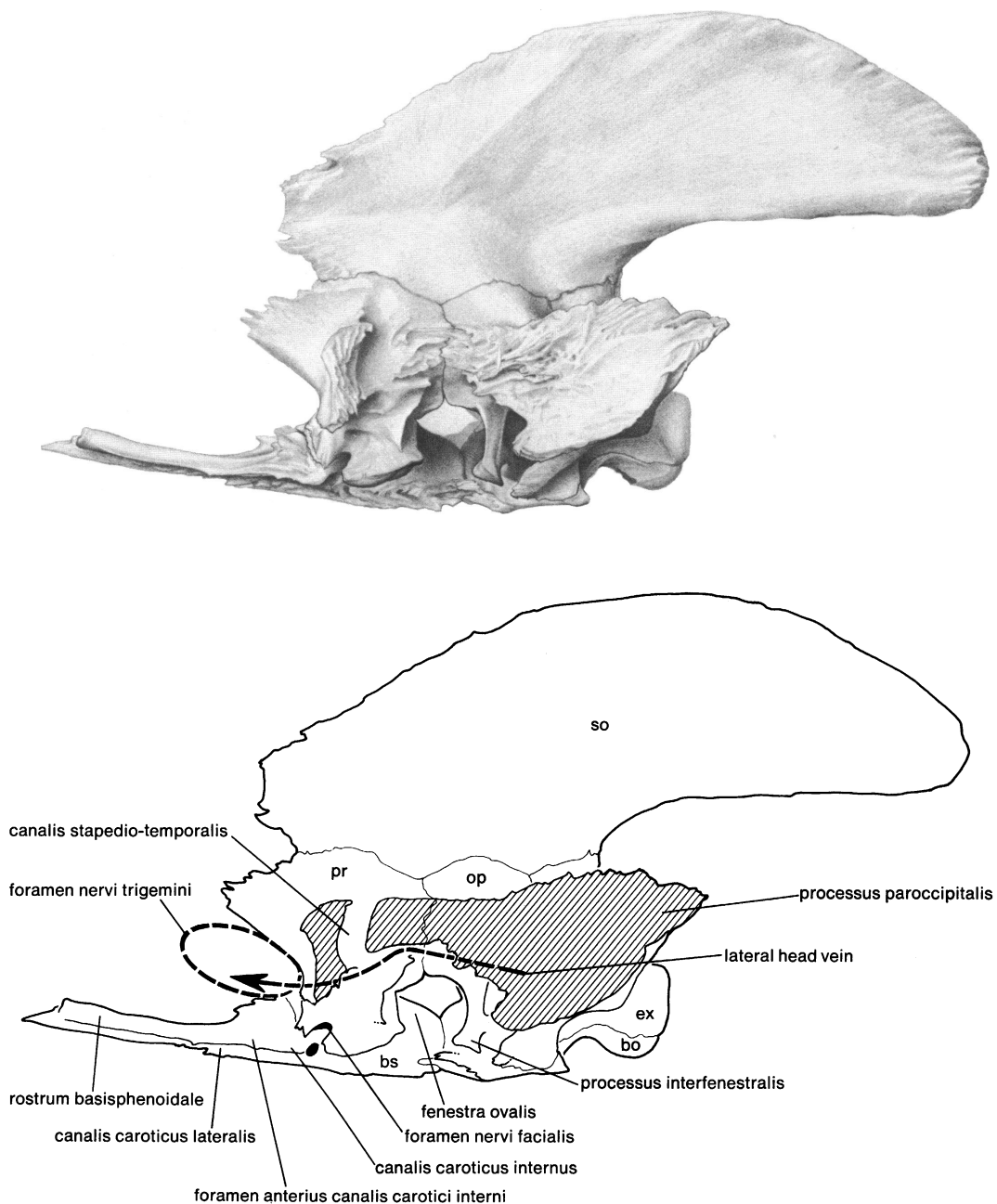


FIG. 4. *Chelydra serpentina*, AMNH (H.) 107387. Lateral view of primary neurocranium in a cryptodire. Hatching indicates sutural contact with palatoquadrate elements above remnants of cranio-quadrate space. Anterior is at left. See figure 5.

articulation is fused and the area of the cranio-quadrate space is nearly obliterated by the broad

sutural contact of the braincase (prootic, opisthotic) and palatoquadrate (quadrate, ptery-

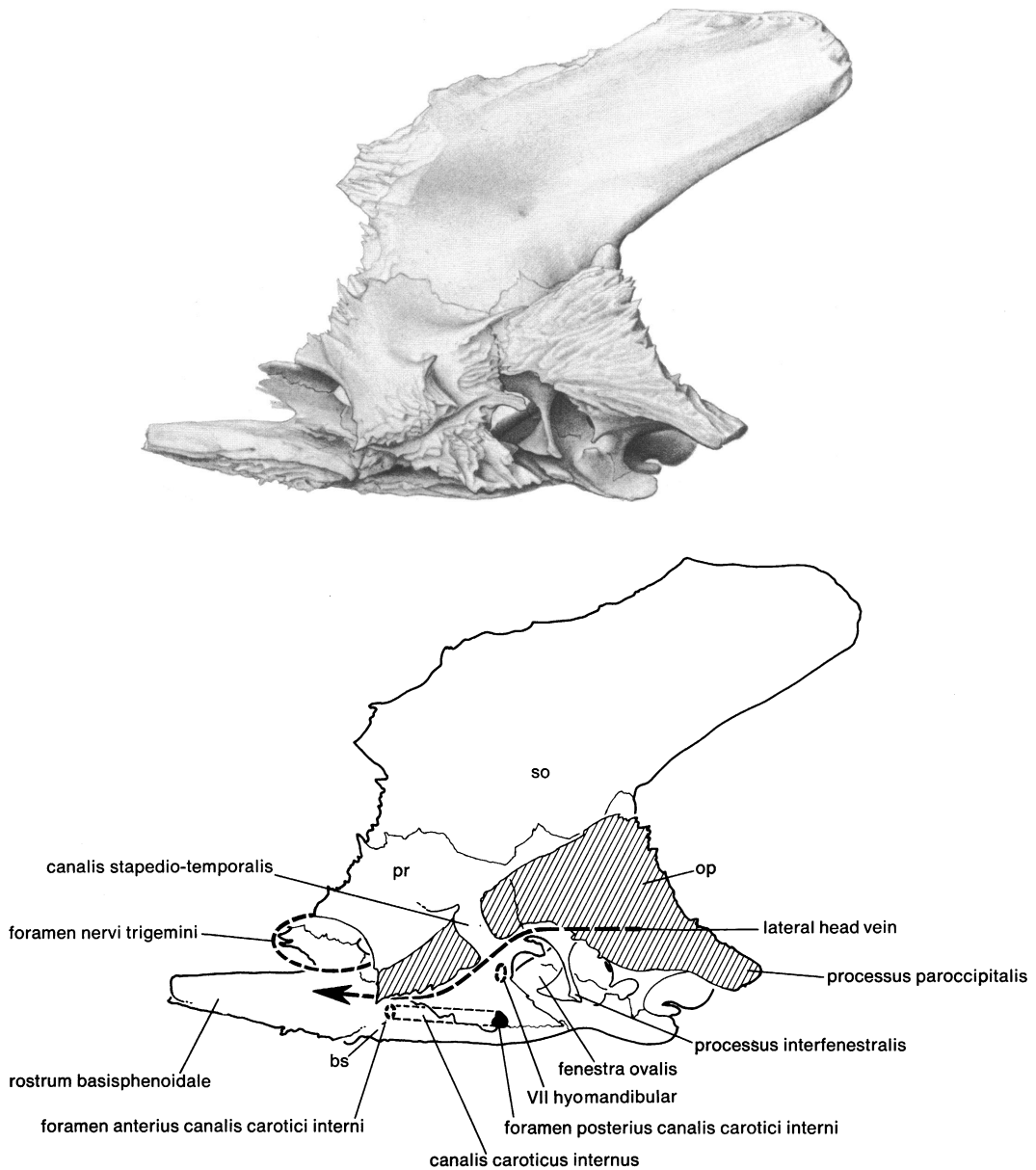


FIG. 5. *Emydura* cf. *australis*, AMNH (H.) 108957. Lateral view of primary neurocranium in a pleurodire. Hatching indicates sutural contact with palatoquadrate elements above remnants of cranio-quadrate space. Anterior is at left. See figure 4.

goid). The akinetic conditions of turtles, then, not only include fusion of the basiptyergoid articulation but also the development of these subsidiary contacts anterior, dorsal, and posterior

to the articulation. It is the nature of these subsidiary contacts that suggests ideas concerning the early history of turtles, because the way in which the fusion has taken place is different in

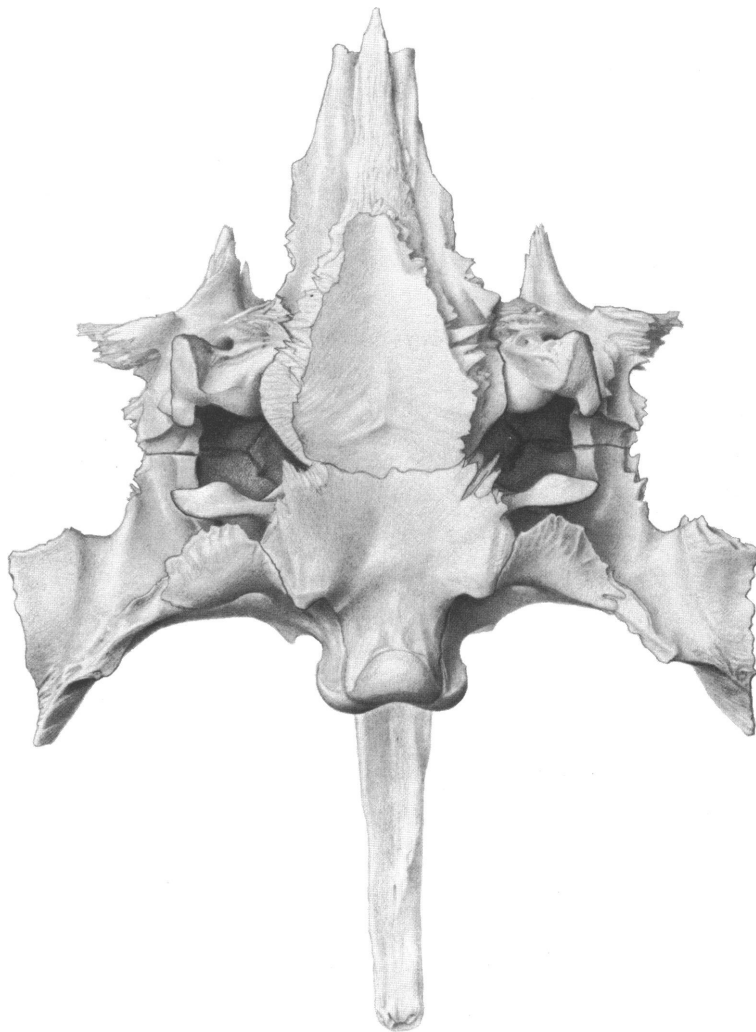


FIG. 6. *Chelydra serpentina*, AMNH (H.) 107387. Ventral view of primary neurocranium in a cryptodire (cf. figs. 8, 9). Anterior is toward top of page.

cryptodires and pleurodires (I am indebted to S. B. McDowell, who first suggested this notion).

I begin an analysis of this region posteriorly, using the processus paroccipitalis of the opisthotic as a reference point. The sutural contact of the processus paroccipitalis to the posterior portion of the quadrate seems to be the same in both cryptodires and pleurodires as there are no consistent morphologic differences in the nature

of the contact. However, anterior and ventral to the stapedia artery (contained in the canalis stapedio-temporalis) there are consistent differences. The most obvious one has already been mentioned above, the quadrate versus pterygoid bracing of the palatoquadrate elements. This difference is also correlated with differences in the structures that run through the remnants of the cranioquadrate space. In all cryptodires the

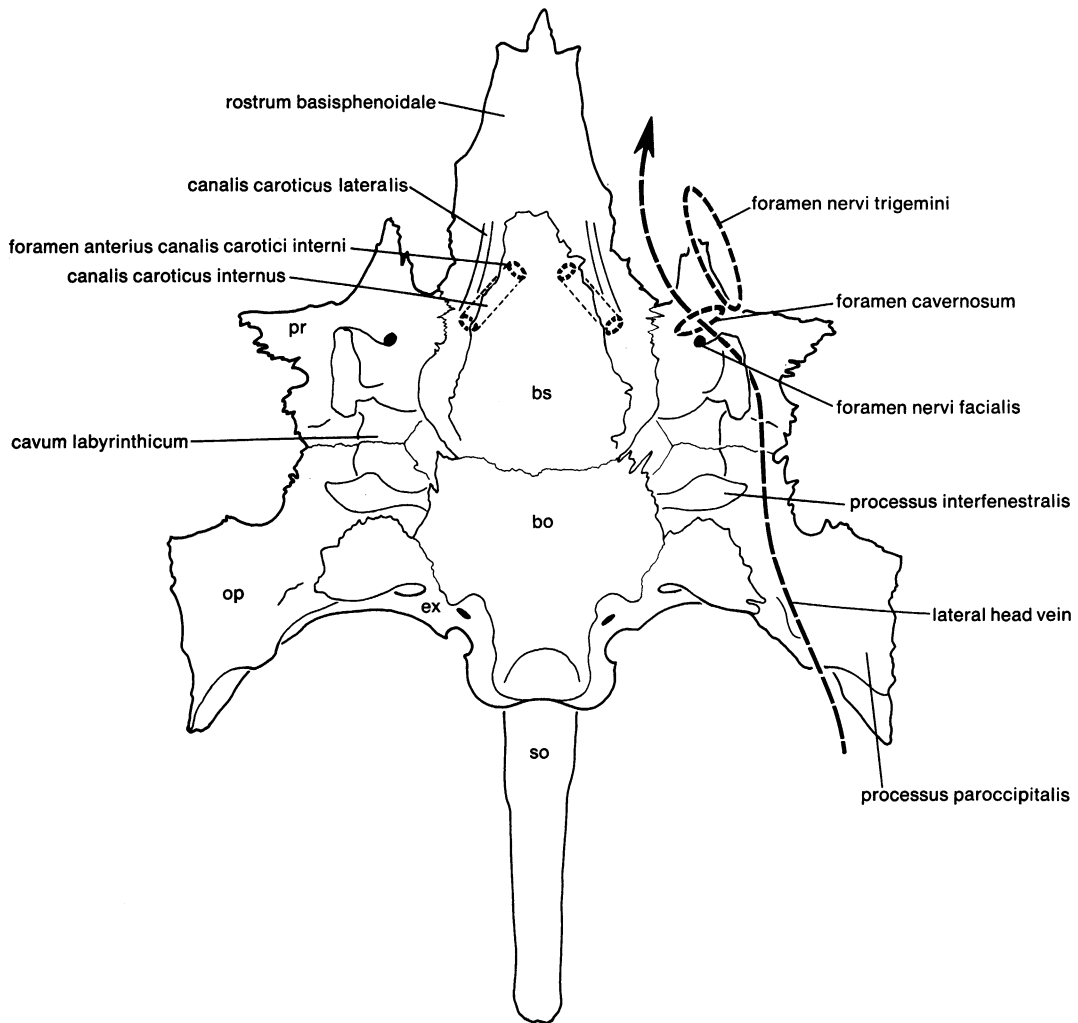


FIG. 7. *Chelydra serpentina*, AMNH (H.) 107387. Key to figure 6.

lateral head vein (vena capitis lateralis) and the hyomandibular branch of the facial (VII) nerve (proximal to the origin of the chorda tympani) run together in the canalis cavernosus, whereas in pleurodires the nerve is more or less separated from the lateral head vein by bone, and therefore, lies outside the canalis cavernosus. The mandibular artery of pleurodires branches from the stapedial artery after the latter leaves the skull via the foramen stapedio-temporale. The mandibular artery of most cryptodires (fig. 14), however, branches off the stapedial artery inside

the skull rather than outside as in pleurodires and usually exits from the foramen nervi trigemini. Although in some cryptodires (the superfamily Trionychoidea of this author) the stapedial artery is reduced or absent and the mandibular artery comes off some other artery inside the skull (usually the palatine or internal carotid) the mandibular artery still exits via the foramen nervi trigemini (in *Caretta* and some *Geochelone* the mandibular artery is partitioned off from the other structures due to subdivision of the foramen nervi trigemini). Most cryptodires,

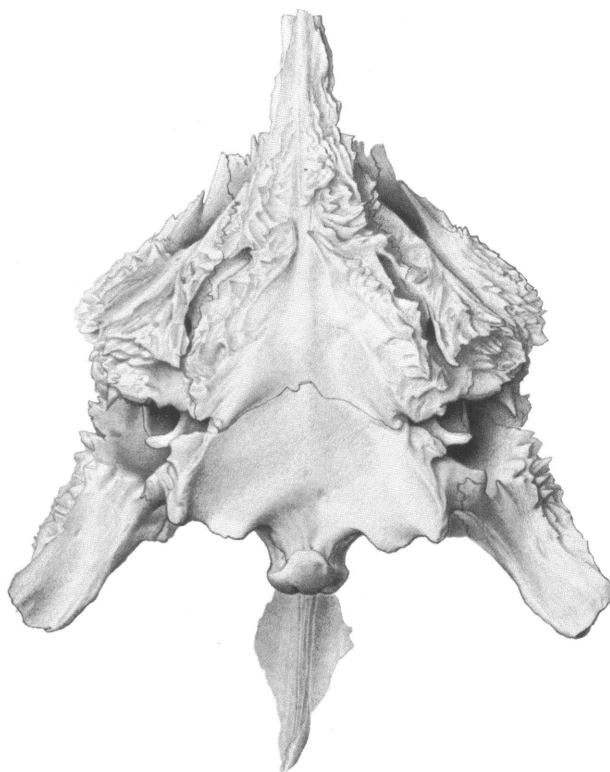


FIG. 8. *Emydura* cf. *australis*, AMNH (H.) 108957. Ventral view of primary neurocranium in a pleurodire (cf. figs. 6, 7). Anterior is toward top of page.

therefore, have the mandibular artery traversing the canalis cavernosus (even in *Caretta* and *Geochelone*), whereas pleurodires do not have the mandibular artery in the canalis cavernosus and it does not exit via the trigeminal foramen.

