

THE JURASSIC TURTLES OF
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EUGENE S. GAFFNEY

*Associate Curator, Department of Vertebrate Paleontology
The American Museum of Natural History
Adjunct Assistant Professor, Department of Geological Sciences
Columbia University*

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ABSTRACT

There are two valid turtle taxa from the North American Late Jurassic Morrison Formation: *Glyptops plicatulus*, distinguished by a fine, pustulose shell ornamentation, last vertebral scute partially dividing the last pair of marginal scutes, and a smoothly convex anterior margin of the plastron; and *Dinochelys whitei*, new genus and species, distinguished by a smooth shell surface, last vertebral scute not dividing the last pair of marginal scutes, and an anterior plastral margin with lobes formed by the gular and intergular scutes. Presumed juveniles of *Glyptops* and *Dinochelys* suggest that prominent carapacial ridges characterize juveniles of these two taxa and that the ridges are lost in adults. *Probaena sculpta* Hay is considered a *nomen dubium* because it is an unidentifiable juvenile, presumably of *Glyptops* or *Dinochelys*. Taxa previously referred to *Glyptops* but here considered indeterminate are:

"*Glyptops*" *pervicax*, "*Glyptops*" *belviderensis*, "*Glyptops*" *caelatus*, "*Glyptops*" *depressus*, and "*Glyptops*" *rueimeyeri*. *Dinochelys* is placed Cryptodira *incertae sedis* because the higher systematics of cryptodires is based on skull morphology and the skull is lacking in this form. A cranial study of *Glyptops* suggests that it and *Mesochelys* form a monophyletic group, the Glyptopsidae, that is characterized by one derived character: the basisphenoid extends the length of, and completely separates, the pterygoids. I follow Evans and Kemp's (1976) suggestion that the Baenoidea of Gaffney (1972 and 1975) is not monophyletic and that the Glyptopsidae is the sister group of the remaining cryptodires. Baenidae and Eucryptodira would form a monophyletic group sharing the derived character: posterior temporal emargination separating or nearly separating parietal and squamosal.

INTRODUCTION

The pre-Cretaceous turtle record in North America is very sparse in comparison to the European record. One of the reasons for this appears to be the common occurrence of marine limestones in the European Upper Jurassic, which in one area alone (Solothurn, Switzerland) has yielded nearly 200 shells. The two North American Jurassic taxa in contrast occur in the freshwater, fluvial Morrison Formation but turtles are unknown in marine Jurassic rocks in North America. Where the Morrison Formation is well exposed, turtle fragments (usually *Glyptops*, fig. 1) are relatively common. Only one good skeleton (AMNH 336,

fig. 2) and two poorly preserved skulls (figs. 12-14) of turtles are known from the North

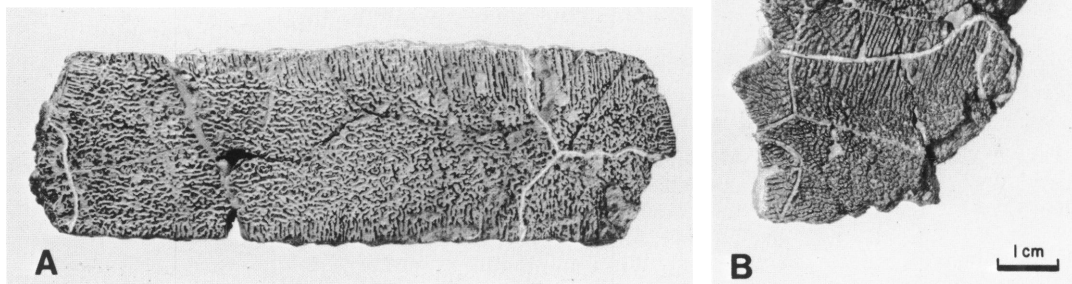


FIG. 1. *Glyptops plicatulus*, type specimen, AMNH 6099, probable source Morrison Formation, near Cañon City, Colorado. A. (?) Third left costal with ornamentation enhanced. B. Portions of left hypoplastron and xiphiplastron.

American Jurassic, again in contrast to the much better European Jurassic material.

My intention in this paper is to (1) determine and diagnose the taxa of North American

Jurassic turtles, and (2) present the cranial morphology and relationships of *Glyptops*, the only one of these taxa known from skull material.

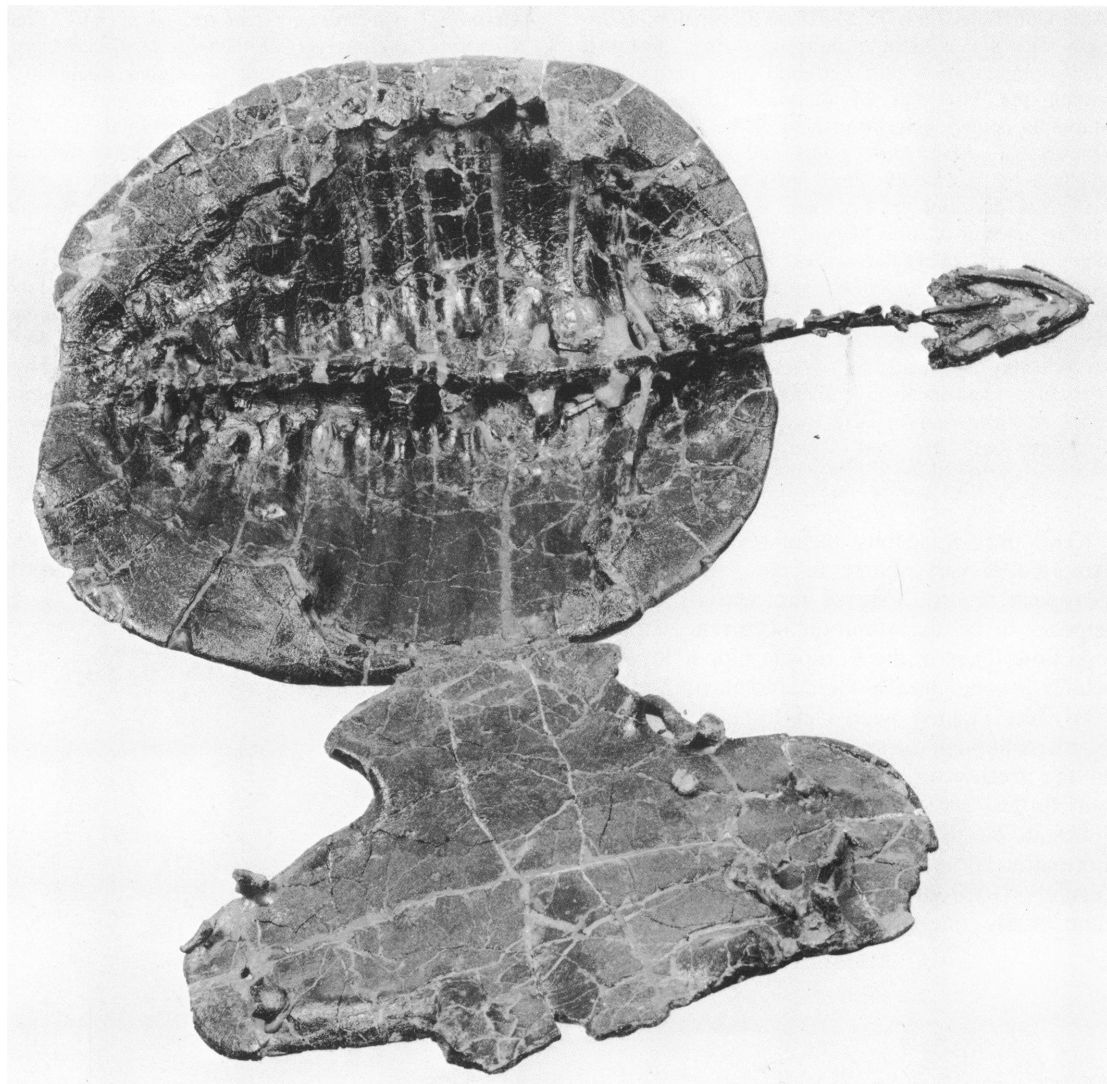


FIG. 2. *Glyptops plicatulus*, AMNH 336, an associated skull, shell, and partial skeleton, Bone Cabin Quarry, Wyoming. This figure is an oblique view of the internal surface of carapace and plastron. See also figure 5.

ABBREVIATIONS

INSTITUTIONS

AMNH, the American Museum of Natural History, New York, N.Y.