These differences can be seen in transverse sections through the canalis cavernosus (figs. 10-17). For example, the canalis cavernosus of the cryptodire *Chelydra* contains the hyomandibular nerve, the mandibular artery, and the lateral head vein. The canalis cavernosus in the pleurodire *Podocnemis*, however, contains only the lateral head vein, with the hyomandibular nerve separated by bone and the mandibular artery absent. The sections also show the medial

extension of the quadrate in *Podocnemis*, and the lateral bracing of the pterygoid in *Chelydra*.

Most cryptodires have an epipterygoid bone but all pleurodires lack this element (figs. 2, 3). The pleurodire condition may be the result of the absence or extreme reduction of the cartilaginous precursor of the epipterygoid in that group. *Dermochelys*, a cryptodire lacking an epipterygoid, does have the cartilaginous precursor of that bone but ossification does not take place (DeBeer, 1937, p. 261). Although Fuchs (1932) and Schwartz (1934) illustrated a few cross sections of an embryonic *Podocnemis* head, the embryology of a pleurodire cranium has never been described, therefore meaningful com-

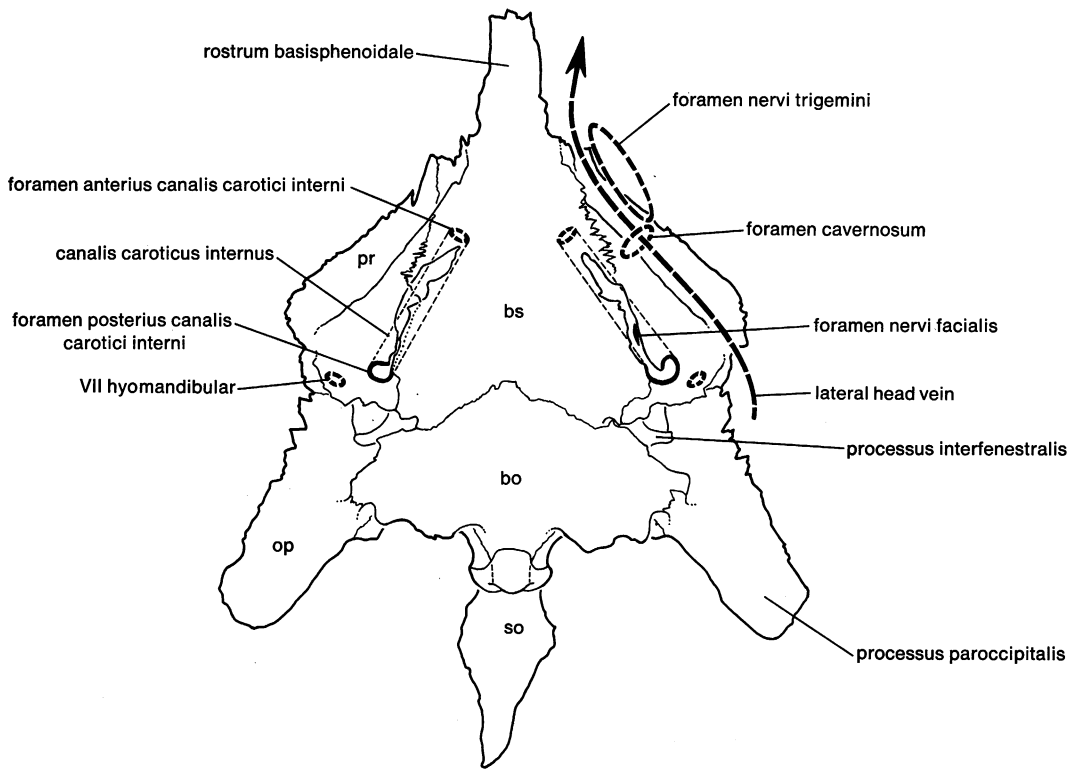


FIG. 9. *Emydura cf. australis*, AMNH (H.) 108957. Key to figure 8.

parisons cannot be made at the present time. Nonetheless, the absence of an epipterygoid in pleurodires does heighten the distinction between the palatoquadrate elements of pleurodires and cryptodires. As is the case with the jaw mechanism, it seems likely that the cryptodire and pleurodire palatoquadrate conditions are both derived with respect to each other and that one did not give rise to the other.

Other cranial features. The position of the foramen palatinum posterius (fig. 23) and its relations to the vidian canal differ in cryptodires and pleurodires. Cryptodires have the foramen palatinum posterius ventral or lateral to the orbit (except in cheloniids in which it is absent), whereas in pleurodires it is behind the orbit. The anterior exit of the vidian canal lies in or close to the foramen palatinum posterius in cryptodires; pleurodires either lack the canal (cheliids) or the exit lies on the ventral surface of the pterygoid.

Although the foramen palatinum posterius of turtles appears to be homologous to the palatine fenestra of other reptiles (Romer, 1956, p. 71), I have no idea which condition is primitive for turtles.

The foramen supramaxillare (Albrecht, 1967; Gaffney, 1972b) is present in most cryptodires but not in pleurodires (Albrecht, personal commun.). This foramen conducts an artery into the nutrient canals of the maxilla. The significance of its absence in pleurodires is not known, and it does not appear to be correlated with the palatoquadrate elements. As this structure does not seem to occur in other reptiles, its presence (or absence) in turtles may be primitive or derived.

In most cryptodires (some trionychids are an exception) the prefrontals possess ventromedial processes (commonly called descending processes) that form an anterior wall for the orbit, a

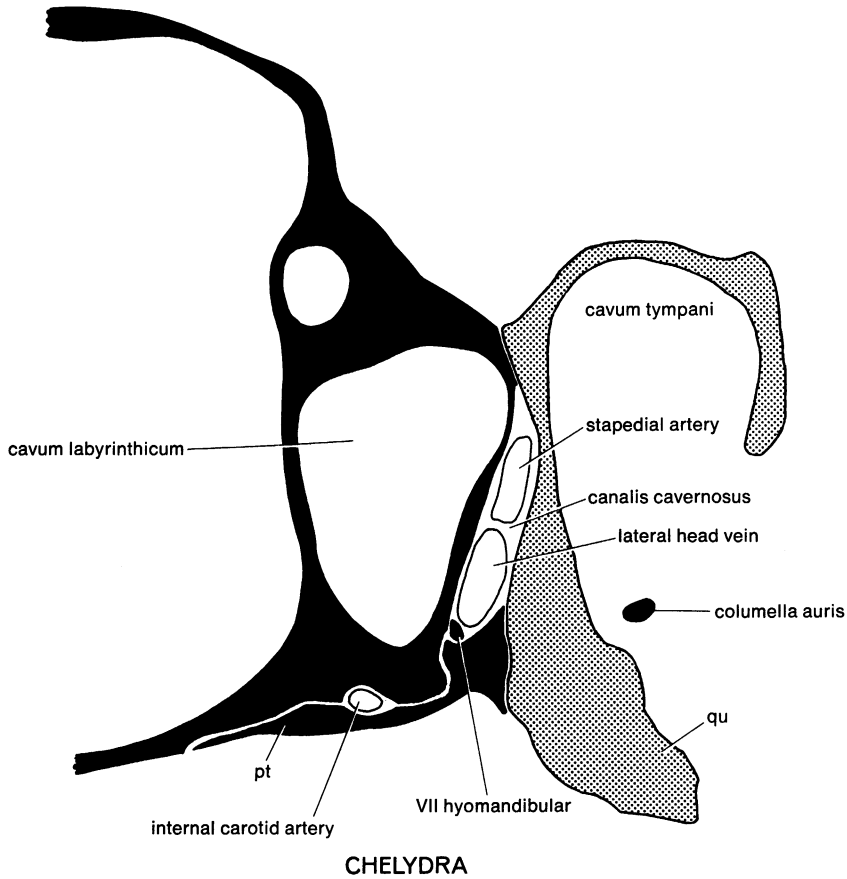


FIG. 10. *Chelydra serpentina*, UT Chely 68. Transverse section through ear region of a cryptodire. Quadrate stippled. Skull midline on left. See figure 11.

posterior wall for the fossa nasalis, and an articulation with the vomer. Pleurodires lack the descending processes and have a fossa nasalis that is largely or entirely open posteriorly. As with the preceding character, I do not know its primitive or derived condition.

HISTORICAL REVIEW OF THE AMPHICHELYDIAN CONCEPT

One of the more obvious novelties of the classification proposed here is the absence of the Amphichelydia, a prominent higher category of most turtle classifications. It seems appropriate to include at this point a brief historical review of this taxon.

In 1884, Dollo (p. 75) suggested that some of the Jurassic turtles belong to a group, the "Thalassemydes," which, he argued, was the common ancestor of all living turtles. He thought that these forms were neither cryptodires nor pleurodires but morphologically intermediate. A few years later, in 1889, Lydekker erected the "Amphichelydia" on a similar basis. In both cases the specimens involved were Jurassic and had plastra with paired indentations, supposedly sutures for the pubis, on the dorsal surface of the xiphiplastra. These indentations were supposed to represent an intermediate stage between the cryptodire condition with a free pelvis and the pleurodire condition with both pubis and ischium sutured to the xiphiplastron. In fact, the

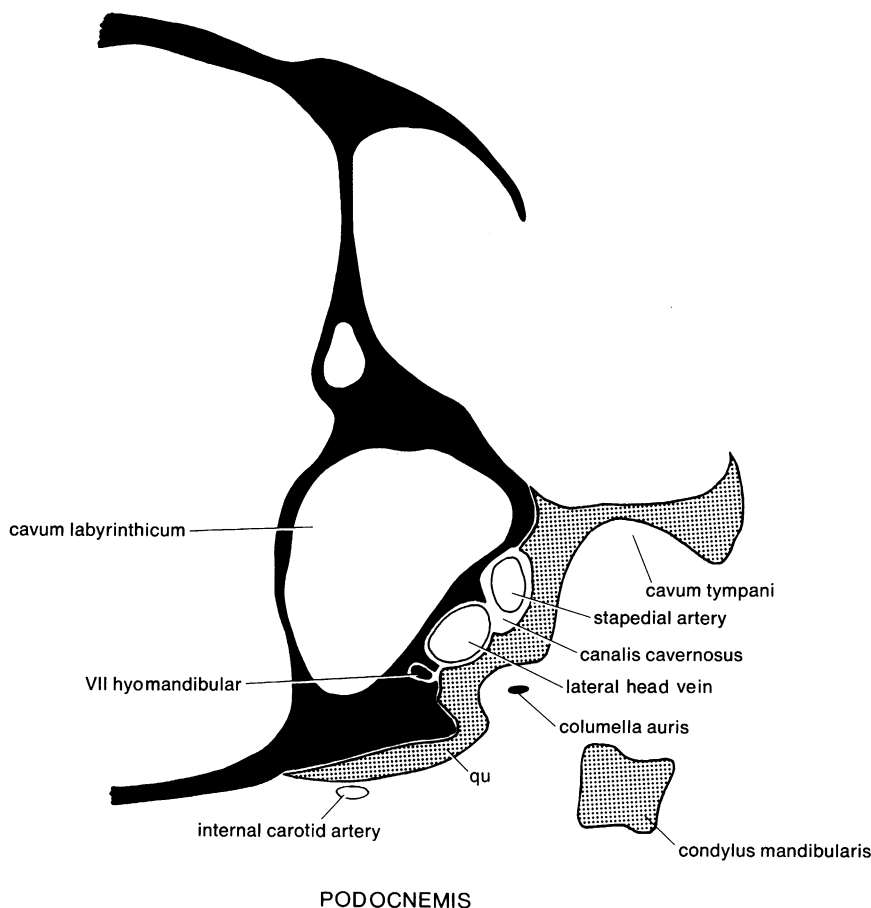


FIG. 11. *Podocnemis expansa*, UT POD III 211. Transverse section through ear region of a pleurodire. Quadrate stippled. Skull midline on left. See figure 10.

indentations occur in most baenoids and appear to represent facets for a movable articulation with the pelvis. Other evidence advanced by Lydekker in support of the Amphichelydia was the presence of mesoplastra and intergular scutes. These elements are lost in many later turtles and appear to represent a primitive condition.

Baur (1891) described the first amphichelydian specimen with an associated skull, *Glyptops* (*Compsemys*) *plicatulus* (YPM 1357) from the Late Jurassic of Wyoming. He supported the Amphichelydia as common ancestors of cryptodires and pleurodires and concluded as follows: "The skull as a whole shows characters which we would expect to find in the ancestors

of Cryptodira and Pleurodira. The quadrate resembles mostly that of the Pinnata [the living sea turtles], the whole arrangement of palate, pterygoid, basisphenoid is that of Cryptodira, the presence of the epipterygoid is also a character of the Cryptodira and so is the union of the descending processes of the prefrontal with the vomer. But the free nasals, the suturally united dentary bones, and the absence of the production of the petrosal are characteristic of the Pleurodira" (1891, p. 414). Baur also compared the vertebrae of *Glyptops* with living turtles and concluded that the cervicals of *Glyptops* were closer to those of pleurodires than to cervicals of cryptodires.

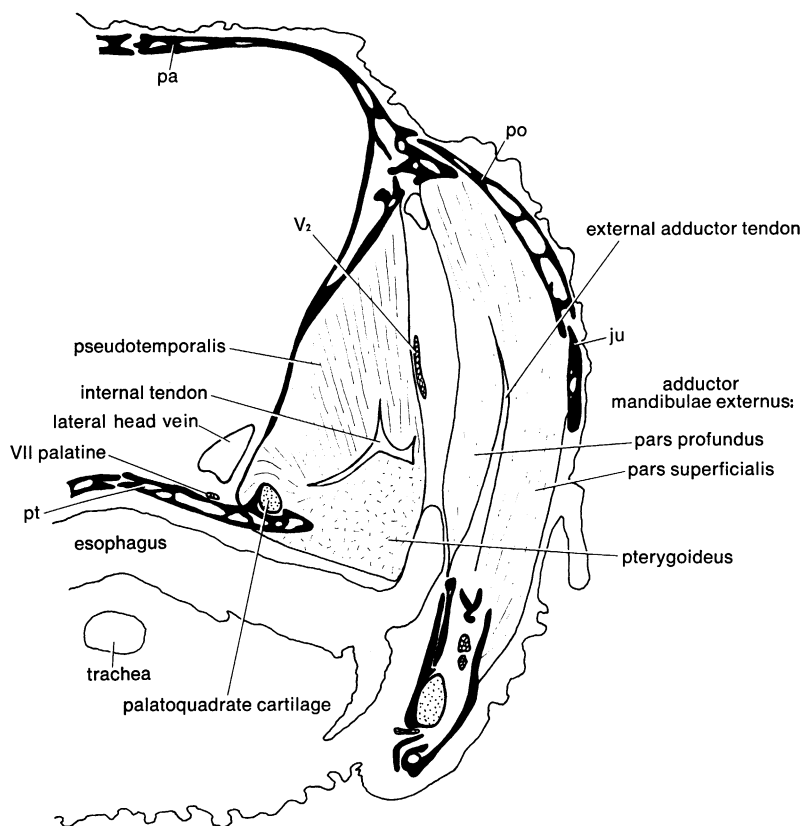


FIG. 12. *Chelydra serpentina*, UT Chely 49. Transverse section through anterior part of fossa temporalis in a cryptodire. This section is in about the same morphologic position as that in figure 13. Skull midline on left.

Hay (1905) presented an extensive discussion of the Amphichelydia and the phylogeny of turtles. In this work, he utilized all aspects of the morphology but stressed the shell. He criticized Baur's description of *Glyptops*, in particular pointing out that *Glyptops* has no real pleurodiran characters (nasals are found in toxochelyid cryptodires but not in pelomedusid pleurodires, the dentaries of *Glyptops* are fused, and some cryptodires have a processus trochlearis oticum as poorly developed as in *Glyptops*). Furthermore, Hay (1905, p. 139) described some new skull material of Amphichelydia that had been discovered recently: "An examination of the skulls of *Compsemys* (= *Glyptops*) and *Baena* (= *Chisternon* and *Eubaena* of Gaffney, 1972a)

shows, it seems to the writer, that where the characters are not primitive they are wholly, or almost wholly, cryptodiran." Although Hay did not diagnose the Amphichelydia in 1905, he did so later (1908, pp. 43-44) when he said: "Thecophorous turtles having a carapace composed of neural, costal, and peripheral bones and a plastron in which the epiplastra are in contact with the hyoplastra. Mesoplastra usually, perhaps always, present. Intergular and inframarginal scutes probably always developed. Skull essentially cryptodiran in structure, but with various primitive elements. Neck short, the vertebrae little differentiated. Limbs, so far as known, fitted for walking."

Hay's characterization relies entirely on the

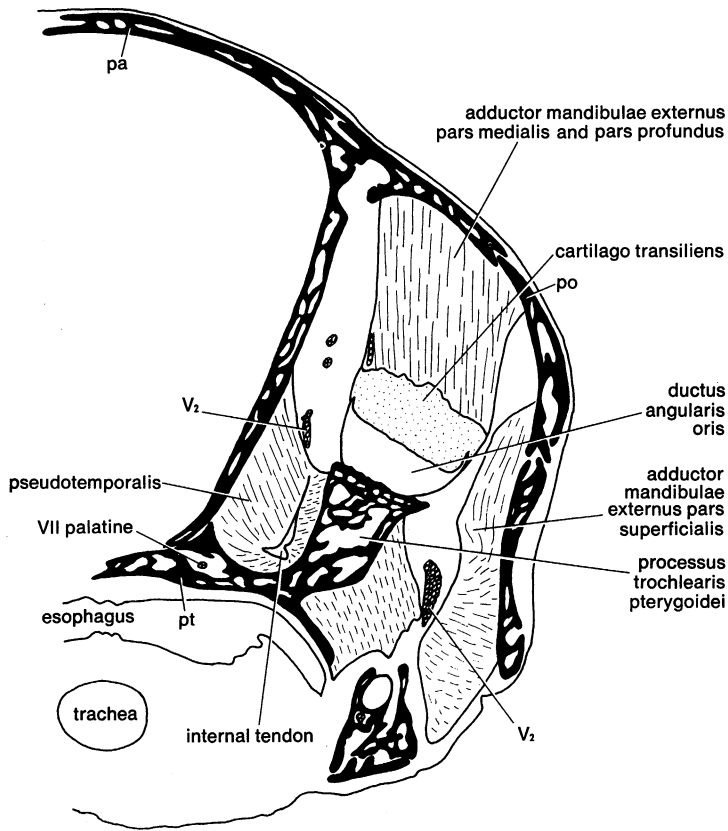


FIG. 13. *Podocnemis expansa*, UT POD III 149. Transverse section through anterior part of fossa temporalis in a pleurodire. This section is in about the same morphologic position as that in figure 12. Skull midline on left.

postcranial elements, primarily on the presence of mesoplastra and an intergular scute in the shell, and the absence of cervical vertebrae specializations. At the time, many Jurassic turtles were being placed rather arbitrarily in either the Cryptodira or the Pleurodira. Apparently, Hay used the Amphichelydia as a taxonomically "practical" solution to the problem of determining the phylogeny of many forms that were too far removed from living groups to be identified adequately. The evidence of the skull morphology was ignored in favor of the postcranial evidence, but, at the time, the systematics of turtles was based almost entirely on the postcranial morphology.

In 1938 (pp. 251-252) Simpson summarized this concept of the Amphichelydia in a description of the meiolaniid *Crossochelys* (Eocene, Patagonia): "The Suborder Amphichelydia, to which the Pleurosternidae, Baenidae, and some other ancient forms are now generally referred, is an essentially horizontal division for a divergent group of early phyla, mostly Mesozoic, which are distinguished from later forms and united with each other by primitive characters. A strictly phyletic classification, were such possible, would reject this suborder as generally defined, but, as so often happens in practical taxonomy, it is now most convenient if not necessary to recognize it."

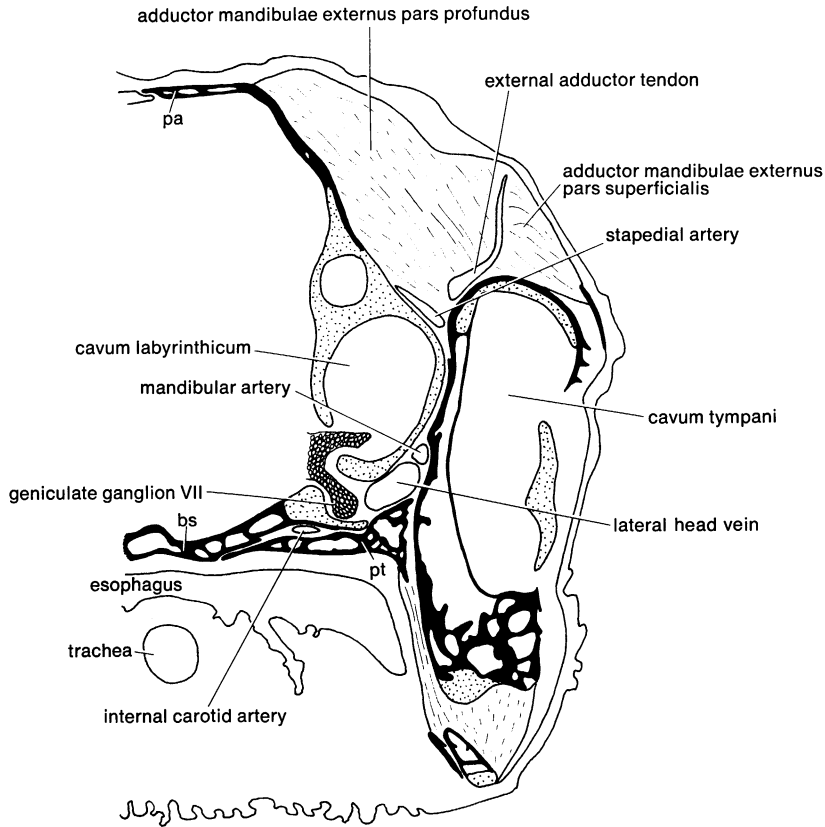


FIG. 14. *Chelydra serpentina*, UT Chely 65. Transverse section through fossa acustico-facialis in a cryptodire. This section is in about the same morphologic position as that in figure 15. Skull midline on left.

Romer (1956, pp. 497-498) also recognized the horizontal nature of the Amphichelydia but he emphasized the supposed intermediate position of the group, that is, as common ancestors of the Cryptodira and Pleurodira: "A third major group, the Amphichelydia, is essentially a Mesozoic one, comprising primitive forms ancestral to both the living suborders. . . . This suborder was erected to contain the older and more primitive turtles, almost entirely Mesozoic in age, which lack the distinctive features of either cryptodires or pleurodires. Certain of them are transitional in structure to these advanced groups, and the group boundaries have varied from author to author. They are here arranged, in superfamilies, in three successive stages: the proganochelyoids,

very primitive Triassic types; the pleurosternoids, typical amphichelydians; and baenoids, advanced forms."

Parsons and Williams (1961) presented a detailed morphologic study of two Jurassic amphichelydian skulls with a review of the origin of turtles based on an examination of the Triassic specimens from Germany. They concluded that the Jurassic skulls were "modern" in the sense that they give no indication of the early stages of the evolution of the turtle skull from nonchelonian ancestors. Their re-examination of the Triassic turtle, *Proganochelys*, demonstrated that this form was much more primitive than any other known turtle and suggested that it be separated from all other turtles (*ibid.*, p. 92).

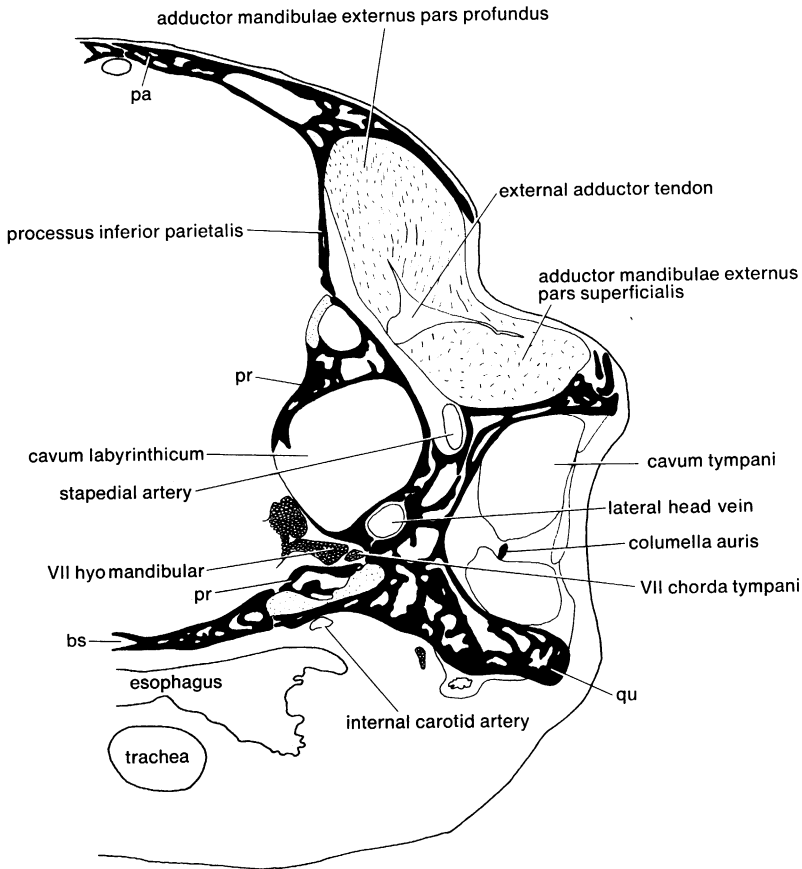


FIG. 15. *Podocnemis expansa*, UT POD III 201. Transverse section through fossa acustico-facialis in a pleurodire. This section is in about the same morphologic position as that in figure 14. Skull midline on left.

This suggestion was followed by Romer (1966, p. 365) to the extent that he elevated the Triassic animals to the subordinal level and recognized the Suborders Proganochelydia, Amphichelydia, Cryptodira, and Pleurodira. In Romer's classification the Triassic turtles are excluded from the Amphichelydia but in another recent classification (Zangerl, 1969) the Amphichelydia consists primarily of the Triassic forms. In fact, there is only one genus common to the Amphichelydia of Romer and Zangerl. Although a consensus hardly exists, it would seem that most authors have used the Amphichelydia as a paraphyletic taxon at best, characterized by variable mor-

phologic criteria usually thought to represent primitive character states.

THE BAENOIDEA COMPARED WITH CRYPTODIRA AND PLEURODIRA

Skull Characters. Table 3 summarizes the criteria most useful in differentiating living cryptodires and pleurodires. Each of these are discussed in relation to baenoids.

1. One of the main osteologic indications of the type of jaw mechanism in a turtle is the position of the trochlea for the sliding cartilage (cartilago transiliens) in the Bodenaponeurosis

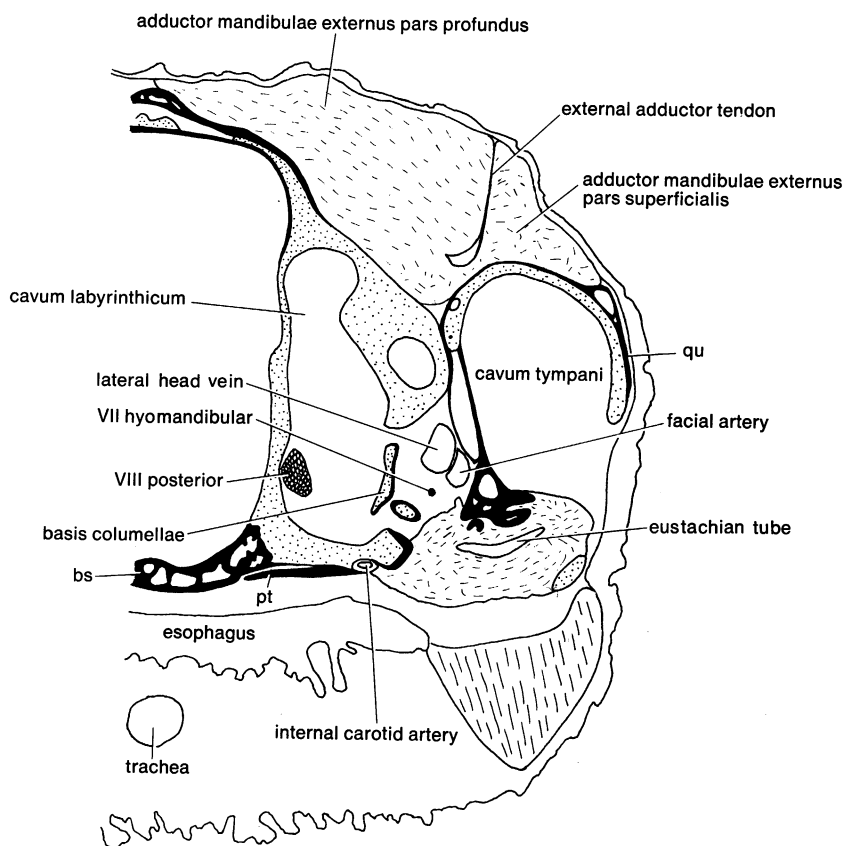


FIG. 16. *Chelydra serpentina*, UT Chely 76. Transverse section through base of columella auris and fenestra ovalis in a cryptodire. This section is in about the same morphologic position as that in figure 17. Skull midline on left.

(main adductor tendon). In baenoids this trochlea is invariably in the same position as it is in cryptodires (fig. 23). There is no indication of a lateral process on the pterygoid for a trochlea as in pleurodires, and no structure is present that could be considered intermediate to the pleurodiran condition. It can be concluded with a high degree of probability that the jaw mechanism of living cryptodires and baenoids is identical.

2. In discussing the differences between cryptodires and pleurodires the structure of the palatoquadrate elements was stressed because this area contains significant shared derived characters. The structure of the pterygoid is particularly sensitive to these differences as it is

involved in flooring the remnants of the cranioquadrate space (figs. 20-22). Furthermore, one of the more prominent features of the cryptodiran akinetic condition involves the bracing of the quadrate to the braincase by means of the pterygoid. A posterior expansion of the pterygoid forms this brace in both Recent cryptodires and baenoids.

3. Another feature related to the palatoquadrate differences in cryptodires and pleurodires is the position of the hyomandibular branch of the facial nerve (VII). Baenoids lack a separate canal for the passage of this nerve as is found in pleurodires. There is complete agreement between cryptodires and baenoids in this feature

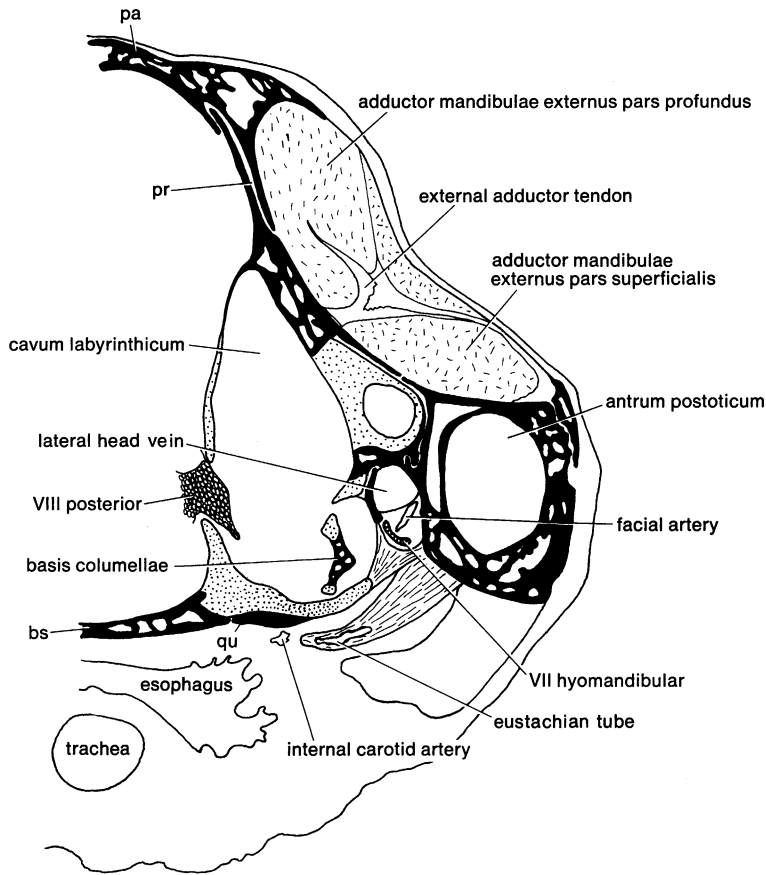


FIG. 17. *Podocnemis expansa*, UT POD III 227. Transverse section through base of columella auris and fenestra ovalis in a pleurodire. This section is in about the same morphologic position as that in figure 16. Skull midline on left.

with no indication of a tendency toward the pleurodire condition in baenoids.

4. The position of the mandibular artery is not determinable in the fossil material.

5. The living cryptodires (with the exception of *Dermochelys*) have an ossified epipterygoid that is usually well developed but is sometimes reduced. Pleurodires all lack epipterygoids. In addition, cryptodires characteristically have a persistent part of the pterygoid cartilage that occupies a small fossa cartilaginis epipterygoidei at the posterior end of the epipterygoid (see Gaffney, 1972b). Pleurodires also lack this structure. *Glyptops* seems to have a free epi-

pterygoid (this is not completely certain, however) but in the Baenidae no sutures are visible. The fossa cartilaginis epipterygoidei is always present in the Baenidae, however, and this suggests that the epipterygoid is either reduced and unossified in the adult (as in *Dermochelys*) or that it has become fused to the parietal. In any case, the condition seems to be very similar to that of other Cryptodira, since in the Pleurodira the cartilage is reduced and apparently does not persist to maturity.