CM, Carnegie Museum of Natural History, Pittsburgh, Pa.

DNM, Dinosaur National Monument, Vernal, Utah
NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

YPM, Yale Peabody Museum, New Haven, Conn.

ANATOMICAL

ang, angular	pal, palatine
art, articular	pf, prefrontal
bo, basioccipital	pm, premaxilla
bs, basisphenoid	po, postorbital
cor, coronoid	pr, prootic
den, dentary	pra, prearticular
epi, epipterygoid	pt, pterygoid
ex, exoccipital	qj, quadratojugal
fr, frontal	qu, quadrate
ju, jugal	so, supraoccipital
mx, maxilla	sq, squamosal
na, nasal	sur, surangular
op, opisthotic	vo, vomer
pa, parietal	

ACKNOWLEDGMENTS

I am grateful to Dr. Theodore White who brought the Dinosaur National Monument turtles to my attention and urged me to work on *Dinochelys*, which he had recognized as distinct from *Glyptops*. Dr. Russell King and Mr. Jim Adams, both of Dinosaur National Monument, considerably aided my work there. Drs. John Ostrom and Jack MacIntosh helped me locate and borrow Yale Quarry Nine material; Dr. Nicholas Hotton III expedited my work on the National Museum of Natural History's Quarry Nine specimens. Drs. David Archibald and Howard Hutchinson kindly took time to review the manuscript.

Ms. Lorraine Meeker did the drawings and reconstructions and Mr. Chester Tarka took the photographs. Both of them produced excellent results with very difficult material and I am grateful to them for their efforts.

I thank the Explorers Club for supporting my fieldwork in the Morrison Formation.

SYSTEMATICS

ORDER TESTUDINES

SUBORDER CASICHELYDIA

INFRAORDER CRYPTODIRA

*INCERTAE SEDIS**DINOCHELYS*,¹ NEW GENUS

TYPE SPECIES: *Dinochelys whitei*, new species.

KNOWN DISTRIBUTION: Late Jurassic of Utah and Wyoming.

DIAGNOSIS: Member of the Cryptodira with external surface of carapace and plastron

smooth and lacking ornamentation seen in *Glyptops* and *Trinitichelys*; carapace oval, nuchal bone slightly indented anteriorly as in *Glyptops*; eight neural bones present; two suprapyrgals, the anterior one large and triangular in contrast to *Pleurosternon* in which it is small and rectangular; nuchal scute rectangular, no accessory nuchal scutes as in *Plesiochelys*; first costal articulates only with first and second peripherals rather than with first through third peripherals as in *Glyptops* and most turtles; supramarginal scutes absent; last vertebral scute completely enclosed by rectangular marginals in contrast to *Glyptops* but as in *Plesiochelys* and *Pleurosternon*; plastral fontanelles absent, at least in presumed adults; anterior edge of plastron produced into lobes by indentations of

¹In reference to the type locality, Dinosaur National Monument.

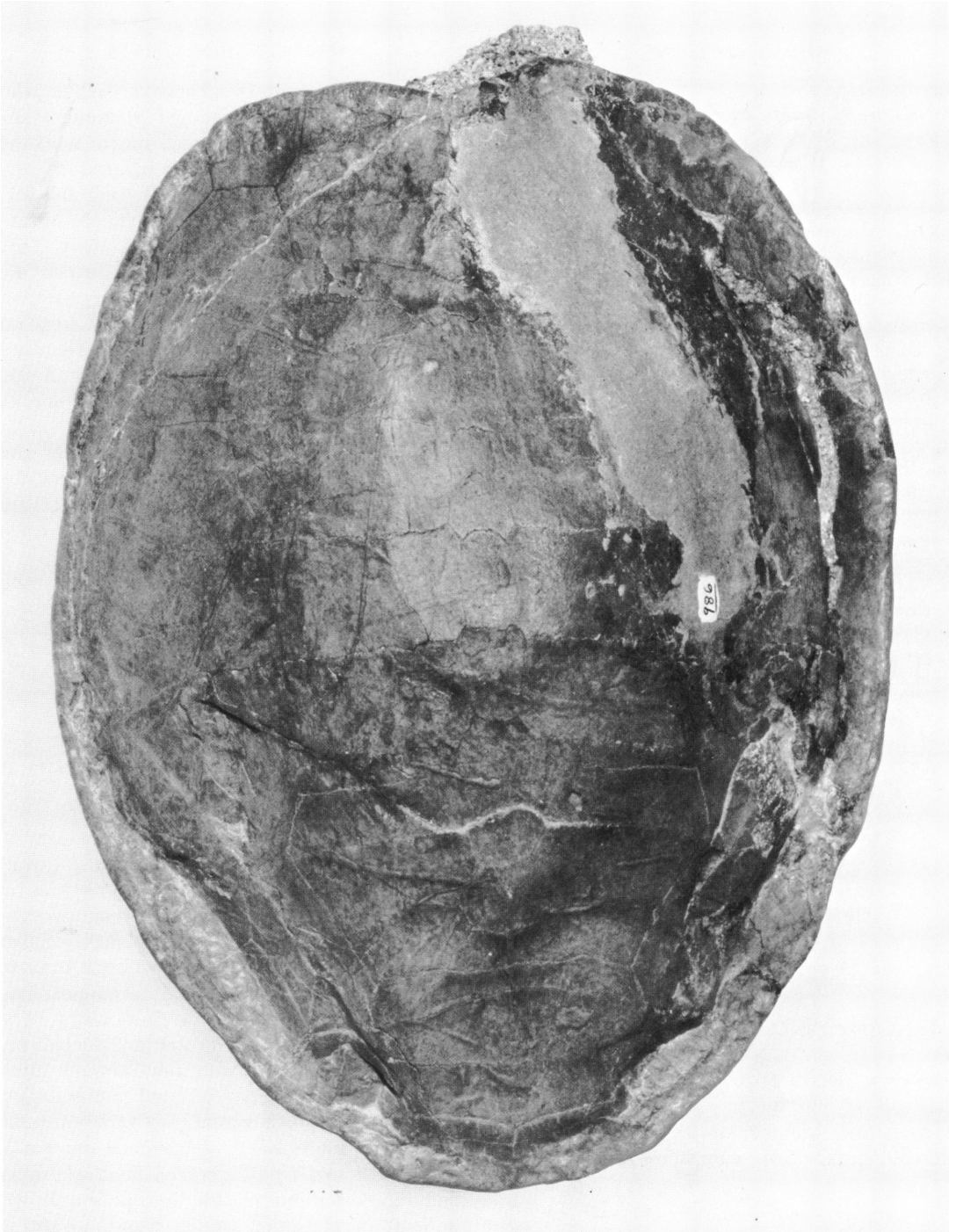


FIG. 3. *Dinochelys whitei*, new genus and species, type specimen, DNM 986, Dinosaur National Monument Quarry, near Vernal, Utah. Dorsal view of shell. Length of midline 310 mm.



FIG. 4. *Dinochelys whitei*, new genus and species, type specimen, DNM 986, Dinosaur National Monument Quarry, near Vernal, Utah. Ventral view of shell. Length of plastron 266 mm.

gular and intergular sulci in contrast to *Glyptops* but similar to *Plesiochelys*; mesoplastra meet in midline; xiphiplastral notch as seen in *Pleurosternon* and *Mesochelys* absent; dorsal surface of xiphiplastron with facet for seemingly movable articulation with pubis, sutural attachment between shell and pelvis absent; one pair of intergular scutes present, extending barely onto entoplastron, and widely separating gular scutes; inframarginal scutes present.

DISCUSSION: See discussion of species following.

Dinochelys whitei,¹ new species

TYPE SPECIMEN (FIGS. 3-5): DNM 986-991, complete shell with associated postcranial elements; still in the matrix with the shell are both pelvis, right humerus and scapula, and left(?) coracoid; about 12 caudal vertebrae, right digits I-V, right tibia; two sacral (?) vertebrae; complete left foot; left femur; left tibia and fibula. Previously figured in Hagood (1976, p. 9) and McIntosh (1977, p. 31).

LOCALITY: Quarry face as exposed inside the Dinosaur National Monument Visitor Center building near Vernal, Utah.

HORIZON: Brushy Basin Member, Morrison Formation, Upper Jurassic.

REFERRED SPECIMENS: All the following specimens are in the Marsh Collection made at Quarry Nine, Como Bluff, Wyoming, Morrison Formation, during the 1880s.