6. Baenoids and testudinoids have very similar articular surfaces, the area articularis mandibularis of chelydrids and baenoids being partic-

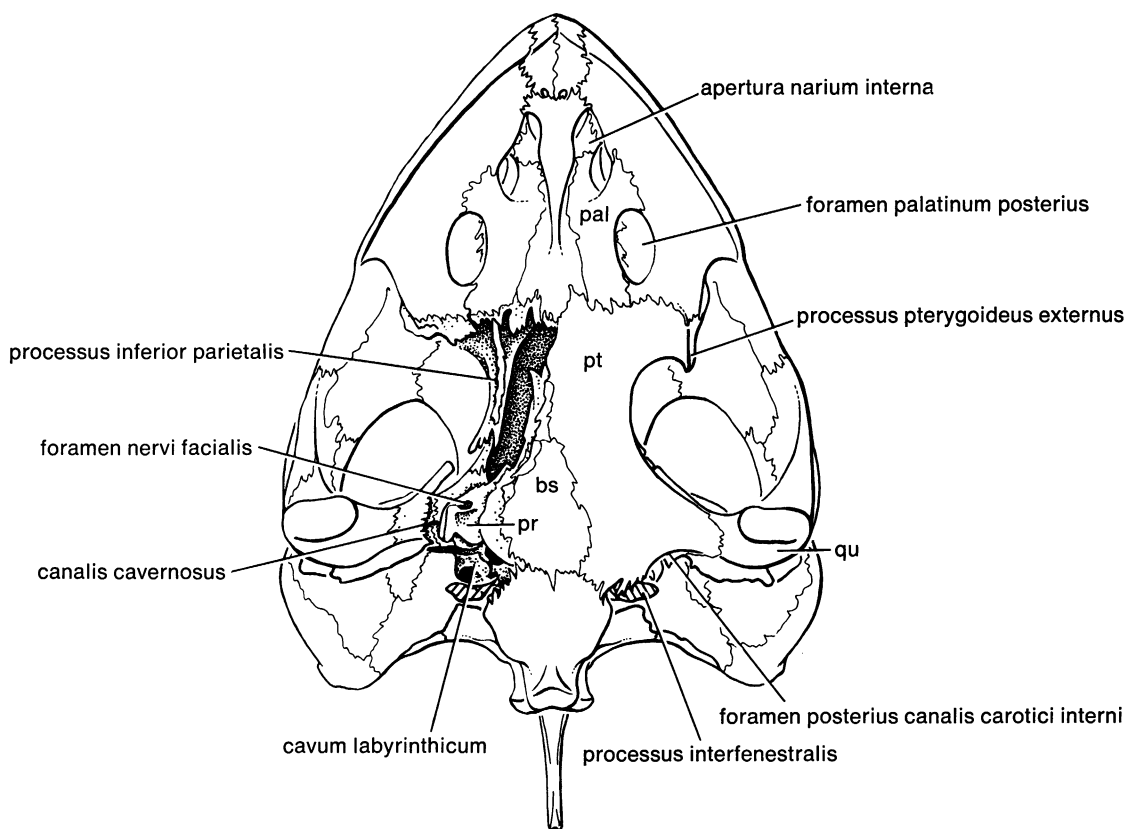


FIG. 18. *Chelydra serpentina*, AMNH (H.) 110446. Ventral view of a cryptodire with right pterygoid removed; stippling shows sutural areas and structures covered by pterygoid. Processus interfenestralis of opisthotic indicated by diagonal lines for a landmark. See figure 19.

ularly similar. Baenoids are not known to have any features in this area that could be considered intermediate between cryptodires and pleurodires.

7. The foramen palatinum posterius, which transmits the inframaxillary artery from the interior of the skull to the ventral surface of the palate, is situated behind the orbit in pleurodires, apparently in conjunction with the development of a bony wall behind the orbit. Baenoids have the foramen palatinum posterius ventral or lateral to the orbit, the same position as it is in cryptodires (with the exception of cheloniids in which the foramen is absent). There is no indication in baenoids of a condition intermediate between cryptodires and pleurodires.

8. The anterior exit of the vidian canal in

baenoids and cryptodires is in or near the posterior wall of the foramen palatinum posterius. In pleurodires the canal does not exit into the foramen (the canal is absent in cheliids and exits on the ventral surface of the pterygoid in pelomedusids).

9. The foramen supramaxillare of baenoids is in the same morphological position as the foramen supramaxillare of cryptodires. Pleurodires lack the foramen, therefore, baenoids agree with cryptodires in this feature.

10. Baenoids possess a prefrontal with a small dorsal plate and only the ventral process remains. Pleurodires lack the ventral process and have a dorsal plate (which may also be small in cheliids). The ventral process of most cryptodires is identical to the ventral process in baenoids. However,

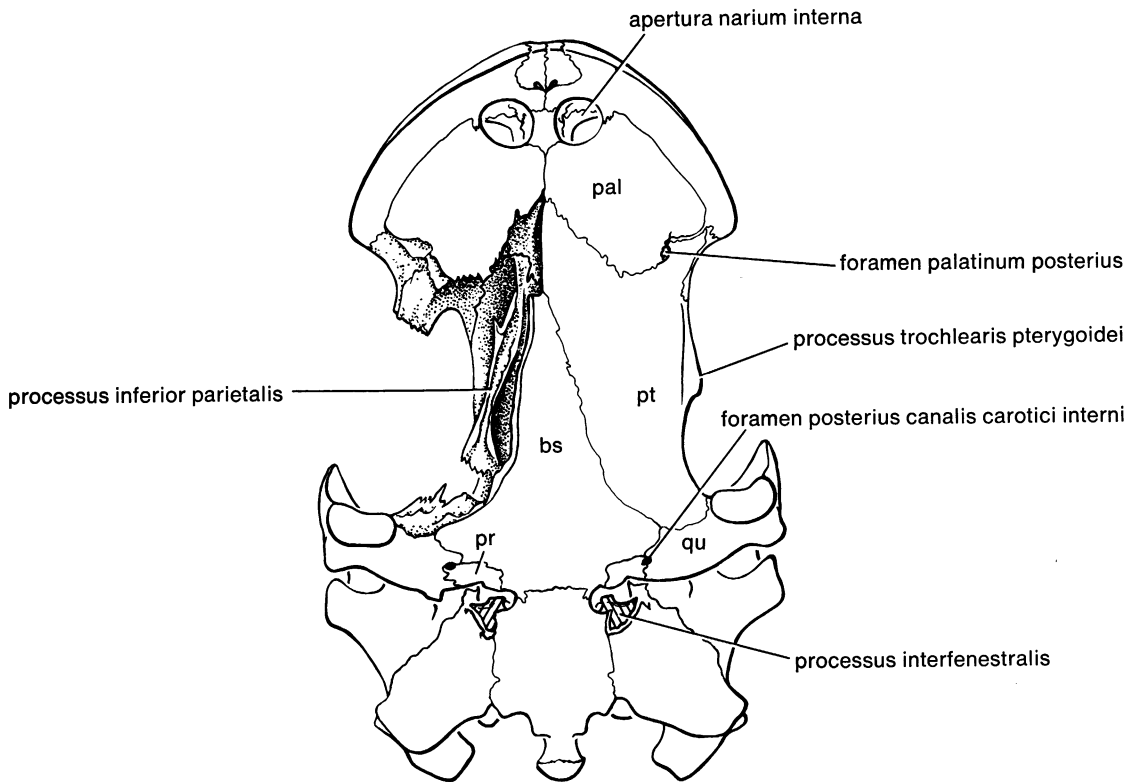


FIG. 19. *Chelodina* sp., AMNH (H.) 108954. Ventral view of a pleurodire with right pterygoid removed; stippling shows sutural areas and structures covered by pterygoid. Processus interfenestralis of opisthotic indicated by diagonal lines for a landmark. See figure 18.

some trionychids have lost the ventral process so the agreement is not total, so far as cryptodires are concerned. Nonetheless, baenoids could not be considered intermediate or even tending toward pleurodires in this feature.

Postcranial Characters. The cervical retraction mechanism in living turtles has been the most widely accepted and utilized character complex for the differentiation of higher categories of chelonians. The absence of a well-developed retraction device in Mesozoic forms has been one of the primary reasons for the recognition of the Amphichelydia. Baenoids lack the cervical specializations of either living cryptodires or pleurodires. Older baenoids (*Glyptops*, Hay, 1908; *Trinitichelys*, Gaffney, 1972a) have amphicoelous cervical vertebrae but later forms have formed articulations (Hay, 1908; Wiman, 1933;

Russell, "1934" [1935]; Case, 1939; Gaffney, 1972a). A careful comparative study of baenoid and other fossil turtle neck vertebrae has yet to be published but at the present time it seems most likely that the baenoid conditions represent primitive states in comparison with the Eucryptodira.

All known pleurodires have the pelvis sutured to the shell, whereas no cryptodire has this condition. Baenoids characteristically have a small facet for the pubis on the xiphiplastron and this condition has been cited as an intermediate feature between cryptodires and pleurodires (Lydekker, 1889, pp. 517-518). However, this does not appear to be even similar to the pelvis-plastron relationship in pleurodires. The baenoid pubis lacks the ventral expansion seen in pleurodires, and it seems to have had only a ligamen-

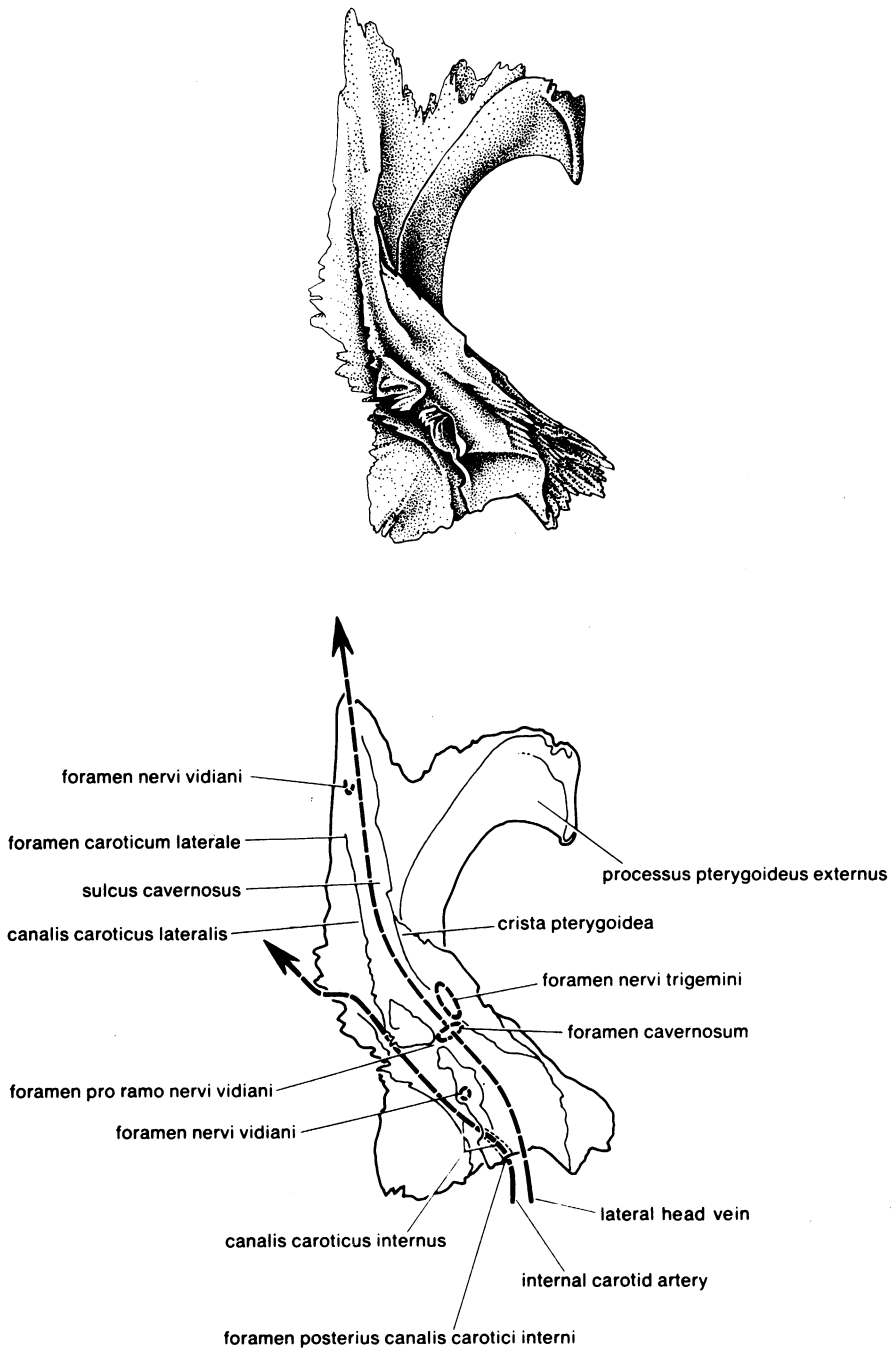


FIG. 20. *Chelydra serpentina*, AMNH (H.) 107388. Dorsal view of right pterygoid in a eucryptodire. See figures 21, 22.

tous attachment with no sutural contact between the pelvis and the plastron. The whole structure is nearly the same as in a living cryptodire, the

only difference being the possibly movable articulation between the pubis and the plastron.

Pleurodires usually have an intergular scute

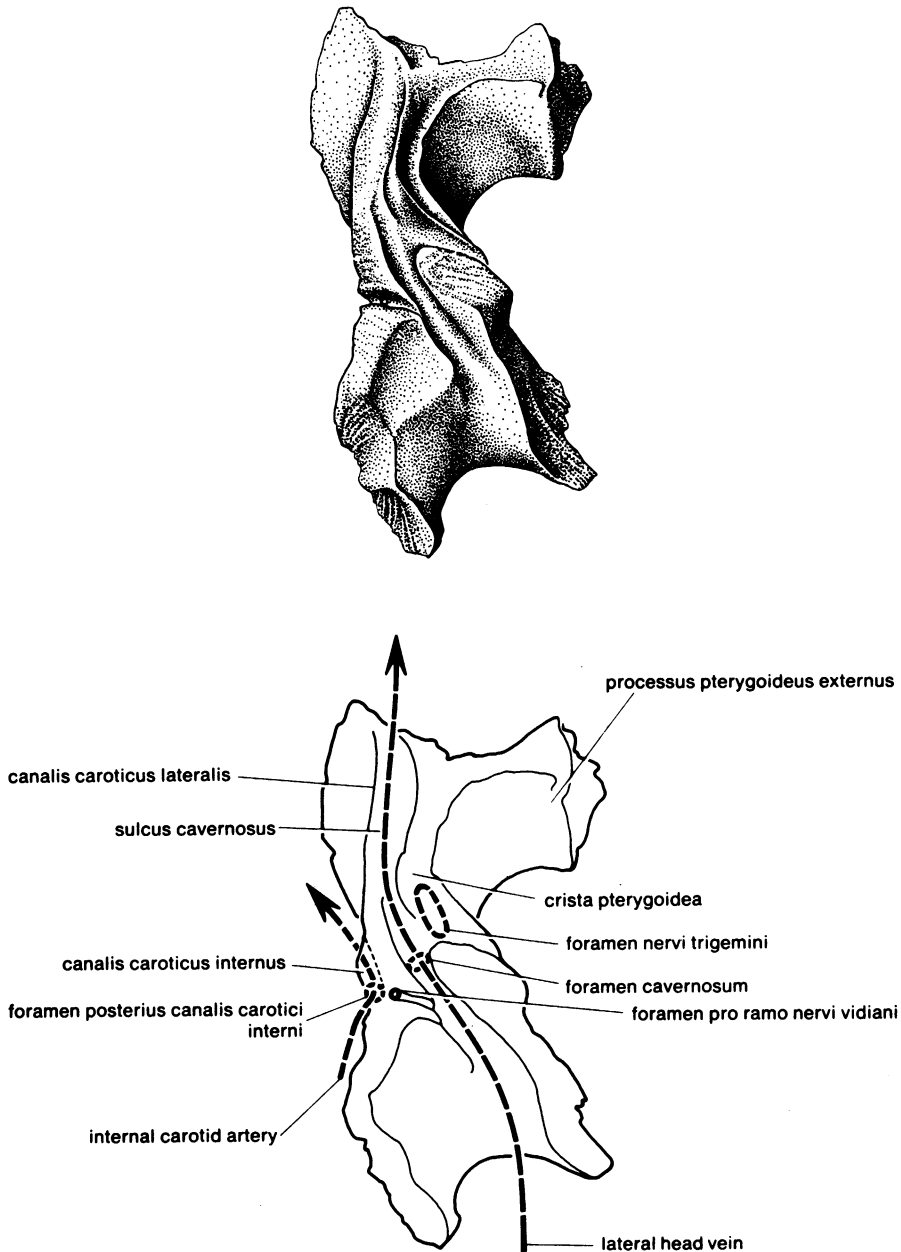


FIG. 21. Family Baenidae, genus indeterminate, Late Cretaceous, MCZ 3563 with added information from MCZ 3566. Dorsal view of right pterygoid in a paracryptodire. See figures 20, 22.

between the paired gular scutes on the plastron, whereas many cryptodires do not. Baenoids usually have paired intergular scutes, but this area is highly variable in individual shells as well as between different taxa. The presence in bae-

noids and in pleurodires (as well as in cheloniid cryptodires) of an intergular scute probably represents the retention of a primitive character and does not demonstrate a special relationship between them.

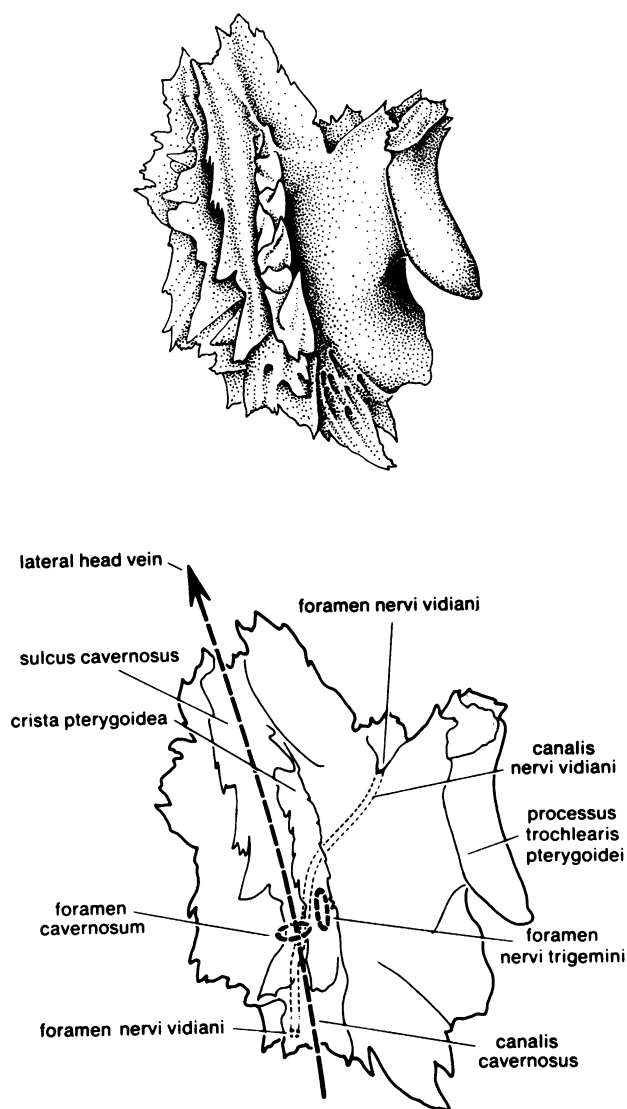


FIG. 22. *Pelomedusa subrufa*, AMNH (H.) 63581. Dorsal view of right pterygoid in a pleurodire. See figures 20, 21.

Baenoids and pelomedusid pleurodires possess paired mesoplastral bones in the plastron, but no living cryptodire has these bones. However, it seems likely that these elements are primitive features of turtles and are not useful as shared derived characters in this context.

In summary, I conclude from the above distri-

bution of derived characters that baenoids have an ancestor in common with the Recent cryptodires (Eucryptodira) that they do not share with other turtles. The following section deals with relationships among the forms here recognized as cryptodires.

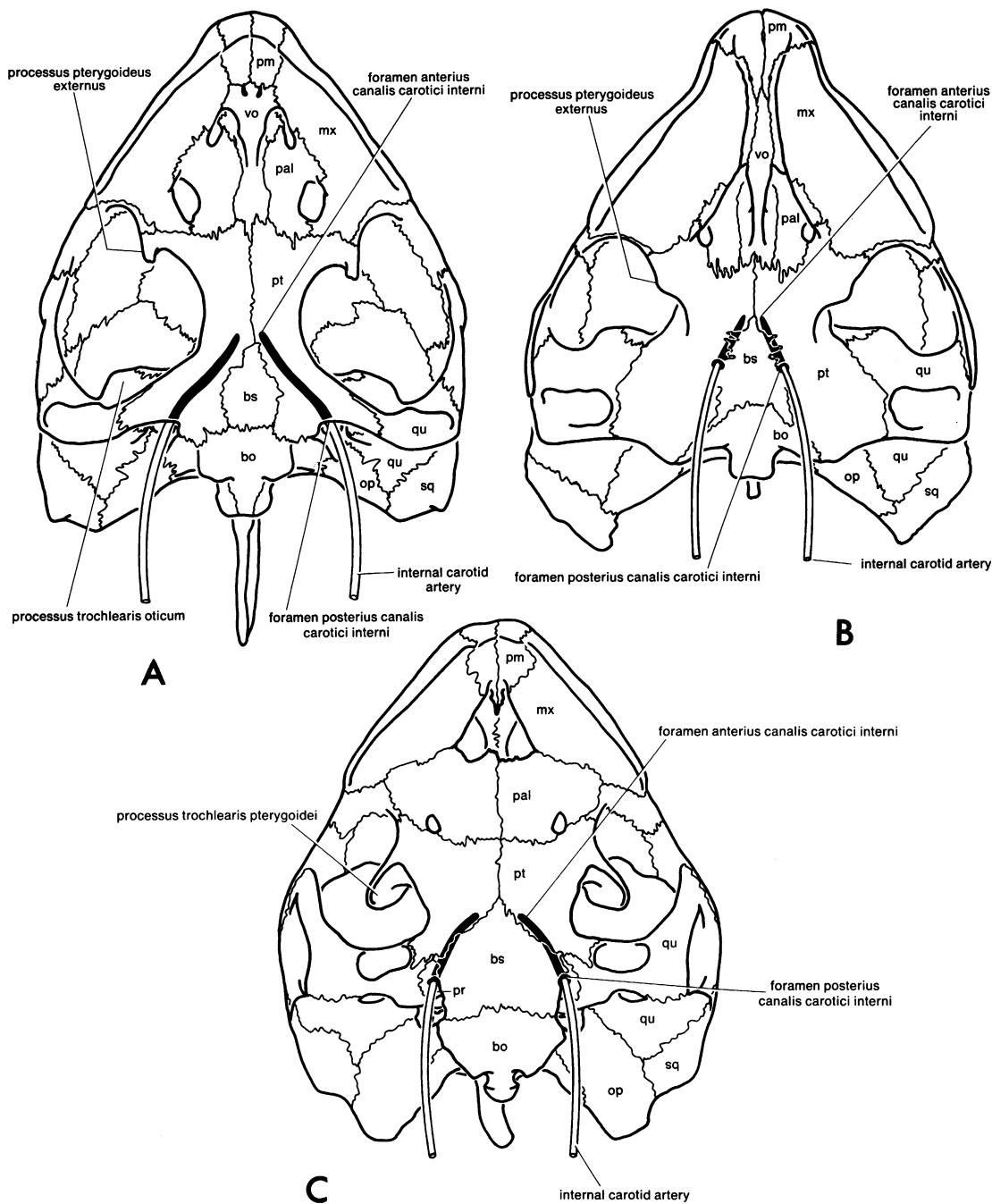


FIG. 23. Comparison of canalis caroticus internus (in black) in three major groups of turtles: A, Eucryptodira (*Chelydra serpentina*); B, Paracryptodira (*Eubaena cephalica*); C, Pleurodira (*Pelusios* sp.). The diameter of the canal is exaggerated for clarity.

THE PARACRYPTODIRA AND EUCRYPTODIRA

When baenoids are compared with other fossil and Recent cryptodires (table 4) certain consistent characters emerge suggesting that most nonbaenoid cryptodires are a monophyletic group. The posterior flange on the pterygoid, characteristic of cryptodires, is intimately involved with the path of the internal carotid artery. The position of the foramen posterior canalis carotici interni is about midway along the length of the pterygoid-basisphenoid suture in baenoids, whereas in the other cryptodires the foramen lies at or near the posterior margin of the pterygoid (fig. 23). Both arterial conditions are here considered to be derived with respect to the Cryptodira as a whole but the primitive condition, as I interpret it, is unknown. However, a hypothetical ancestral condition can be speculated upon. I suggest that the two cryptodire groups diverged before the posterior flange was completely developed, but after the development of a difference in position of the carotid artery. During further extension of the flange the carotid became fixed in position.

An alternative hypothesis is to consider one of the known carotid positions primitive and the other derived. The age and association of other primitive characters with the baenoids suggest consideration of the baenoid carotid pattern as primitive with respect to the eucryptodires, but the morphology does not substantiate this alternative. Although the more anterior position of the foramen posterior canalis carotici interni in baenoids agrees with the pleurodire condition rather than with the eucryptodire condition, the bones forming the foramen are different (pterygoid and basisphenoid rather than prootic) and the baenoid condition is not a structural intermediate between the pleurodire and eucryptodire conditions. Morphologic intermediates between baenoid and eucryptodire carotid states are also not known.

Other characters tend to support the contention that eucryptodires are the more derived (or apomorphic) of the two groups. The nasals are usually lost and the prefrontals usually have an expanded dorsal lappet that meets in the midline and occupies the position of the nasals. This

feature appears to have arisen independently in the pelomedusid pleurodires. Some eucryptodires (e.g., toxochelyids, plesiochelyids) retain nasals and some (*Rhinochelys*, Collins, 1970; *Desmatochelys*, Zangerl and Sloan, 1960) have prefrontals that do not meet in the midline. The postcranium of baenoids also has retained primitive features: the cervical vertebrae are not modified for neck retraction to the extent seen in most eucryptodires, and mesoplastra and intergular scutes are usually retained in baenoids but lost in eucryptodires.

RELATIONSHIPS WITHIN THE EUCRYPTODIRA

The past 20 years have witnessed the general recognition of three main groups of living cryptodires: sea turtles, soft shell turtles (triony-chids), and tortoises plus the remaining freshwater forms. Wermuth and Mertens (1961) formally recognized these groups as superfamilies: Chelonioidea, Trionychoidea, and Testudinoidea. The main departure from this sort of classification has been the maintenance of separate superfamilies for the highly derived living species (plus a few presumed fossil relatives) *Dermochelys coriacea* and *Carettochelys insculpta* beginning with Williams (1950) and continued by Romer (1956, 1966). Wermuth and Mertens include these forms in the Chelonioidea and Trionychoidea respectively, and in this section I present arguments that these two superfamilies (as construed by Wermuth and Mertens) are strictly monophyletic. As with the preceding parts of this paper, I am developing these hypotheses primarily on the basis of shared derived characters in the skull. Nonetheless, postcranial features are dealt with to some extent but this is mostly done from the literature.

SUPERFAMILY TRIONYCHOIDEA

McDowell (1961) and Albrecht (1967) studied the cranial arterial patterns in living turtles with special reference to kinosternids and triony-chids. More recently Albrecht (unpublished ms) has increased the taxonomic breadth of the work, and the major cranial arteries of turtles are now relatively well known. The following shared derived character analysis of the arterial patterns

agrees with some of the above authors' conclusions but not with others.

In general two basic patterns of relative diameter size exist in the internal carotid system of living turtles (fig. 25). In one pattern (found in trionychids, carettochelyids, kinosternids, and dermatemydids) the stapedia artery is distinctly smaller and a more medial branch of the internal carotid is larger, whereas in the other pattern (found in all other turtles except living cheloniids) the stapedia artery is distinctly larger and the more medial branches of the internal carotid are smaller. McDowell (1961) and Albrecht (1967) suggested that the pattern seen in living cheloniids, in which both arterial branches have about the same diameter, was primitive for turtles and that later turtles enlarged one or the other branch. Comparison with other reptiles and other turtle groups, however, does not substantiate this notion. To begin with, other chelonoids, *Toxochelys* (Zangerl, 1953, pl. 9 and personal observ.), *Eochelone* (Casier, 1968, fig. 6 and personal observ.), and *Notochelone* (personal observ.), have a small foramen caroticum laterale as in testudinoids, and this indicates that the medial branch is reduced with respect to the stapedia branch. More importantly, however, baenoids, pleurodires, and most living reptiles also have a smaller palatine artery and a larger stapedia artery strongly suggesting that the cheloniid condition is derived and not primitive for cryptodires or all turtles. The enlargement of the medial internal carotid branch and the reduction of the stapedia artery then would appear to be a derived character shared by dermatemydids, kinosternids, trionychids, and carettochelyids and would imply that these groups share a common ancestor not shared by other turtles.

A recent phenetic analysis of turtle hind-limb morphology (Zug, 1971) also supports this theory of relationships. Zug obtained measurements of the distribution of muscle attachment sites and osteology of the pelvic girdle and hind limb in a series of modern turtles. He then entered this information into a computer program designed to determine overall phenetic similarity between the included taxa for these characters. Even though the trionychids and *Dermatemys* are categorized as swimmers and the kinosternids as bottom walkers, the similarity method

linked trionychids with kinosternids. I examined Zug's morphologic descriptions and although it is difficult to determine primitive and derived states for most of the musculature characters, I did find one character shared by kinosternids, *Dermatemys*, and trionychids that is not found in other turtles. The caudifibularis muscle exists only in those groups and would appear to be a good shared derived character (also noted by Frair, 1972).

In view of the hypothesis that dermatemydids, kinosternids, carettochelyids, and trionychids are a monophyletic group, I would extend the superfamily Trionychoidea to include these families. Within this superfamily two subgroups may be recognized also on the basis of the arterial pattern. The kinosternids and *Dermatemys* have enlarged the palatine artery while the trionychids and *Carettochelys* have enlarged a more medial branch of the internal carotid (termed by Albrecht the pseudopalatine artery, but which appears to be in the same morphologic position as the orbital artery of kinosternids and testudinids).

SUPERFAMILY CHELONIOIDEA

Determining shared derived characters for living chelonoids (cheloniids and *Dermochelys*) is not too difficult. Nick (1912) and later workers (Pehrson, 1945; Wegner, 1959; see their references) have produced extensive studies of the head of *Dermochelys* comparing it with other turtles, particularly cheloniids, and a number of the characters presented may be used as shared derived characters for the group cheloniids plus *Dermochelys*. As opposed to the trionychoids and the testudinoids, however, examination of the fossil record reveals a considerable diversity of forms possibly related to the living chelonoids (see Romer, 1956, pp. 507-512, for a summary). Although much of this fossil material is represented by skulls with well-preserved basicrania, very little of it is prepared to the extent necessary for comparisons to be made using the criteria developed for the living forms. Furthermore, the most derived of the living forms, *Dermochelys*, has apparently utilized neoteny as a modifying mechanism, and the cartilaginous nature of much of the skull makes comparison

with fossil forms difficult, since cartilage is usually not preserved in fossils.

The region around the basisphenoid appears to offer the best derived characters applicable to fossil and Recent chelonoids. Nick (1912), Pehrson (1945), and Zangerl (1953) have been the principal developers of these criteria, and I think that together with considerations of postcranial morphology (see below) they offer a good complex of shared derived characters.

1. The ossified trabeculae lie close together for their whole length and are partially or completely fused to form a rostrum basisphenoidale.

2. The foramina anterius canalis carotici interni are close together and separated by a relatively thin bar of bone.

3. The sella turcica is reduced or absent due to approximation of the trabeculae or ossification of the taenia intertrabecularis (see below).

4. The dorsum sellae is high and separated from the sella turcica and foramina anterius canalis carotici interni by a prominent bone surface that usually has a sagittal ridge. In the other superfamilies the dorsum sellae overhangs the sella turcica.

The state of the above characters is relative and their condition is meaningful only in comparison to the other cryptodire superfamilies. The above features are seemingly interrelated and may be explained by the presence of a structure, the taenia intertrabecularis, that Nick (1912) and Pehrson (1945) described. This structure, a rod-like element positioned in the midline just above the trabeculae and anterior to the dorsum sellae, is found only in the cheloniids and *Dermochelys* among living turtles. In *Dermochelys* it does not ossify (as is the case with much of the basicranial morphology) and must be studied in cartilaginous preparation (or sections, as provided by Nick). In living cheloniids the taenia intertrabecularis ossifies as part or all of the rostrum basisphenoidale resulting in the obliteration of the sella turcica. The actual presence of a taenia intertrabecularis in fossils is difficult to demonstrate because developmental information is really necessary for its identification but in any case the list of characters is valid whether or not they are related to the taenia intertrabecularis.

Some information on the basicranium is avail-

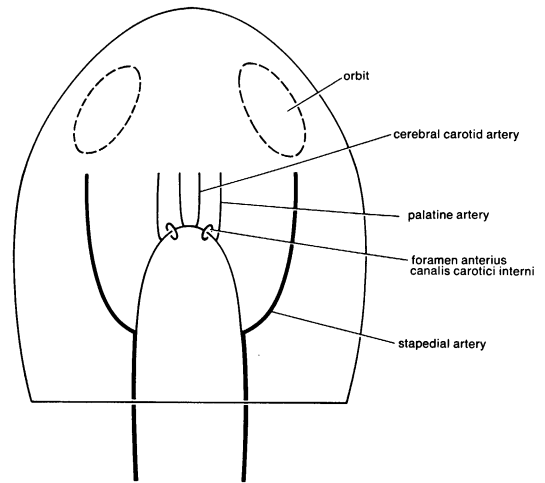


FIG. 24. Diagrammatic dorsal view of a turtle head showing relative diameters and positions of branches of the internal carotid artery. The arterial pattern shown here is suggested as the primitive condition for turtles and is repeated as A in figure 25.

able for fossil chelonoids and the following forms are known to possess the above characters: *Toxochelys moorevillensis* (Zangerl, 1953), *Toxochelys latiremis* (AMNH 1042 and 1835), *Ctenochelys tenuitesta* (Zangerl, 1953), *Rhinochelys* sp. (Collins, 1970), *Eochelone brabantica* (Casier, 1968), *Puppigerus camperi* (Moody, 1974), *Corsochelys haliniches* (Zangerl, 1960), and *Notochelone costata* (Queensland Museum F6587).