YPM 6057, right epiplastron, entoplastron, left hyoplastron, right and left hypoplastra, right and left xiphiplastra, and two left bridge peripherals. YPM 6078, right epiplastron; YPM 6068, costal fragment and two bridge peripherals; YPM 6089, right sixth costal; YPM 6069, left seventh costal and associated neural; various costal fragments: YPM 6056, 6079, 6081, 6084, 6085, 6090, 6092, 6093, 6096; various peripherals: 6070, 6071, 6072, 6073, 6074, 6075, 6080, 6103, 6104, 6106, 6113, 6119.

¹For Dr. Theodore White, formerly Paleontologist at Dinosaur National Monument.

DNM 993 (fig. 10), a complete shell with right hind foot, very questionably referred to *Dinochelys* (see section below on *Probaena*). Brushy Basin Member, Morrison Formation, Dinosaur National Monument Quarry near Vernal, Utah. Figured (upside down) in McIntosh (1977, p. 34).

DISCUSSION: *Dinochelys* (see table 1, fig. 5) is most similar to *Glyptops* but differs from it in lacking any ornamentation on the shell, in having distinctive lobes formed by the gular and intergular scutes on the anterior lobe of the plastron, in having relatively broad vertebral scutes, and in having the last vertebral scute completely enclosed by the last marginal scutes. A comparison of left and right epiplastra in *Glyptops* and *Dinochelys* (fig. 6) makes some of these features particularly apparent. Of the taxa possessing medially meeting mesoplastra, *Pleurosternon* is also similar to *Dinochelys* but differs in that the latter lacks a xiphiplastral notch but has a nuchal scute and large triangular anterior suprapygal as well as broad vertebral scutes. *Mesochelys* is so poorly known from shell material that comparisons are difficult but that genus has scalloped peripheral bones and a xiphiplastral notch, both lacking in *Dinochelys*.

Dinochelys is most similar to *Glyptops* but all the characters in common I judge to be primitive for Cryptodira. I cannot make a useful argument for allying *Dinochelys* with any particular cryptodire or group of cryptodires and, to some, this will be a good reason to retain the paraphyletic group "Amphichelydia." However, *Dinochelys* is a diagnosable taxon, and even though I hesitate to inflict another *incertae sedis* shell taxon on fellow turtle workers, I see no advantage in refraining from naming it. It can be proposed that *Dinochelys whitei* would be better as a new species of *Glyptops* rather than as a new genus, but I have not done this because it would be an explicit statement that the two species are sister taxa and there is no reason to think that this is the case. Nonetheless, I realize that naming a new genus does not clarify the situation either. Cranial material of *Dinochelys* should help this problem.

TABLE 1
Shell Features of Selected Jurassic and Early Cretaceous Turtles

Character	<i>Dinochelys</i>	<i>Glyptops</i>	<i>Trinitichelys</i>	<i>Plesiochelys</i>	<i>Pleurosternon</i>	<i>Mesochelys</i>
Surface ornamentation	Smooth	Raised ridges and tubercles	As in <i>Glyptops</i>	Smooth	Similar to <i>Glyptops</i> but less pronounced	Similar to <i>Glyptops</i>
Number of neurals	8	8	Indeterminant	6-8	8	Indeterminant
Anterior suprapygal	Triangular, large	Triangular, large	Indeterminant	Triangular, large	Rectangular, small	Indeterminant
Scalloped peripheral bones	No	No	No	No	No	Yes
Nuchal scute	Present	Present	Present	Present	Absent	Indeterminant
Accessory nuchal scutes	Absent	Absent	Absent	Present	Absent	Indeterminant
Last vertebral scute barely enclosed by tapering margins	No	Yes	Indeterminant	No	No	Indeterminant
Inframarginal scutes	Present	Present	Present	Present	Present	Indeterminant
Vertebral scutes	Broad	Narrow	Narrow	Narrow to broad	Narrow	Indeterminant
Mesoplastra meet in mid-line	Yes	Yes	Yes	Mesoplastra absent	Yes	Indeterminant
Plastral fontanelles	Absent	Absent	Absent	Present and absent	Absent	Indeterminant
Anterior edge of plastron produced into lobes by gular and intergular sulci	Yes	No	No	Yes	No	Indeterminant
Xiphiplastral notch	Absent	Absent	Indeterminant	Absent	Present	Present
Relative thickness of bone in plastron (in presumed adults)	Thick	Thin	Thin	Thin	Thin	Indeterminant

The Marsh collections from Quarry Nine, Como Bluff, Wyoming, now at the Yale Peabody Museum, contain a number of disarticulated turtle shell bones that are smooth and lack the distinctive ornamentation of *Glyptops*. Study of this material is difficult because of the lack of association, but a partial plastron (YPM 6057, fig. 7) was fitted together and seems to belong to one individual. This plastron is about 20 percent larger than the type and indicates that *Dinochelys* reached a larger size than *Glyptops*. Appendicular and vertebral elements are available for both *Glyptops* and *Dinochelys* and study of this material might bear phylogenetic fruit, but it would require a more extensive comparative background than I am willing to acquire at present.

FAMILY GLYPTOPSIDAE MARSH, 1890

TYPE: *Glyptops* Marsh, 1890.

KNOWN DISTRIBUTION: Late Jurassic of Utah, Wyoming, and Colorado; Early Cretaceous of Britain.

REVISED DIAGNOSIS: Casichelydian turtles (see Gaffney, 1975) having as their sole unique feature an elongate basisphenoid extending the length of and completely separating the pterygoids; skull relatively long and narrow; nasals present; well-developed prefrontal lappets not meeting medially; posterior temporal emargination poorly developed in comparison to Baenidae and most Eucryptodira, well-developed parietal-squamosal contact; foramen posterius canalis carotici interni formed by

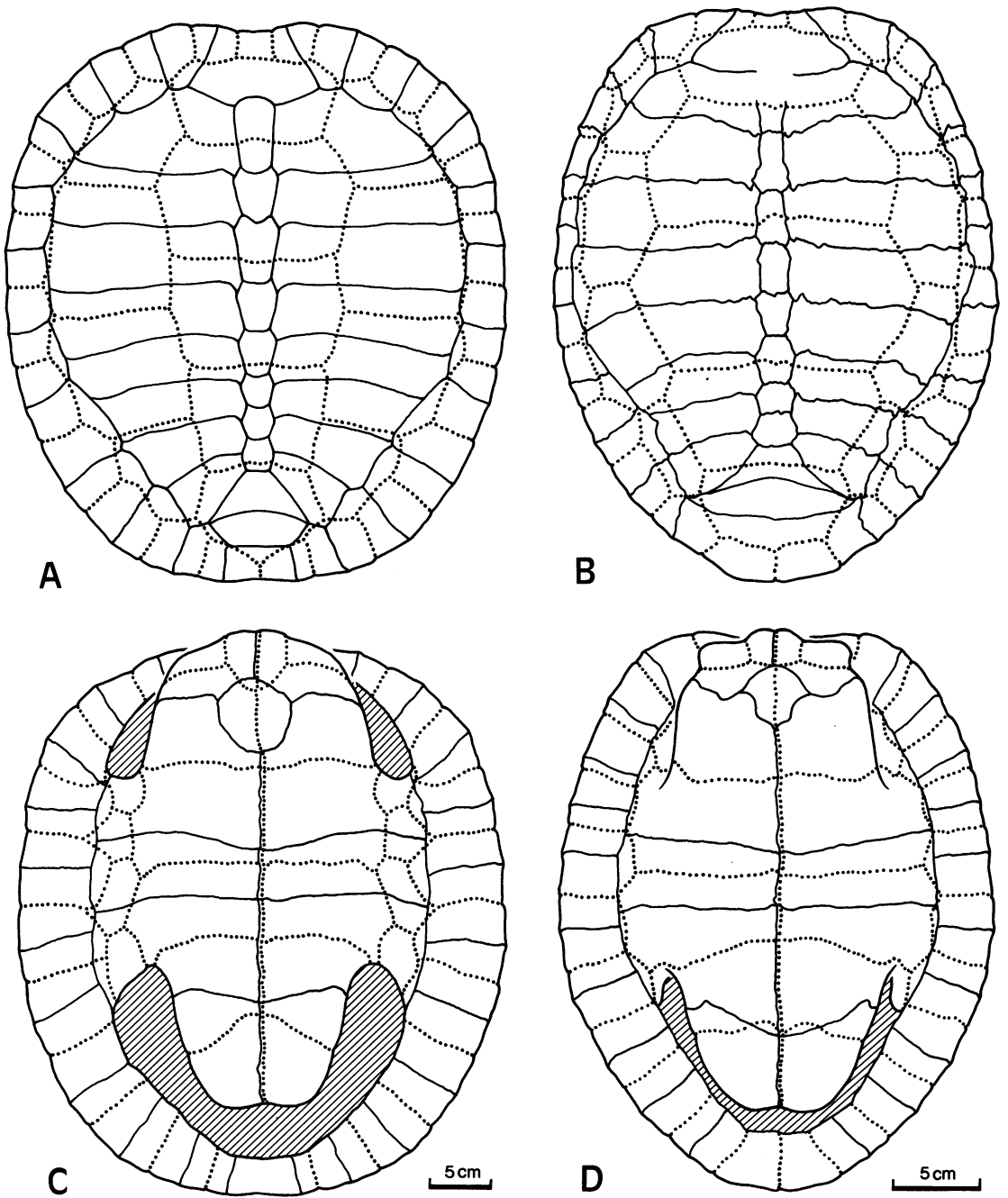


FIG. 5. Partially restored views of the shell in *Glyptops plicatulus* (A, C) and *Dinochelys whitei* (B, D). *Glyptops* is based primarily on AMNH 336 with additions from AMNH 5458; *Dinochelys* is based on DNM 986.