As I interpret the postcranial characters used by previous workers, two character complexes, the forelimbs and the shell, emerge as potential derived characters for the Chelonioidea. The development of a flipper-type locomotion in the front limbs has involved a series of changes that are recognizable to a varying degree. For example, Zangerl has argued (1953) that although toxochelyid front limb and girdle elements lack the extreme modifications seen in the living cheloniids, they do possess changes in a flipper direction in comparison to *Chelydra* and other testudinoids. Zangerl and Sloan (1960, pp. 34-38) use features of the limb complex as the primary basis for a diagnosis of the Chelonioidea

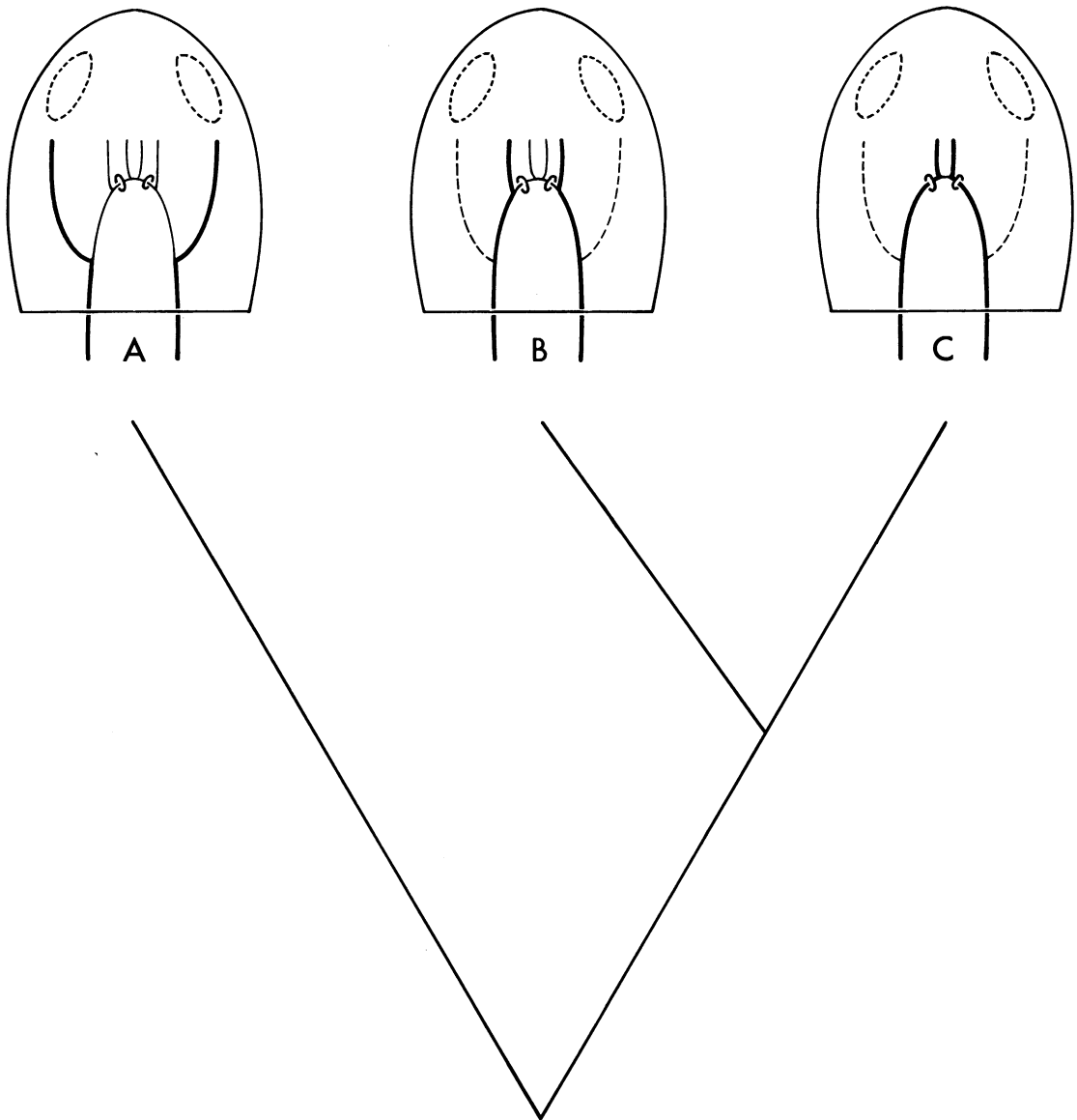


FIG. 25. A cladogram showing relationships of trionychoid turtles based on arterial patterns in the head. A, primitive condition for turtles; B, pattern found in Kinosternidae and Dermatemydidae; C, pattern found in Carettochelyidae and Trionychidae. See figure 24 for identification of arteries.

and consider that the families Toxochelyidae, Protostegidae, Dermochelyidae, and Cheloniidae possess these features in varying degrees.

Shell morphology has also been a classic source of characters for differentiating sea turtles

but here the determination of homologous features appears more difficult than with the forelimb. Strictly speaking one can assume that fontanelle development is derived with respect to a solid shell for all turtles, but further use of shell

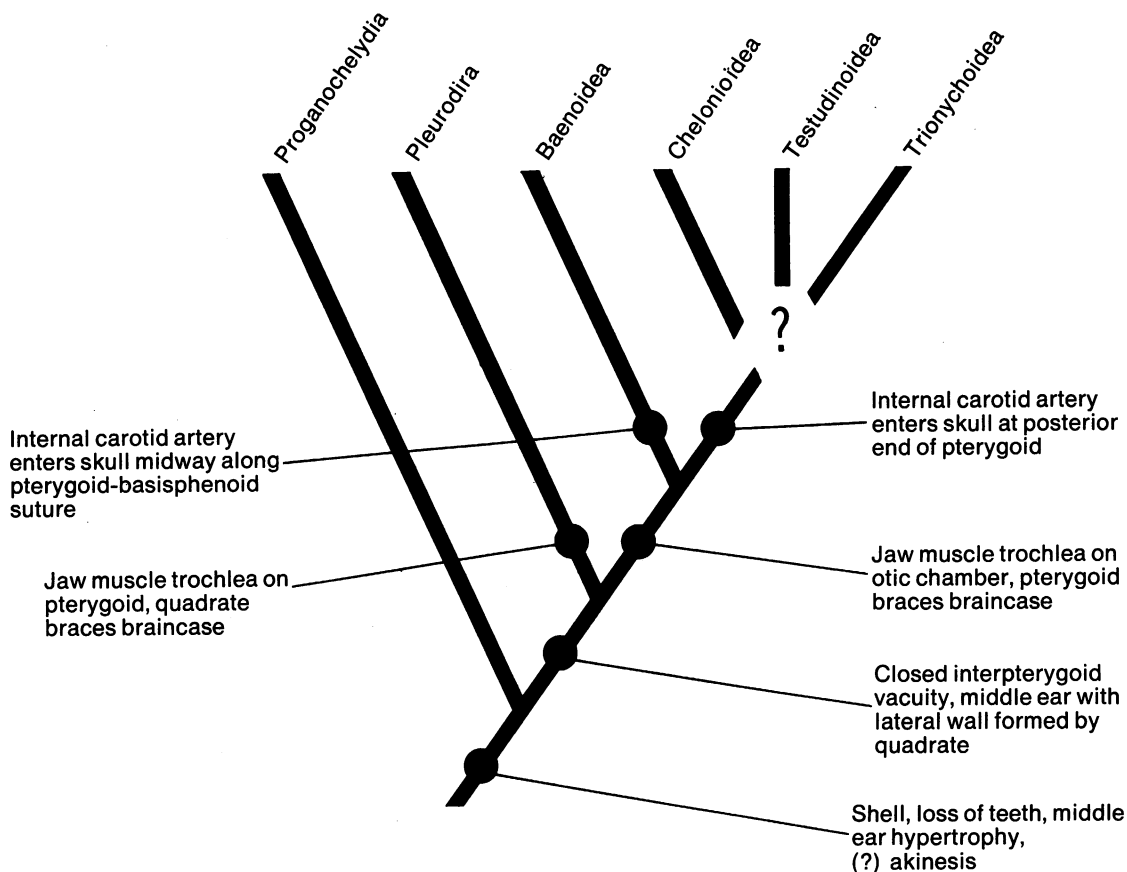


FIG. 26. A theory of relationships among the higher categories of turtles. This cladogram indicates the relative position of common ancestors and a few shared derived characters diagnostic of particular lineages. Other morphologic and temporal parameters are not expressed.

reduction is difficult. Most chelonioid shells, particularly plastra, are reduced in some ways but determining primitive and derived states between them and forms such as *Chelydra* and *Macrolemys* is difficult.

SUPERFAMILY TESTUDINOIDEA

I have attempted to show that the two previous superfamilies can be hypothesized as monophyletic units on the basis of shared derived characters. However, the Testudinoidea have no shared derived characters that I have been able to find. If the argument that the cheloniid arterial pattern is primitive for eucryptodires is correct then the reduction of the medial carotid branch

would be a good derived character. In that case, however, independent reduction would have had to take place in at least three different lines—pleurodires, baenoids, and noncheloniid chelonioids to say nothing of other reptiles. My interpretation, then, of the testudinoidean arterial pattern is that it is primitive for turtles and, therefore, not useful for arguing the monophyletic nature of the Testudinoidea.

THE EARLY HISTORY OF TURTLES

Turtles have long been considered a “primitive” or relict reptile group that has maintained a consistent morphologic structure since its origin, but an alternative interpretation of chelonian

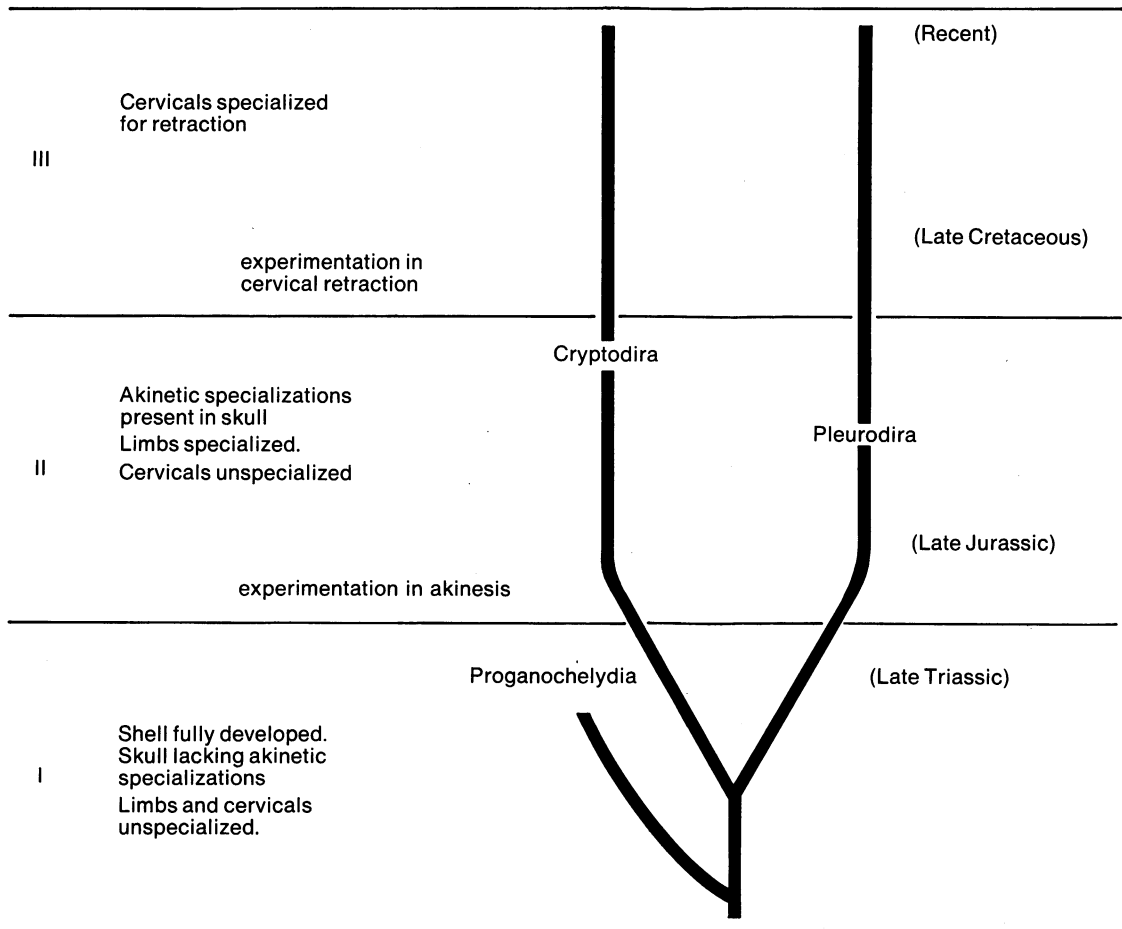


FIG. 27. A speculative history of turtle adaptations in terms of levels of organization (see text for explanation). Major horizontal divisions refer to adaptive levels and not to stratigraphic units. Approximate stratigraphic age is indicated on the right.

history may be more accurate. It seems more likely that two major lineages (cryptodires and pleurodires) arose early in the history of turtles and passed through similar stages during their phylogeny and repeatedly evolved parallel adaptations. Furthermore, as opposed to previous ideas on conservatism in turtles, a number of unique and structurally profound adaptations arose throughout chelonian history.

As the preceding comparison of pleurodires and cryptodires emphasizes, most of the cranial differences between the two groups are related to the palatoquadrate elements. The differences are summarized below:

1. Nonhomologous trochlear structure in the jaw mechanism
2. Method of bracing palatoquadrate elements to braincase
3. Position of structures in cranioquadrate space
4. Epipterygoid
5. Position of foramen palatinum posterius.

The trochlear apparatus of turtles is unique among vertebrate adductor systems and has, apparently, evolved in conjunction with the expansion of the otic region. The paracapsular network, a fluid filled sinus in the middle ear of turtles, is hypertrophied compared with most

other tetrapods and is enclosed in a chamber formed from palatoquadrate and braincase elements. The development of this otic chamber reduced the space for the adductor musculature and probably stimulated the formation of the trochlear apparatus. The trochlear system is a mechanism for translating anteroposterior forces into a vertical plane, enabling the adductor musculature to insert above and behind the expanded otic chamber. The morphology of the trochlear apparatus in pleurodires and cryptodires is different but the mechanism is the same, suggesting that the lineages diverged before the development of the trochlea but after the beginning of ear hypertrophy. Akinesis probably preceded or directly followed trochlear formation because of the close relationship between the quadrate and the paracapsular system. The method of achieving akinesis, as in the method of trochlear formation, is different in cryptodires and pleurodires, again suggesting independent acquisition. The different position of structures traversing the space (the cranioquadrate space) between the palatoquadrate and the braincase in the two groups, and the development of a pterygoid brace in cryptodires and a quadrate brace in pleurodires are significant indications that akinesis was attained independently in the two groups. Thus, the differences between cryptodires and pleurodires can be interpreted as arising in two closely related lineages that were subject to similar selection pressures and evolved similar, but not homologous, structures in response to these selection pressures.

A summary of the possible events in the history of chelonians can be assembled from the above interpretations and current knowledge of the fossil record (fig. 27). *Proganochelys* (Jaekel, 1916; Parsons and Williams, 1961; Romer, 1966) shows that turtles evolved the shell before the skull, vertebrae, and limbs were characteristically modified. The skull at this stage (level I in fig. 27) lacked marginal teeth and in life probably had a horny bill as in Recent turtles. However, the palatoquadrate elements, particularly the structures related to the cranioquadrate space, do not seem to be modified in either the cryptodiran or pleurodiran manner: "Posteriorly also the situation is primitive; [in *Proganochelys*] the

quadrate ramus of the pterygoid does not send any flange inward to floor the cranio-quadrate passage as in all other known turtles [actually only in cryptodires; pleurodires have a flange of the quadrate flooring the cranio-quadrate space and bracing the palatoquadrate against the braincase], and the foramina for the vena capitis lateralis, the internal carotid, and the stapedia artery, as well as the fenestra ovalis are all exposed in ventral view" (Parsons and Williams, 1961, p. 91). Kinesis may or may not have been present. As far as can be determined, then, the Triassic *Proganochelys* supports the hypothesis advanced here and presents us with a good morphologic ancestor for cryptodires and pleurodires.

Following *Proganochelys*, there was a probable period of experimentation during the development of advanced features of akinesis and a trochlear mechanism. During or before this period the pleurodire and cryptodire lineages split. The next level (II) is characterized by akinetic skulls, specialized limbs, and unspecialized cervical vertebrae. The two lineages were essentially "modern" in all aspects of their osteology except the neck. In the Late Jurassic and Early Cretaceous cryptodire cervicals appear to lack formed central articulations (they are amphicoelous) but in the Late Cretaceous formed centra appear and one double-jointed centrum (an advanced cryptodiran feature) is known from the Maestrichtian Hell Creek Formation (R. Estes, personal commun.). Some Late Cretaceous pleurodire vertebrae (*Taphrophys*, Maestrichtian, New Jersey) are still more primitive than Recent pleurodire cervicals but are definitely specialized in that direction, whereas other Cretaceous pleurodire vertebrae (*Podocnemis*, Wood, personal commun.) appear identical to some living pleurodires. The latest period of chelonian history (level III) then, is characterized by the fully developed cervical retractile mechanisms that are the most obvious feature of living cryptodires and pleurodires.