basisphenoid and lies midway along its length in close proximity to the pterygoid suture; epipterygoid present and well developed; cervical vertebrae amphicoelus.

DISCUSSION: I follow Evans and Kemp's (1975) addition of *Mesochelys* to the previously monotypic Glyptopsidae but modify their diagnosis by arguing that the two taxa have a derived character in common, namely basisphenoid morphology (see section on relationships for discussion).

GLYPTOPS MARSH, 1890

Compsemys Leidy, 1856, p. 312.

TYPE SPECIES: *Compsemys plicatulus* Cope, 1877, p. 195.

KNOWN DISTRIBUTION: Late Jurassic of Wyoming, Utah, and Colorado.

DIAGNOSIS: A glyptopsid turtle that differs from *Mesochelys* (see table 2) the only other genus in the Glyptopsidae, in the following features: hooked premaxillae; narrower interorbital distance; small or absent nasal-prefrontal contact; narrower maxillary triturating surface relatively large palatine; jugal widely separated from orbit by well-developed postorbital-maxilla contact; carapace with smooth outline; xiphiplastral notch absent.

External surface of skull and shell with a

distinctive ornamentation consisting of tubercles and raised ridges in a vermiculate pattern as in *Trinitichelys*; carapace oval (shell poorly known in *Mesochelys*, see table 1), nuchal bone slightly indented anteriorly, as in *Dinochelys*; eight neural bones present; two suprapygals, the anterior one large and triangular as in *Dinochelys* but in contrast to *Pleurosternon*; nuchal scute rectangular, no accessory nuchal scutes as in *Plesiochelys*; supramarginal scutes absent; last vertebral scute barely enclosed by tapering marginal scutes; plastral fontanelles absent, at least in presumed adults; anterior lobe of plastron smoothly convex, not produced into lobes

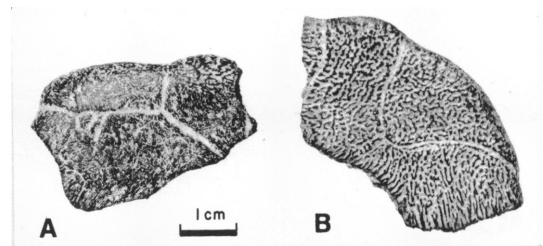


FIG. 6. Epiplastra enhanced to show surface morphology. A. Right epiplastron of *Dinochelys whitei*, new genus and species, YPM 6078; B. Left epiplastron of *Glyptops plicatulus*, YPM 6077. Both specimens from Quarry Nine, Como Bluff, Wyoming.

TABLE 2
Comparison of *Glyptops* and *Mesochelys*

	<i>Glyptops</i>	<i>Mesochelys</i>
Hooked premaxilla	Present ^a	Absent
Interorbital distance	Narrow	Broad
Well developed nasal-prefrontal contact	Probably absent	Present
Maxillary triturating surface	Narrow	Broad
Incisura columellae auris	Probably wide	Narrow
Palatine	Relatively large	Relatively small
Jugal	Widely separated from orbit	Just entering orbit
Carapace	Without emarginate peripherals	With at least one emarginate peripheral
Xiphiplastral notch	Absent	Present

^aBroken off in specimens but present in figure in Hay (1908a).

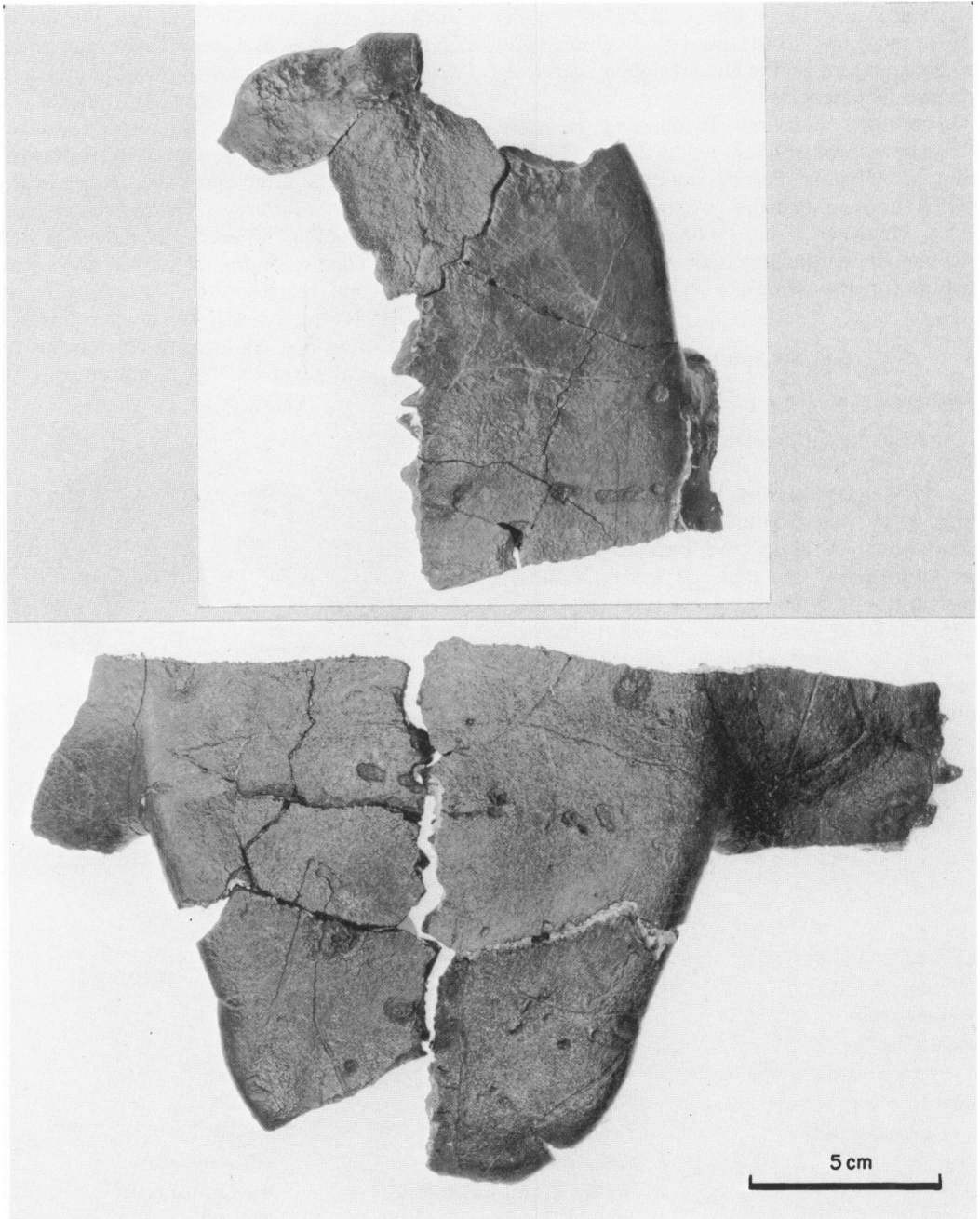


FIG. 7. Ventral view of plastron, *Dinochelys whitei* YPM 6057, Quarry Nine, Como Bluff, Wyoming.

as in *Dinochelys*; mesoplastra meet in midline; xiphiplastral notch, as seen in *Pleurosternon*

and *Mesochelys*, absent; dorsal surface of xiphiplastron with facet for seemingly movable

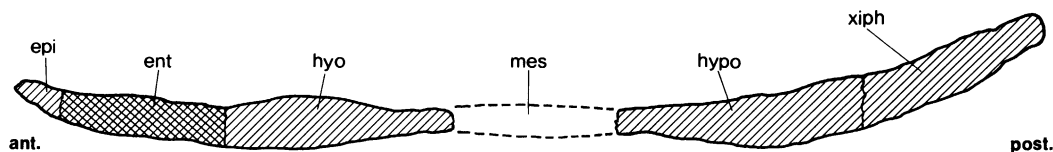


FIG. 8. *Dinochelys whitei*, new genus and species, YPM 6057. Cross-section of plastron seen in fig. 7. Abbreviations: ant, anterior; ent, entoplastron; epi, epiplastron; hyo, hyoplastron; hypo, hypoplastron; mes, mesoplastron; post, posterior; xiph, xiphiplastron.

articulation with pubis, sutural attachment between shell and pelvis absent; one pair of intergular scutes, barely extending onto entoplastron, and widely separating gular scutes; inframarginal scutes absent.