CLASSIFICATION

Most controversy and misunderstanding concerning cladism arises from classification rather

TABLE 1
A Comparison of *Captorhinus* and Turtles

Character	<i>Captorhinus</i>	Testudines
Maxillary and mandibular teeth	Well-developed	Absent or rudimentary
Basipterygoid articulation	Movable	Fused ^a
Hypertrophy of middle ear	Absent	Present
Pineal foramen	Present	Absent ^b
Ectopterygoid	Absent ^c	Absent
Lacrimal, postfrontal, supratemporal, postparietal, septomaxilla	Present	Absent ^d
Vomer	Paired	Single
Processus paroccipitalis of opisthotic sutured to quadrate	No	Yes

^aPossibly movable in *Proganochelys*; see discussion under Proganochelydia.
^bPresent as an abnormality in some forms—Zangerl, 1957.
^cPresent in other Captorhinomorpha.
^dSee discussion under Proganochelydia.

than phylogeny reconstruction. Although nearly all systematists emphasize the importance and value of classification, there is little agreement, even among cladists, as to the specific procedures or governing principles used in erecting a classification. In my opinion a phylogenetic diagram, cladistic or not, is more useful and to be preferred over a classification for most biologic purposes. Arguments for or against a particular classification in a situation where the phylogeny is essentially agreed upon by the persons involved seems fruitless. Nonetheless, I am here proposing a new classification of turtles. This classification differs from previous ones because I have tried to maintain strictly monophyletic taxa to the extent that this is possible. For the most part previously erected taxa are maintained and phylogeny is reflected by the addition of new categories at intermediate levels. My only purpose in this classification is the naming of monophyletic groups and the reflection of the phylogenetic hypotheses advanced here.

The erection of new categories (i.e., Parv-order) is not unusual, but it is rarely done by vertebrate systematists. After I decided on a strictly monophyletic classification, it was a question of how to express this in the idiom of the Linnaean hierarchy. I have chosen to do this by maintaining previously named monophyletic groups at "conventional" levels and inserting new categories where necessary. If one accepts my

phylogeny (as a useful, testable hypothesis, that is), but finds my classification radical, impractical, or simply offensive, then I would urge ignoring my classification.

CLASSIFICATION OF RECENT AND FOSSIL TURTLES

ORDER TESTUDINES¹ LINNAEUS, 1758

Diagnosis. Anapsid sauropsids with mandibular and maxillary teeth rudimentary or absent, functionally replaced by a horny sheath, basipterygoid articulation fused (see discussion under *Proganochelys*); middle ear hypertrophied for the housing of a fluid-filled paracapsular sinus; pineal foramen absent; ectopterygoid, postfrontal, supratemporal, postparietal, and septomaxilla absent; vomer single; lacrimal duct absent; processus paroccipitalis of opisthotic sutured to quadrate.

Discussion. Romer (1956, p. 495) should be consulted for the rather useful postcranial features diagnostic of turtles. The cranial features listed above would probably be amplified considerably if the Triassic proganochelyids were better known. I have tried to indicate here those characters that would be most important in a comparison of turtles and captorhinomorphs (see table 1).

¹Hunt (1958) discussed the ordinal name for turtles.

TABLE 2
A Comparison of Proganochelydia and Casichelydia

Character	Proganochelydia	Casichelydia
Floor of cavum acustico-jugulare	Open	Closed
Interpterygoid vacuity	Open	Closed
Middle ear (cavum acustico-jugulare) with lateral wall formed by quadrate	Absent	Present
Cultriform process on parasphenoid	Present	Absent
Palatal teeth	Present	Absent
Apertura narium externa divided by dorsal process of premaxillae	Yes	No (see discussion)
Expanded crista supraoccipitalis	Absent	Present
Antrum postoticum	Absent	Present
Well-developed median tubercle on (?) basioccipital	Present	Absent

SUBORDER PROGANOCHELYDIA ROMER, 1966

Diagnosis. Turtles with open interpterygoid vacuity and cultriform process; floor of cavum acustico-jugulare open; middle ear (essentially the cavum acustico-jugulare) without a lateral wall formed by the quadrate; kidney-shaped cavum tympani absent; palatal and rudimentary marginal teeth present; apertura narium externa divided by dorsal processes of premaxillae; crista supraoccipitalis not developed as in other turtles; antrum postoticum absent; well-developed median tubercle on (?) basioccipital; lacrimal apparently present.

Discussion. The above characters are for the most part based on the works of Jaekel (1916) and Parsons and Williams (1961). The latter authors have particularly modified knowledge of *Proganochelys*, but the cranial morphology of that form still awaits thorough description. A figure in Romer (1966, fig. 166) also changes previous ideas about the skull of *Proganochelys*. This figure shows no supratemporal or post-frontal elements, absent in all later turtles but long presumed to be present in *Proganochelys*. If correct, the 1966 figure shows that the only "extra" bone present in *Proganochelys* is the lacrimal, and that is indicated by a dashed suture. In the above diagnoses of Testudines and Proganochelydia I have assumed that this figure is correct; however, I do not know if it is based on original examination of the specimen or interpretation of the photographs. There is, therefore, some doubt about these features.

The presence of a fused basiptyergoid articulation in *Proganochelys* is based solely on my interpretation of the figures given by Parsons and Williams. Poor preservation or preparation could very well make a kinetic skull look akinetic and this doubt should also be kept in mind.

The suggestion made by Lydekker (1889) that some "amphichelydians" had the pelvis partially fused to the plastron has been shown (see preceding section on baenoids) to be in error, and the pelvis in *Pleurosternon*, *Plesiochelys*, and baenoids is free from sutural contacts with the shell. I have not been able to find any turtles with a pelvis that is neither completely fused with the shell as in pleurodires nor free as in cryptodires and I advance the suggestion (see discussion of Pleurodira) that the fused pelvis may be a derived character for pleurodires. *Proterochersis* Fraas (1913) from the Late Triassic of Germany has usually been included with *Proganochelys* but it has a pelvis that is fused to the shell. The original description and a good cast (AMNH 3867) show a pelvic morphology that agrees closely with other pleurodires. Fraas originally identified this form as a pleurodire, and the only basis for removing it from the Pleurodira seems to be its age and the presence of presumably primitive characters such as two pairs of mesoplastra. Cranial material may clarify the relationships of *Proterochersis* but presently no one has successfully negated the hypothesis that *Proterochersis* shares an ancestor with other Pleurodira. In any case, I am specifically removing it from the Proganochelydia which, for the

present, rests entirely on the forms described by Jaekel (1916) and Parsons and Williams (1961).

SUBORDER CASICHELYDIA GAFFNEY, 1975a

Diagnosis. Turtles with closed interpterygoid vacuity and no trace of cultriform process on parasphenoid (parasphenoid nearly always fused with basisphenoid); floor of cavum acusticojugulare with lateral wall formed by quadrate; kidney-shaped cavum tympani present; all indications of teeth absent; apertura narium externa usually not divided; crista supraoccipitalis expanded dorsally and/or posteriorly in comparison with other reptiles; antrum postoticum present; median tubercle on basioccipital absent; lacrimal absent.

Discussion. The erection of what may seem to

some to be another superfluous higher taxon of turtles (for example, see Bergounioux, 1955; Zangerl, 1969; Chkhvadze, 1970) is defended here only on the assumption that a classification should completely reflect phylogenetic relationships. This group is monophyletic and can be recognized by a series of shared derived characters, and that is why I have named it.

The name has been coined from two Greek words, *kasis*—sister or brother—and *chelys*—turtle—in allusion to the supposition that this is the sister group of the Proganochelydia.

INFRAORDER PLEURODIRA (COPE, 1868)

Diagnosis. Casichelydians with trochlear surface for cartilago transiliens developed on lateral process of pterygoid; processus trochlearis ptery-

TABLE 3
A Comparison of Cryptodires and Pleurodires

Character	Cryptodira	Pleurodira
Trochlear surface upon which cartilago transiliens articulates	A true synovial capsule formed on the processus trochlearis oticum, the anterior edge of the otic chamber	A joint surface consisting of the infolded oral mucosa formed on the lateral process of the pterygoid
Bracing of quadrate to braincase	Pterygoid extends posteriorly between quadrate and braincase	Quadrate sends a ventral process medially to the braincase
Position of hyomandibular branch of facial nerve (VII) in the cranio-quadrate space	Traverses the canalis cavernosus	Travels outside the canalis cavernosus in its own canal for most of the distance
Position of mandibular artery	Usually exits from foramen nervi trigemini, usually travels through canalis cavernosus	Does not exit from foramen nervi trigemini, branches off stapedial artery after latter exits from foramen stapedio-temporale, does not travel through canalis cavernosus
Epipterygoid	Present (except in <i>Dermochelys</i>), pterygoid cartilage persistent in fossa cartilaginis epipterygoidei	Absent, pterygoid cartilage not persistent, fossa cartilaginis epipterygoidei greatly reduced or absent
Lower jaw articulation	Lacks hemispherical articular	Usually has hemispherical articular
Foramen palatinum posterius	In floor of orbit (absent in cheloniids)	Behind orbit
Anterior exit of the canalis nervi vidiani	In posterior wall of foramen palatinum posterius	Absent in cheliids, in ventral surface of pterygoid in pelomedusids
Descending process of prefrontal meets vomer ventromedially	Yes	No

goidei never on otic chamber; joint surface of trochlea consisting of infolded oral mucosa rather than true synovial capsule; quadrate sending process medially to braincase elements, pterygoid rarely extending posteriorly but in any case not preventing quadrate contact with braincase; hyomandibular nerve contained in own canal separate from canalis cavernosus; mandibular artery failing to exit from foramen nervi trigemini but branching off stapedial artery after latter leaves otic region of skull to enter temporal fossa; epipterygoid not ossifying, epipterygoid cartilage apparently absent or greatly reduced in adult, fossa cartilaginosa epipterygoidei therefore greatly reduced or absent; articular usually hemispherical; foramen palatinum posterius behind orbit; descending process of prefrontal reduced, not meeting vomer ventromedially.

Head withdrawn by horizontal flexure of neck in advanced forms with attendant development of narrowly spaced zygapophyses, laterally developed transverse processes, and formed central articulations; pelvis suturally united to carapace and plastron; cervical (nuchal) scute, intergular scute and mesoplastra present or absent.

Discussion. I have discussed most of the above features earlier in this paper, but the absence of a posterior extension on the pterygoid appears to have an exception in a Cretaceous pleurodire, *Bothremys* (Gaffney and Zangerl, 1968), and needs to be dealt with. In *Bothremys* the articulation with the lower jaw is on a level posterior to the occipital condyle, a very rare condition in pleurodires and presumably specialized. The relations of the quadrate and the neurocranial elements are still basically the same as in other pleurodires but the posterior movement of the quadrate has "pulled" the quadrate ramus of the pterygoid posteriorly. The pterygoid flange of cryptodires is still entirely absent and *Bothremys* is not an exception to the characters listed.

The sutural union of all three pelvic bones with the shell appears to be a good shared derived character for pleurodires. The free pelvic condition presumably precedes the fused one and, until some argument is developed to the contrary, the free condition can be hypothesized as primitive and the fused one as derived. Furthermore, of taxa known from both skull and

pelvis, the cryptodiran cranial features are invariably associated with a free pelvis and pleurodiran cranial features with the sutured pelvis. Supposed partially sutured pelves (e.g., *Plesiochelys*, *Pleurosternon*) actually have the free condition and lack any sutural connection.

Platychelys oberndorferi (see Bräm, 1965) from the Late Jurassic of Europe can be identified as a pleurodire because it has a sutured pelvis. Its other features, a single pair of mesoplastra and an intergular scute, are primitive chelonian features also occurring in baenoids and pleurodires. *Proterochersis* (see discussion above) from the Late Triassic can also be postulated as a pleurodire. This form is older and has other primitive or perhaps uniquely derived features in its shell but again, assuming that a fixed pelvis is a derived character and, in the absence of conflicting derived characters, the hypothesis that these forms are pleurodires cannot be negated.

INFRAORDER CRYPTODIRA (COPE, 1868)

Diagnosis. Skull with trochlear surface for cartilago transiliens developed on processus trochlearis oticum, never on process of pterygoid; pterygoid extending posteriorly between quadrate and braincase; hyomandibular nerve traversing cranioquadrate space in canalis cavernosus; mandibular artery usually exiting from foramen nervi trigemini; epipterygoid usually present, when absent pterygoid cartilage persistent, resulting in fossa cartilaginosa epipterygoidei; no development of hemispherical articular on lower jaw; foramen palatinum posterius in floor of fossa orbitalis; vidian nerve exiting in or near foramen palatinum posterius (absent in chelonians); descending process of prefrontal meeting vomer ventromedially.

Head withdrawn by vertical flexure of neck in advanced forms with attendant development of widely spaced zygapophyses, reduced transverse processes, and formed central articulations; these features absent or slightly developed in primitive members; pelvis not suturally united to carapace and plastron; cervical (nuchal) scute usually present; intergular scute absent in advanced forms, present primitively; mesoplastra absent in advanced forms, present in primitive members.

TABLE 4
A Comparison of Paracryptodira and Eucryptodira

Character	Paracryptodira	Eucryptodira
Position of foramen posterius canalis carotici interni	Midway along length of basisphenoid-pterygoid suture	Posterior end of pterygoid
Prefrontals meet on skull roof midline	No	Yes ^a
Nasals	Present	Usually absent
Cervical vertebrae	Not fully retractile	Usually fully retractile
Mesoplastra	Present	Absent

^aNot in some specimens of *Rhinochelys* (Collins, 1970) and *Desmatochelys* (Zangerl and Sloan, 1960).

Discussion. It should be noted that I made an error in the original published diagnosis of cryptodires (Gaffney, 1972a, p. 249). The fifth and sixth lines of the diagnosis which read: "hyomandibular nerve in its own canal traversing cranio-quadrate space. . ." should read as follows: "hyomandibular nerve traverses cranio-quadrate space in canalis cavernosus. . ."

PARVORDER PARACRYPTODIRA GAFFNEY,
NEW

Diagnosis. Cryptodiran turtles tending to retain primitive features; skull with nasals; prefrontals not meeting on skull roof midline; foramen posterius canalis carotici interni lying midway along length of basisphenoid-pterygoid suture; well-developed stapedial artery, reduced orbital and palatine arteries (inferred from foramina); cervical vertebrae lacking well-developed retraction mechanism, early forms lacking formed central articulations; shell with mesoplastra and paired intergular scutes.

Discussion. The category "parvorder" is derived at the suggestion of McKenna from the Latin word *parvus*—little. The Paracryptodira comes from the Greek *para*—near, beside—combined with the Greek derived Cryptodira in allusion to its relationships with the Eucryptodira.

Essentially, the Paracryptodira consists of the Baenoidea as defined in a paper by me (Gaffney, 1972a). Since the publication of that paper I have examined a newly prepared specimen of *Kallokibotium* (Nopsca, 1923) that shows the diagnostic baenoid features of the foramen poste-

rius canalis carotici interni occurring midway along the pterygoid-basisphenoid suture.

Meiolaniids have been considered baenoids but an examination of basicrania (*Meiolania platyceps*, Australian Museum F 208B, F 1209, F 43183; *Crossochelys corniger*, AMNH 3161; see also Anderson, 1925, and Simpson, 1938) suggests that they are eucryptodires. The foramen posterius canalis carotici interni lies at the posterior edge of the pterygoid, the most important diagnostic character of the Eucryptodira.

PARVORDER EUCRYPTODIRA GAFFNEY, 1975a

Diagnosis. Cryptodiran turtles tending to possess advanced features in comparison with Paracryptodira; skull often without nasals; prefrontals nearly always meeting on skull roof midline; foramen posterius canalis carotici interni lying at or near posterior edge of pterygoid and usually formed primarily by pterygoid; stapedial, orbital, and palatine arteries varying from primitive condition (see Paracryptodira) to various derived conditions involving reduction of stapedial artery and/or enlargement of more anterior carotid branches; cervical vertebrae characteristically with formed central articulations adapted for skull retraction in vertical plane; transverse processes usually reduced, zygapophyses usually placed laterally, primitive forms possibly even amphicoelous, however; shell usually with fewer bones and scutes than in Paracryptodira, mesoplastra and intergular scutes usually absent.

Discussion. The term "eucryptodira" is formed

TABLE 5
A Comparison of the Eucryptodire Superfamilies

Character	Trionychoidea	Chelonioidea	Testudinoidea
Stapedial artery reduced or absent	Yes	No	No
Foramen stapedio-temporale reduced or absent	Often	No	No
Dorsal process on palatine present	Yes	No	No ^a
Ossified trabeculae of rostrum basisphenoidale lie close together or are fused	No	Yes	No
Foramina anterius canalis carotici interni lie close together	No	Yes	Rarely
Sella turcica reduced or obliterated	No	Yes	No
Dorsum sellae high and separated from sella turcica by bone surface	No	Yes	No
Posterior portion of sella turcica concealed by overhanging dorsum sellae	Usually	No	Yes
Caudifibularis muscle present	Yes	No	No

^aSmall process present in some Batagurinae.

from the Greek *eu*—true plus *cryptodira*—in allusion to the idea that members of this group typically (but not universally) have well-developed retractile neck mechanisms.

Although I am here proposing three superfamilies in the Eucryptodira, there are other forms recognizable as eucryptodires, but not members of these superfamilies. For example, *Solnhofia* (Gaffney, 1975b) and the meiolaniids can be identified as eucryptodires but I cannot be more specific about their relationships.