Glyptops plicatulus (Cope)

Compsemys plicatulus Cope, 1877, p. 195.

Glyptops ornatus Marsh, 1890, p. 177.

Glyptops utahensis Gilmore, 1916, p. 7.

TYPE SPECIMEN: AMNH 6099, a (?) third left costal (fig. 1, also figured in Hay, 1908a, pl. 5, fig. 1), fragmentary left hypoplastron and xiphiplastron (fig. 1), plus various shell fragments. Also present are some non-turtle fragments. The original label with the material reads "2352 *Compsemys plicatulus* No. 9." I have no idea what this refers to. There is no information on association and if there is ever any question about the association of these carapace and plastral fragments, the costal should be considered the type specimen.

LOCALITY: "Dakota Beds of Colorado" (Cope, 1877). The specimen was apparently found with sauropods and presumably comes from Garden Park near Cañon City (see Ostrom

and McIntosh, 1966, fig. 1, for map and historical background).

HORIZON: Presumably the Morrison Formation, Late Jurassic.

COLLECTOR: O. W. Lucas, one of Cope's collectors, probably in 1876 or 1877.

DIAGNOSIS: The genus is monotypic.

REFERRED SPECIMENS: Marsh's collections from Quarry Nine at Como Bluff, Wyoming, and now housed in the Yale Peabody Museum and the National Museum of Natural History contain many turtle shell fragments that can be identified on the basis of ornament as *Glyptops plicatulus*. This material is uncatalogued and not listed here.

AMNH 336 (figs. 12-14, 16; Hay, 1908a, pp. 47-52, figs. 17, 19-27; pl. 5, figs. 3, 4; pl. 6), a nearly complete skeleton with skull. Field no. 86. Probably prepared and mounted for exhibition by A. Thomson, about 1901, with the plastron turned back, on a hinge, to show the inside of the carapace with vertebrae and skull in position (fig. 2). Locality: Bone Cabin Quarry of the American Museum of Natural History, in the Medicine Bow Anticline, Wyoming, (see Osborn, 1904; Colbert, 1968, p. 149, for locality map and description). I have

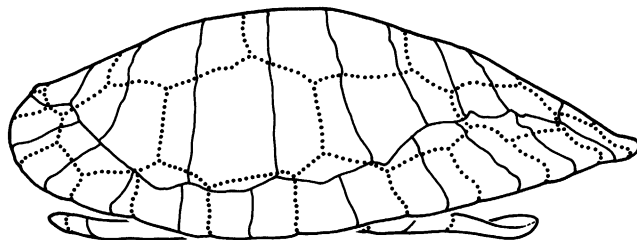


FIG. 9. Lateral view of shell, *Dinochelys whitei*, new genus and species, type specimen, DNM 986. See also figure 5.

been unable to locate the specimen on quarry diagrams. Horizon: Morrison Formation, Late Jurassic. Collector: American Museum Expedition, 1898, consisting of Wortman, Granger, Menke and Kaisen.

YPM 1784 (figs. 12-15; type of *Glyptops ornatus* Marsh, 1890, p. 177, pl. 7, fig. 1; Marsh, 1897, fig. 63; Hay, 1908a, pl. 5 fig. 2), a laterally compressed skull without lower jaws. Locality: Reed's YPM Quarry 9 (mammal quarry), T 22 N, R 77 W, sec. 12, Como Bluff, Wyoming (see Ostrom and McIntosh, 1966, for background, maps, and quarry list). Horizon: Morrison Formation, Late Jurassic. Collector: William H. Reed.

YPM 1357 (figured by Marsh as *Glyptops ornatus*, 1890, pl. 7, fig. 2; Hay, 1908, fig. 18), carapace (not seen). The same data as YPM 1784.

YPM 4742, anterior end of right lower jaw ramus. Same data as YPM 1784.

YPM 4721, fragmentary left dentary. Same data as YPM 1784.

YPM 4717, braincase (fig. 19-22) consisting of basisphenoid, basioccipital, exoccipitals and prootics. Same data as YPM 1784.

YPM 5821, left lower jaw (figs. 24,25). Same data as YPM 1784.

YPM 2753, left lower jaw. Same data as YPM 1784.

YPM 6077, left epiplastron. Same data as YPM 1784.

NMNH 26370, basioccipital. Same data as YPM 1784.

NMNH 26371, basioccipital. Same data as YPM 1784.

CM 3412 (type of *Glyptops utahensis* Gilmore, 1916, pp. 7-12, figs. 1, 2, pl. 1), a complete shell. Locality: "Carnegie Dinosaur Quarry, near Jensen, Uinta County, Utah." This is now Dinosaur National Monument.

Horizon: Morrison Formation, Late Jurassic. Collector: Earl Douglas, 1913.

CM 3380 (referred specimen of *Glyptops utahensis* in Gilmore, 1916). Same data as CM 3412.

NMNH 5458 (Hay, 1908b, pp. 161-162, fig. 1), posterior part of carapace.

Locality: ". . . it was collected by a member of one of Professor O. C. Marsh's party at Como Bluff, Wyoming, in 1884."

DNM 1122, shell. Locality: Dinosaur National Monument Quarry, near Vernal Utah. Horizon: Morrison Formation, Late Jurassic.

DNM 994, badly fractured shell. Same data as DNM 1122.

DNM 995, entoplastron, both hyoplastra. Same data as DNM 1122.

DISCUSSION: In 1877, Cope described the new species *Compsemys plicatulus* based on a costal bone and plastron fragments from the Jurassic of Colorado. He apparently referred it to Leidy's *Compsemys* on the basis of ornamentation. Marsh, in 1890, described a skull from the Jurassic of Wyoming, creating the taxon *Glyptops ornatus* for its reception. Hay (1908a), having an associated skull and shell (AMNH 336) from the Jurassic of Wyoming, recognized that Cope's *Compsemys plicatulus* was the same as Marsh's *Glyptops ornatus*, and produced the new combination, *Glyptops plicatulus*.

Glyptops utahensis Gilmore is here synonymized with *G. plicatulus* because Gilmore's diagnostic criteria (1916, p. 11) are within my subjectively determined limits of species demarcation. One criterion, however, shell shape, appears to be different in the two supposed forms because the Utah shells are only slightly deformed, if at all, whereas the AMNH shell is considerably flattened.

FORMS INADEQUATELY KNOWN BUT PREVIOUSLY REFERRED TO *GLYPTOPS*

"*Glyptops*" *pervicax* Hay, 1908a.

TYPE SPECIMEN: AMNH 1018 (incorrectly given as AMNH 1910 in both Hay, 1908a and

Ostrom, 1970), a poorly preserved carapace and plastron.

LOCALITY AND HORIZON: According to Os-

from (1970, p. 60), the most likely source of the type specimen is Push Creek, 13 miles east of Pryor, Montana, Sykes Mountain Formation or Thermopolis Shale.

DISCUSSION: Although Hay's (1908a, p. 46) key indicated that the primary diagnostic feature of *G. pervicax* was the stratigraphic position, he did compare it with other taxa (*ibid.*, p. 55): "To *Glyptops* is provisionally referred *G. pervicax*, which in some respects approaches more closely *Pleurosternon*, more especially in having the plastron slightly notched behind. On the other hand, the bridge is longer than in *Glyptops plicatulus*. It is not improbable that it represents an undescribed genus." The information about the posterior edge of the plastron came from the referred specimen (AMNH 6071, "... collected by Barnum Brown, 1904, in the Crow Reservation, Montana, at a point about 50 miles southeast from Billings and about 25 miles east of Pryor, *ibid.*"). The label gives the horizon as "Middle Cretaceous, Benton Formation." This specimen is somewhat better preserved but as in the type, most of the sutures are difficult to determine. Most of the sulci painted on both specimens by Hay are also doubtful, particularly on the carapace.

The absence of sutures in the material (perhaps fused or possibly due to preservation) prevents any definite statement about the taxonomic position of this form. The internal surface of the plastron in the type shows that the pelvis was not sutured in the pleurodiran manner and further shows an ischial tuberosity on the right side. This tuberosity is commonly found in *Glyptops* and baenids but also occurs in other groups and can hardly be used as a diagnostic feature. The material cannot be differentiated from *Glyptops*, *Trinitichelys* or, as Hay suggested, from European Jurassic material.

"*Glyptops*" *belviderensis* (Cragin, 1894).

TYPE SPECIMEN: The figures (Cragin, 1894), show four costals and one neural but the description indicates more material. "In Colorado College, Colorado Springs, Colorado" (Hay, 1908a, p. 53). I have been unable to determine

the whereabouts of this specimen, and it would appear that Hay did not see it either.

LOCALITY AND HORIZON: "... about half a mile south of the railway station at Belvidere, Kansas, at the upper limit of the black shale that constitutes No. 4 of the "Belvidere section" (Cragin, 1894, p. 71).

DISCUSSION: Cragin (1894) originally described this specimen as a new species of *Plesiochelys*, differentiating it from *P. solodurensis*. Hay (1908a) referred it to *Glyptops*? on the basis of the ornament seen in Cragin's figures. Although the figures are somewhat crude, in my opinion the ornament as figured is also consistent with *Peritresius*, a toxochelyid studied by Baird (1964). In any case, the taxon as presently known is not diagnosable because so little of the shell morphology is known.

"*Glyptops*" *caelatus* Hay, 1908a.

TYPE SPECIMEN: NMNH 5800 (originally no. 1930 and reported as such in Hay, 1908a), a first right costal and first and second right peripherals.

LOCALITY AND HORIZON: Muirkirk, Maryland, Potomac Formation, early Cretaceous, collected by J. B. Hatcher, 1887 (Hay, 1908a, p. 52).

DISCUSSION: Although the sculpture pattern of the type is the same as the pattern seen in *Glyptops* and *Trinitichelys*, the scanty nature of the specimen precludes identifying it with one of these taxa; the presence of this ornament pattern alone is insufficient to identify the specimen.

"*Glyptops*" *depressus* Hay, 1908a.

TYPE SPECIMEN: NMNH 5731, mentioned by Hay as having "packing number 1998." Consisting of a poorly preserved shell lacking most of the bone surface and edges.

LOCALITY AND HORIZON: Hay (1908a, p. 55) stated: "It appears to have been secured by one of Professor O. C. Marsh's collectors in 1889, inasmuch as it bears his packing number '1998, Box 3.' With the specimen comes a statement by Mr. Whitman Cross, of the United States Geological Survey as follows: 'No. 2 Box B. '89' (Cannon's designation). An

isolated fragment. (I think this fossil is from the Denver beds, from the nature of the sandstone between the shells and the apparently zeolitic material in cells of the bone.)" Strictly speaking, there appears to be no useful locality data.

DISCUSSION: Sutures (but not sulci) are determinable and Hay's figures (1908a, figs. 33, 34) agree closely with the specimen. Medially meeting mesoplastra suggest the baenids but because this is a primitive chelonian character it is not diagnostic. Most of the bone surface has been worn away so that ornamentation and sulci are not visible.

"*Glyptops*" *ruetimeyeri* (Lydekker, 1889).

TYPE SPECIMEN: BM(NH) 40676 (*vide* Lydekker, 1889), consists of carapace lacking all peripherals except the first and second on the left and the first on the right. Not seen in the course of this study.

LOCALITY AND HORIZON: "Purbeck of Swanage, Dorsetshire" (Lydekker, 1889, p. 149), Early Cretaceous.

DISCUSSION: Watson (1910) identified two shells in the Manchester Museum (L. 7017, L. 9520) as pertaining to Lydekker's "*Thalassemys*" *ruetimeyeri*. Both were from the Purbeck beds of Swanage, as was the type specimen. Watson argued that on the basis of the medially meeting mesoplastra the taxon could not be

assigned to *Thalassemys* but should be assigned to *Glyptops*. Although Watson noted the similarity to *Pleurosternon* he differentiated "*G.*" *ruetimeyeri* by the "... presence of a nuchal shield and [by] the emarginate anterior-edge" (Watson, 1910, p. 314). The emarginate anterior edge is not demonstrated by Watson's figures and there is no convincing evidence in the literature that the two authors were working with the same taxon. In any case, glyptopsids (*Mesochelys*) do occur in Europe (Evans and Kemp, 1975) and it would be impossible at present to argue that any of the shells identified as "*Glyptops*" *ruetimeyeri* were *Glyptops* and not *Mesochelys*, which lacks a useful shell.

"*Glyptops*" sp.

SPECIMEN: Laboratory of Vertebrate Paleontology, Academia Sinica, V374, a partial fourth right costal (Chow, 1954, fig. 1, p. 404; also Yeh, 1963). Not seen in the course of this study.

LOCALITY AND HORIZON: Chingkongkou, Laiyang, Shangtung, Peoples' Republic of China; Wangshih Formation, Late Cretaceous (Chow, 1954).

DISCUSSION: I mention this identification because of its zoogeographic interest. Unfortunately on the basis of published data there is no reason to identify this specimen as *Glyptops*. It is a turtle, however.

THE STATUS OF *PROBAENA SCULPTA* HAY

Hay (1903; see also 1908a, pl. 7) described a small turtle shell from the Cañon City, Colorado region of the Morrison Formation as a new genus, *Probaena sculpta*. Although Hay noted at the time that the individual might be a juvenile because of its small size and the presence of a central fontanelle on the plastron, he argued that the distinctive radiating ridges on the carapace were unknown in the only other Morrison turtle, *Glyptops*, and that the ridges were similar to those found in the Eocene *Baena*. He therefore concluded that *Probaena*, juvenile or not, was distinct from *Glyptops* and related to *Baena*. While making a search of the USNM and YPM Quarry Nine collections, I found a

few dozen small isolated shell bones and later White brought to my attention some small shells collected at Dinosaur National Monument which are about the same size as the type of *Probaena*, but are much better preserved. Study of these specimens suggests that they (as well as the type of *Probaena*) are juveniles, assignable to either *Glyptops* or *Dinochelys* and that the radiating ridges on the carapace are a feature peculiar to juveniles and lost in the adults.

The bone surface is relatively well preserved in the Dinosaur National Monument shells but the type specimen of *Probaena* (CM 917) has a badly eroded and broken surface. All three

shells, nonetheless, display the radiating ridges noted by Hay as diagnostic of *Probaena*. These ridges occur in the areas covered in life by the five vertebral scales. Within each scale area the ridges radiate anteriorly and laterally from a point on the midline at the posterior margin of the scale. Usually three or four nearly parallel ridges are present on the midline, whereas the more lateral ridges extend anterolaterally. DNM 993 (fig. 10) also has concentric ridges paralleling the sulci but these are not evident on DNM 992 (fig. 11). There are also parasagittal ridges in the region covered by the pleural scales, one ridge per scale. These can be seen in CM 917 and DNM 992, but not in DNM 993, because most of the pleural region in that specimen is unossified. Fine, *Glyptops*-like ornament covers the shell in DNM 992 but DNM 993 lacks this feature. The surface pattern in CM 917, unfortunately, is not sufficiently well preserved to determine.

This radiating ornament is quite similar to that figured for *Desmemys* (Wegner, 1911), a shell from the Wealden of Gronau. This shell is 180 mm. in length and has well-developed plas-

tral and costo-peripheral fontanelles, which led Wegner to place it in the Thalassemydidae, a "waste-basket" taxon of "Amphichelydia" having presumed marine adaptations. But large mesoplastra are present, a feature absent in other "thalassemydids." The nuchal area is missing and the systematically important ventral surface of the plastron is not figured by Wegner, precluding further comparison.