SUPERFAMILY TRIONYCHOIDEA GRAY, 1870

Diagnosis. Eucryptodires with distinctly reduced stapedial artery, usually (but not always) reflected by a reduction or loss of foramen stapedio-temporale and canalis stapedio-temporalis; foramen posterius canalis carotici interni and canalis caroticus internus relatively larger in diameter in comparison with those structures in Testudinoidea; foramen caroticum laterale or foramen anterius canalis carotici interni conspicuously enlarged in comparison with these structures in Testudinoidea; palatine usually with variably developed dorsal process that contributes to side wall of braincase (cavum epiptericum); ossified trabeculae of basisphenoid well separated lateral to a prominent sella turcica and not fused into rodlike rostrum basisphenoidale; foramina anterius canalis carotici interni separated by prom-

inent bone area in contrast to most Chelonioidea; sella turcica well developed, not reduced; dorsum sellae low and overhanging foramina anterius canalis carotici interni and concealing posterior portion of sella turcica, bone surface as seen in Chelonioidea not developed; caudifibularis muscle present.

Included Families. Kinosternidae, Dermatemydidae, Carettochelyidae, Trionychidae.

SUPERFAMILY CHELONIOIDEA BAUR, 1893¹

Diagnosis. Eucryptodires with well-developed stapedial artery reflected by a relatively large foramen stapedio-temporale; foramen posterius canalis carotici interni and canalis caroticus internus usually smaller in diameter than in Trionychoidea but sometimes larger than in Testudinoidea; foramen anterius canalis carotici interni as in Testudinoidea and never enlarged as in Trionychoidea but foramen caroticum laterale (and palatine artery) enlarged in Chelonidae; palatine without dorsal process; ossified trabeculae of basisphenoid usually close together or fused into rodlike rostrum basisphenoidale; foramina anterius canalis carotici interni close together and separated by relatively thin bar of bone; sella turcica reduced or obliterated due to approximation of trabeculae and/or development of taenia inter-

¹Kuhn (1964) indicated "Baur 1889" as the original appearance of this name but I have been unable to find this name in any of Baur's papers before 1893.

trabecularis; dorsum sellae high and separated from sella turcica and foramina anterius canalis carotici interni by prominent bone surface that usually has a sagittal ridge; posterior portion of sella turcica not concealed by overhanging dorsum sellae; caudifibularis muscle absent.

Included Families. Plesiochelyidae (Gaffney, 1975a), Toxochelyidae, Protostegidae, Dermochelyidae, and Cheloniidae.

SUPERFAMILY TESTUDINOIDEA BAUR, 1893

Diagnosis. Eucryptodires with well-developed stapedial artery reflected osteologically by relatively large foramen stapedio-temporale and canalis stapedio-temporalis; foramen posterius canalis carotici interni and canalis caroticus internus distinctly smaller in relative diameter than those structures in Trionychoidea; foramen

anterius canalis carotici interni and foramen caroticum laterale distinctly smaller in diameter than foramen stapedio-temporale; palatine usually without dorsal process (small process present in some Batagurinae); ossified trabeculae of basisphenoid usually well separated lateral to prominent sella turcica and not fused into rodlike rostrum basisphenoidale; foramina anterius canalis carotici interni usually separated by prominent bone area in contrast to most Chelonioidea; sella turcica well developed, not reduced; dorsum sellae low and overhanging foramina anterius canalis carotici interni and concealing posterior portion of sella turcica; bone surface as seen in Chelonioidea not developed; caudifibularis muscle absent.

Included Families. Chelydridae (plus *Platysternon*, Gaffney, In press), Emydidae, Testudinidae.

A CLASSIFICATION OF TURTLES

- Order Testudines Linnaeus, 1758
 - Suborder Proganochelydia Romer, 1966
 - Family Proganochelyidae (Triassic)
 - Suborder Casichelydia Gaffney, 1975a
 - Infraorder Pleurodira (Cope, 1868)
 - Family Pelomedusidae (Cretaceous-Recent)
 - Family Chelidae (Eocene-Recent)
 - Infraorder Cryptodira (Cope, 1868),
 - Parvorder Paracryptodira, new
 - Superfamily Baenoidea Williams, 1950
 - Family Glyptopsidae (Jurassic)
 - Family Baenidae (Cretaceous-Eocene)
 - Parvorder Eucryptodira Gaffney, 1975a
 - Superfamily Trionychoidea Gray, 1870
 - Family Kinosternidae (Oligocene-Recent)
 - Family Dermatemydididae (Cretaceous-Recent)
 - Family Carettochelyidae (Eocene-Recent)
 - Family Trionychidae (Cretaceous-Recent)
 - Superfamily Chelonioidea Baur, 1893
 - Family Plesiochelyidae (Jurassic)
 - Family Protostegidae (Cretaceous)
 - Family Toxochelyidae (Cretaceous-Eocene)
 - Family Dermochelyidae (Eocene-Recent)
 - Family Cheloniidae (Cretaceous-Recent)
 - Superfamily Testudinoidea Baur, 1893
 - Family Chelydridae (Paleocene-Recent)
 - Family Emydidae (?Paleocene-Recent)
 - Family Testudinidae (Eocene-Recent)

SUMMARY

Basicranial characters provide the basis for a new theory of relationships among major groups of Recent and extinct turtles. The method used here to develop phylogenetic hypotheses is based on the distribution of shared derived characters; a strategy expounded by Hennig (1966) and others and often called cladism or phylogenetic systematics. Although I emphasize phylogenetic reconstruction I also present a new classification of turtles that consists of strictly monophyletic groups (to the extent that I can determine them) and is a direct reflection of the phylogeny.

1. Shared derived characters diagnostic of the order Testudines include: a shell, loss of marginal teeth, middle ear hypertrophy, and probably akinesis.

2. Two suborders are recognized within the Testudines. The suborder Proganochelydia consists of the Triassic genus *Proganochelys* and is characterized by predominantly primitive features such as an open interpterygoid vacuity and a laterally open middle ear cavity. All other turtles are contained in the suborder Casichelydia which can be diagnosed using shared derived characters; the most important being a closed interpterygoid vacuity and a middle ear with the lateral wall present.

3. The Casichelydia consists of two infraorders. The infraorder Pleurodira possesses the following shared derived characters: jaw muscle trochlea on pterygoid, quadrate braces braincase. The infraorder Cryptodira has these shared derived characters: jaw muscle trochlea on otic chamber, pterygoid braces braincase.

4. Within the Cryptodira two monophyletic taxa are recognized. In the parvorder Paracryptodira (consisting only of the superfamily Baenoidea) the internal carotid artery enters the skull midway along the pterygoid-basisphenoid suture, whereas in the parvorder Eucryptodira the internal carotid artery enters at the posterior end of the pterygoid.

5. The Eucryptodira contains three superfamilies. The superfamily Chelonioidea is characterized by the following series of shared derived characters: sella turcica reduced or obliterated,

dorsum sellae high and does not overhang carotid foramina, carotid foramina closely apposed. The Chelonioidea contains the Plesiochelyidae, Protostegidae, Toxochelyidae, Dermochelyidae, and Cheloniidae. The primary shared derived character defining the superfamily Trionychoidea is the reduction or absence of the stapelial artery. The families Kinosternidae, Dermatemydidae, Carettochelyidae, and Trionychidae are placed in the Trionychoidea on this basis. I have not been able to diagnose the superfamily Testudinoidea using shared derived characters and the group may be paraphyletic because it is delimited only by primitive features. The families Testudinidae, Emydidae, and Chelydridae make up the Testudinoidea.

The "Amphichelydia" is a higher taxon characterized by primitive features and supposedly containing the ancestors of Recent turtles. The development of a strictly monophyletic classification requires the rejection of this taxon and the redistribution of its included taxa.

Although most turtle fossils consist only of shells or shell fragments, there are a sufficient number of skull-shell associations to allow the development of a speculative history of the group. The acquisition of a shell (Late Triassic or earlier) preceded the characteristic akinetic modifications (although kinesis may have actually been lost at that time or earlier) and the development of cervical and limb specializations. Adaptations for cervical retraction (Late Cretaceous) appear well after the akinetic and palatoquadrate features diagnostic of cryptodires and pleurodires (Late Jurassic). However, identification of pleurodires in the Late Jurassic (*Platychelys*) and Late Triassic (*Proterochersis*) suggest that the pleurodire-cryptodire dichotomy took place very early in the history of turtles.

ZUSAMMENFASSUNG

Die Charakteristiken der Gehirnschalenbasis bilden die Grundlage für eine neue Theorie der verwandtschaftlichen Beziehungen zwischen grösseren Gruppen neuzeitlicher und ausgestor-

bener Schildkröten. Die hier zur Entwicklung phylogenetischer Hypothesen angewandte Methode basiert auf der Verteilung gemeinsamer, hergeleiteter Eigenschaften, eine Strategie, die von Henning (1966) und anderen erläutert wurde und oft Cladismus oder Phylogenetische Systematik genannt wird. Obwohl ich die phylogenetische Konstruktion in den Vordergrund stelle, führe ich auch eine neue Klassifizierung der Schildkröten ein, welche aus streng monophyletischen Gruppen (soweit ich sie bestimmen kann) besteht und eine direkte Widerspiegelung der Phylogenie darstellt.

1. Die gemeinsamen, hergeleiteten Eigenschaften, welche für die Gattung Testudines kennzeichnend sind, bestehen aus: einer Schale, Verlust der Randzähne, Hypertrophy des Mittelohres und wahrscheinlich Akinese.

2. Zwei Unterabteilungen werden innerhalb der Testudines anerkannt. Die Unterabteilung Proganochelydia besteht aus der triassischen Art *Proganochelys* und ist gekennzeichnet durch überwiegend primitive Merkmale wie eine offene interpterygoide Lücke und einem seitlich geöffneten Hohlraum des Mittelohres. Alle anderen Schildkröten gehören zu der Untergruppe Casichelydia, welche dadurch diagnostiziert werden kann, dass gemeinsame, abgeleitete Kennzeichen beobachtet werden; das wichtigste Kennzeichen sind ein geschlossener interpterygoider Hohlraum und ein Mittelohr, welches eine seitliche Wand aufweist.

3. Die Casichelydia bestehen aus zwei untergeordneten Gruppen. Die Untergruppe Pleurodira besitzt die folgenden gemeinsam, hergeleiteten Merkmale: trochlea Kiefermuskel an Pterygoid, Quadratknöchel festigt Gehirnschale. Die Untergruppe Cryptodira weist diese gemeinsamen, hergeleiteten Merkmale auf: trochlea Kiefermuskel an der Ohrenkammer; Pterygoid festigt Gehirnschale.

4. Innerhalb der Cryptodira werden zwei monophyletische Klassen anerkannt. In der Parvorder Paracryptodira (die nur aus der Oberfamilie Baenoidea besteht) tritt die innere Halsschlagader halbwegs entlang der pterygoid-basisphenoid Naht in den Schädel ein, während in der Parvorder Eucryptodira die innere Halsschlagader am hinteren Ende der Pterygoid eintritt.

5. Die Eucryptodira besteht aus drei Oberfamilien. Die Oberfamilie Chelonioidea ist durch die folgende Reihe gemeinsamer, abgeleiteter Merkmale charakterisiert: sella turcica reduziert oder verschwunden, dorsum sellae hoch und hängt nicht über carotiden Öffnungen, carotide Öffnungen dicht nebeneinander. Die Chelonioidea umschließt die Plesiochelyidae, Protostegidae, Toxochelyidae, Dermochelyidae und Cheloniidae. Das hauptsächlich gemeinsame, hergeleitete Merkmal, welches die Oberfamilie Trionychoidea bestimmt, ist die Reduzierung oder das Fehlen der stapediale Arterie. Die Familien Kinosternidae, Dermatemydidae, Carettochelyidae und Trionychidae werden auf dieser Grundlage in die Trionychoidea eingereiht. Ich war nicht in der Lage, die Oberfamilie Testudinoidea unter Verwertung gemeinsamer, hergeleiteter Merkmale zu diagnostizieren und die Gruppe kann paraphyletisch sein, weil sie nur durch primitive Grundzüge abgegrenzt ist. Die Familien Testudinidae, Emydidae und Chelydridae runden die Testudinoidea aus.

Die "Amphichelydia" ist eine höhere Art, die sich durch primitive Grundzüge kennzeichnet und angeblich die Ahnen der neuzeitlichen Schildkröte einschließt. Die Entwicklung einer streng monophyletischen Klassifizierung erfordert den Ausschluss dieser Art und die Neueinstufung der dazu gehörenden Artgruppen.

Obwohl die meisten Fossilien von Schildkröten nur aus Schalen oder Schalenteilen bestehen, so ist doch eine genügende Anzahl von Gruppierungen von Schädel-Schalen vorhanden, um die Entwicklung einer theoretischen Geschichte der Gruppe zu ermöglichen. Der Erwerb einer Schale (späte triassische Periode oder früher) ging den charakteristischen akinetischen Veränderungen voraus (obwohl die Kinesis tatsächlich zu jener Zeit oder früher verloren gegangen sein mag) und der Entwicklung von Hals- und Glieder Spezialisierungen. Anpassungen für die Zurückziehung des Halses (späte cretacäische Periode) erscheinen beträchtlich später als die akinetischen und palatoquadraten Eigenschaften, welche für Cryptodires und Pleurodires (späte jurassische Periode) diagnostisch sind. Die Identifizierung von Pleurodires in der späten jurassischen Periode (*Platychelys*) und in der späten triassischen Periode (*Proterochersis*) weist jedoch

darauf hin, dass die pleurodire-cryptodire Dichotomie sich sehr früh in der Geschichte der Schildkröten vollzog.

КРАТКОЕ ИЗЛОЖЕНИЕ

Базикранические признаки служат основой для новой теории взаимоотношений среди больших групп современных и вымерших черепах. Применяемый здесь метод для развития филогенетического гипотеза основан на распределении общих унаследованных признаков. Это стратегия изложен Хенningом (в 1966 году) и другими и часто называется кладизмом или филогенетической систематикой. Хотя я подчеркиваю филогенетическую реконструкцию, я также представляю новую классификацию черепах, которая состоит из строго монофилетических групп (насколько я мог определить) и является прямым отражением филогенетики.

1. Общие унаследованные признаки, определяющие отряд черепах включают: панцирь, потерю краевых зубов, гипотрофию среднего уха и, по всей вероятности, акинезию.

2. Черепахи подразделяются два признанных подотряда. Подотряд Proganochelydia состоит из рода Proganochelys триасового периода и характеризуется преобладающими примитивными особенностями, как например, открытой интерптеригоидной полостью и поперечно открытой полостью среднего уха. Все остальные черепахи входят в подотряд Casichelydia, который может быть определен применением общих унаследованных признаков, самым важным из которых является закрытая интерптеригоидная полость и среднее ухо с присутствием поперечной стенки.

3. Casichelydia состоят из двух инфраотрядов. Pleurodira обладают следующими общими унаследованными признаками: трохлеями мышц челюсти на крыловидной кости, квадратной костью, подкрепленной к черепной коробке. Инфраотряд Cryptodira обладает следующими общими признаками: трохлеями мышц челюсти на ушной полости, крыловидной костью, подкрепленной к черепной коробке.

4. В инфраотряде Cryptodira распознаются

две монофилетические классификации. В парвотряде Paracryptodira (состоящем только из надсемейства Baenoidea) внутренняя сонная артерия входит в череп на середине шва крыловидной кости и базисфеноида, в то время как в парвотряде Eucryptodira внутренняя сонная артерия входит с задней стороны крыловидной кости.

5. Eucryptodira содержат три надсемейства. Надсемейство Chelonioidea характеризуется следующей серией общих унаследованных признаков: уменьшенным или облитерованным турецким седлом, высокой спиной седла, не выступающей над протоками сонной артерии, протоками сонной артерии расположенными тесно бок о бок. Chelonioidea содержит Plesiochelyidae, Protostegidae, Toxochelyidae, Dermochelyidae и Cheloniidae. Основным общим унаследованным признаком, определяющим надсемейство Trionychoidea является уменьшение или отсутствие артерии стремечки. Семейства Kinosternidae, Dermatemyidae, Carettochelyidae и Trionychidae включены в надсемейство Trionychoidea на этом основании. Я не сумел определить надсемейство Testudinoidea при помощи общих унаследованных признаков, группа может быть парафилетической, так как она разграничена примитивными признаками. Семейство Testudinidae, Emydidae и Chelydridae составляют надсемейство Testudinidae.

Amphichelydia является более высокой таксоном, характеризующим примитивными признаками, якобы содержащим предков современных черепах. Развитие строго монофилетической классификации требует отрицания этого таксона и перераспределения таксисимеющихся в его составе. Хотя многие ископаемые остатки черепах состоят только из панцирей или фрагментов панцирей, существует достаточное количество черепнопанцирных ассоциаций, разрешающих развитие гипотетической истории группы. Приобретение панциря (поздняя триаса или раньше) предшествовало характеристической акинетической модификации (хотя кинесис мог в действительности быть потерянным в это время или раньше) и развитию шейных и конечностных специализаций

Приспособление к втягиванию шеи (поздний меловый период) появляется намного позже акинетических и небо-квадратнокостных признаков, определяющих cryptodires и pleurodires (поздний юрский период). Однако, опознование pleurodires в позднем юрском периоде (*Platychelys*) и поздней триасе (*Proterochersis*) предлагает, что дихотомия pleurodire-cryptodire произошла очень рано в истории черепах.

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