The carapace bones and sulci in CM 917 are nearly impossible to determine but I can agree with Hay's (1903 and 1908a) description of them. DNM 993 differs strikingly from CM 917 and DNM 992 in the presence of extensive costo-peripheral fontanelles. CM 917 has no extensive costo-peripheral fontanelles but a slight space, as seen in DNM 992, may be present.

The most remarkable difference in the plastron among the specimens is the development of fontanelles and varying degrees of ossification. DNM 992 has the smallest central fontanelle and few, if any, bridge-peripheral openings, whereas DNM 993 has a relatively large central fontanelle and greatly developed

TABLE 3
A Comparison of Three Possibly Juvenile Shells
(Measurements in millimeters.)

Feature	CM 917	DNM 992	DNM 993
Midline carapace length as preserved	105 ^a	95 ^b	101
Maximum carapace width as preserved	72	66	81
Radiating ridges on bone underlying vertebral scutes	yes	yes	yes
Costo-peripheral fontanelles	absent or only slightly developed	slightly developed	extensive
Midline plastron length as preserved	77 ^a	77 ^a	86
Plastron width at base of anterior lobe	37	30	38
Epiplastra	lost in preservation	lost in preservation	present
Central fontanelle on plastron, maximum width as preserved	15 ^b	6	9
Central fontanelle, maximum length as preserved	13	11	20
Central fontanelle separating hypoplastron	probably	no	yes
Shape of central fontanelle	circular	oval	oval
Bridge-peripheral fontanelle on plastron	small or absent	small or absent	extensive

^aSignificant portions missing.

^bSmall portions missing.

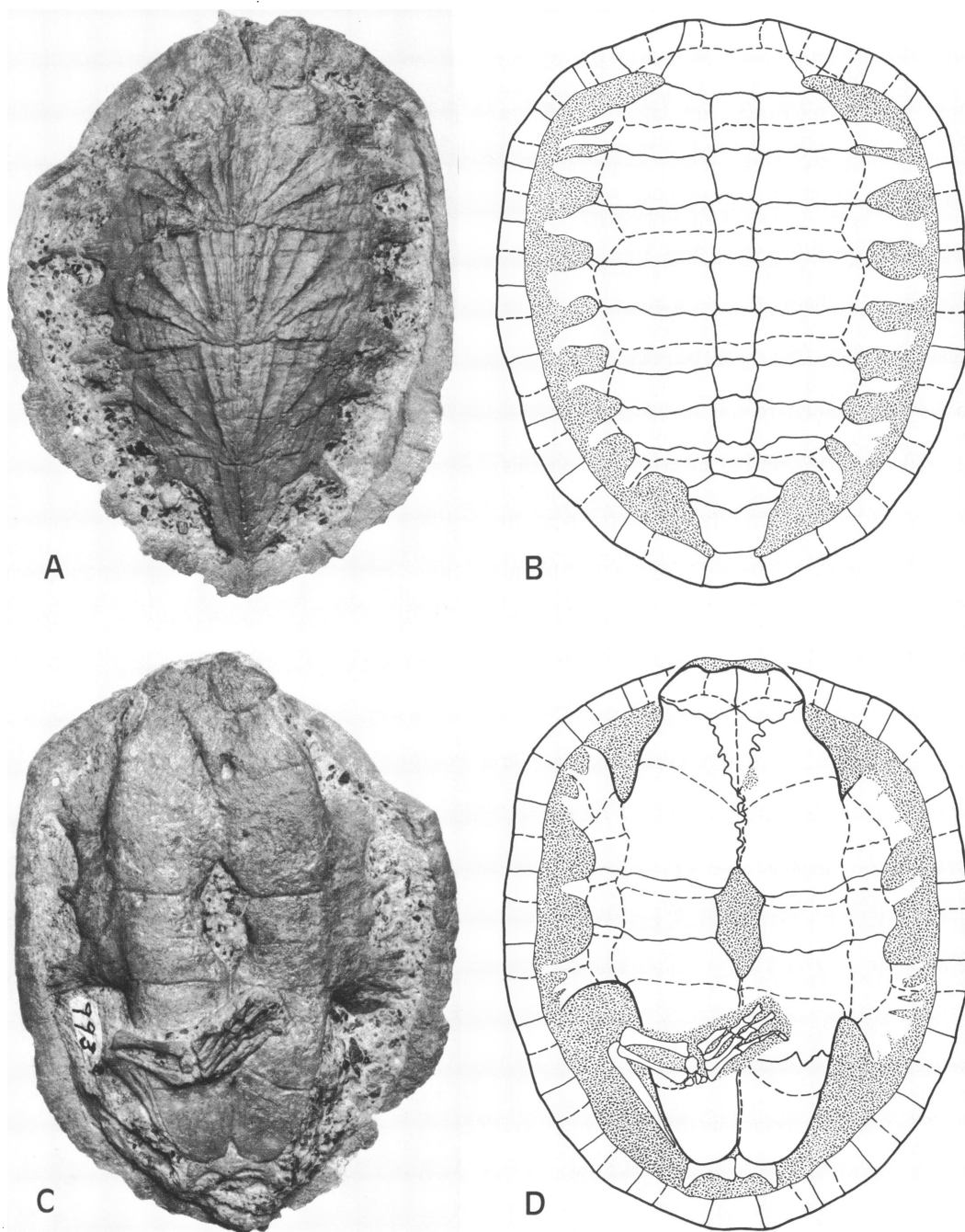


FIG. 10. Presumed juvenile shell, possibly belonging to *Dinochelys whitei*, DNM 993, Dinosaur National Monument Quarry, near Vernal, Utah. Dorsal views (A, B) and ventral views (C, D), with B and D partially restored. Midline length 101 mm.

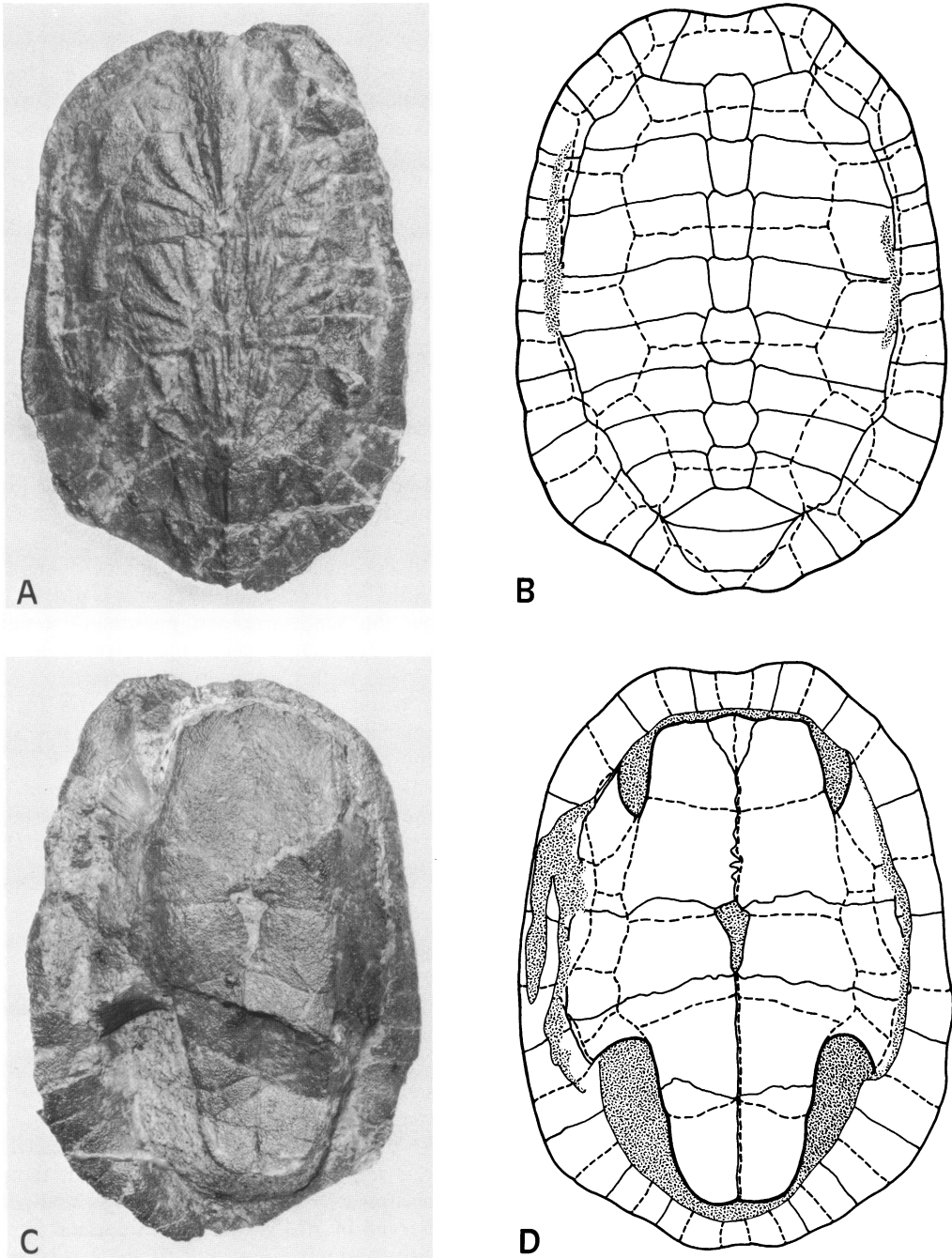


FIG. 11. Presumed juvenile shell of *Glyptops plicatulus*, DNM 992, Dinosaur National Monument Quarry, near Vernal, Utah. Dorsal views (A, B) and ventral views (C, D) with B and D partially restored. Midline length as preserved 95 mm.

bridge-peripheral fontanelles. CM 917 has a circular central fontanelle that contains about the same area as the oblong central fontanelle in DNM 993 but has few, if any, bridge-peripheral openings. The epiplastra are lost in CM 917 and DNM 992 but in DNM 993 they are developed into anterolateral lobes suggesting the adult condition of *Dinochelys*. Other features of the shells in these specimens are compared in table 3 and can be seen in the accompanying figures.

DNM 992 is particularly useful in falsifying the hypothesis that these shells represent a separate taxon characterized by radiating carapacial ridges because it can be identified as *Glyptops*. It has a fine ornament pattern similar to but not quite as well defined as *Glyptops* and, most importantly, it has the last vertebral scute partially dividing the last pair of marginal scutes, a diagnostic feature of *Glyptops*. DNM 992 is about 95 mm. in length and has well-developed carapacial ridges, whereas DNM 496 is about 165 mm. in length and has the ridging very low and nearly gone. This latter specimen is not well preserved but narrow costo-peripheral fontanelles are visible and the anterior lobe of the plastron has a smooth margin as in *Glyptops* and in contrast to *Dinochelys*.

DNM 993 may possibly be a juvenile *Dinochelys* but here the diagnostic features are less apparent. The condition of the last vertebral scute is not determinable but the anterior lobe

of the plastron is lobate as in *Dinochelys*. The lobes, however, do not have the same proportions as in presumed adult *Dinochelys*. One can ascribe this to growth differences but any differences between presumed juveniles and presumed adults can be explained in this way, resulting in a very weak argument. DNM 993 does lack any surface ornament, as in *Dinochelys*. The Quarry Nine collection at Yale shows that disarticulated costals that I estimate came from shells in the 100 to 200 mm. range can be readily placed in two groups, those with *Glyptops*-like ornament (YPM 5793, YPM 5799, YPM 5801, YPM 5803, YPM 6094) and those that are smooth (YPM 5792, YPM 5794, YPM 6076). I think that since this distinction does not seem gradational or age-dependent, it can be used tentatively as a criterion for identifying these small shells as *Dinochelys* or *Glyptops*.

In conclusion, even though there are three shells (CM 917, DNM 992, and DNM 993) of about the same size and possessing a unique feature (carapacial ridges) not found in other Morrison turtles, they do not represent a separate taxon. I advance the hypothesis that the carapacial ridges are age dependent and occur in the juveniles of *Glyptops* and *Dinochelys* but are lost in older individuals. The type of *Probaena sculpta* Hay is too poorly preserved to allow identification as either *Glyptops* or *Dinochelys* and is therefore a *nomen dubium*.

CRANIAL MORPHOLOGY OF *GLYPTOPS*

SKULL ROOF (FIGS. 12, 14, 26, 27)

The poor preservation of the skulls precludes a detailed study of the skull roof. The few sutures that appear on the restoration (figs. 26, 27) are thus open to question. The anterior end of *Glyptops*, as interpreted here, is quite similar to *Mesochelys*. There is a long suture between nasal and frontal, and the prefrontal is a lappet barely (if at all) contacting the nasal and not meeting in the midline. This interpretation may be wrong because YPM 1784 has transverse cracks dividing the nasal bone (fig. 12) and these cracks may be sutures. If so, an alternative interpretation might show the prefrontals

(or maxillae) nearly meeting in the midline to separate nasals and frontals.

The frontal enters the margin of the orbit posterior to its contact with the prefrontal. The posterior limits, however, are dubious. The most likely position of the frontal-parietal suture is indicated in the restoration but the area is occupied by matrix in YPM 1784 and poorly preserved in AMNH 336. The parietal appears to be extremely long, and, if the lateral limits indicated are correct, it is extremely narrow, in contrast to *Mesochelys* and most other turtles. The posterior and posterolateral limits of the parietal are not determinable. The posterior

temporal emargination appears to be very slight, and not any greater than that seen in *Mesochelys* and possibly less.

The postorbital can be distinguished on the right side of YPM 1784. It broadly enters the orbit, has a parasagittal contact with the parietal dorsally and an anteroventral contact with the maxilla. Posterior to the maxilla contact the postorbital lies above the jugal. The posterior areas of the postorbital are indeterminant. The jugal is also distinguishable in YPM 1784. It does not enter the orbit and lies between the maxilla (ventrally) and the postorbital (dorsally); its posterior limits are indeterminant. The postorbital and jugal morphology, as interpreted here, are as seen in *Mesochelys*. A limited cheek emargination may have been present, but if so, it was probably not as extensive as in *Mesochelys*.

Fragmentary remnants of the squamosal and quadratojugal are visible in both skulls but sutures can be seen only in AMNH 336. In that skull the quadrate-quadratojugal suture, C-shaped as in most turtles, is apparent. The respective positions of contacts between parietal, squamosal, post-orbital, and quadrate in this region are indeterminant; the available cracks and fissures are consistent with a number of interpretations. Contrary to an earlier statement (Gaffney, ms), an antrum postoticum is present. It appears to be shallow but extensive crushing and bone loss prevents useful statements about it.

Hay (1908a, p. 48) stated with regard to AMNH 336: "On the upper surface there is observed on each side a groove, or sulcus, which starts about 8 mm. from the midline at the hinder border of the temporal roof, runs first forward and inward to near the midline, then toward the orbit. Similar sulci are seen in *Chelydra* and it is thus rendered probable that the surface of the head was covered with horny scutes." These "sulci" can be seen on the left side, but are all cracks. There is no evidence for the presence of sulci on either skull.

PALATAL ELEMENTS (FIGS. 13, 28)

The premaxilla is poorly represented. Hay (1908a, p. 47, pl. 5, fig. 2) indicated that the premaxilla in YPM 1784 was a distinct ele-

ment, forming a hooked beak as in the living *Chelydra*. It is clear that YPM 1784 has lost most of this area since it was figured and AMNH 336 also has little of the area preserved. I cannot distinguish the bone in either specimen at the present time, but I have restored the area (fig. 26) using Hay's figure.

The anterior portion of the palate is not preserved in AMNH 336 and is badly crushed in YPM 1784. There is clearly a median concavity, at the end of the snout, similar to the one seen in most turtles. The vomer makes up the posterior half of this concavity with the premaxillae apparently forming the anterior half. Only a very slight ridge separates the triturating surfaces from the median concavity.

The vomer can be seen anteriorly and posteriorly between the palatines but the intervening area is broken. The opening of the nares, the apertura narium interna, seems to be more anterior than in *Mesochelys* or *Trinitichelys* but this area is dubious. On the right side of the vomer in YPM 1784, one edge of the apertura is preserved. In the same specimen a break reveals the contact of the vomer and prefrontal in cross section.

The maxilla of *Glyptops* bears a triturating surface that is very narrow compared to *Mesochelys*, *Trinitichelys* and most turtles. The labial ridge has a sharp edge and is V-shaped in cross section. There is a low, narrow channel between the labial and lingual ridges. The maxilla-palatine suture follows the low lingual ridge posteriorly to the jugal. Only a small portion of the jugal is visible ventrally, in the anterolateral corner of the fenestra subtemporalis.

The foramen palatinum posterius is formed by the palatine and pterygoid with no contribution from the maxilla. The ventral surface of the pterygoid is best seen in AMNH 336. There is a well-developed processus pterygoideus externus which is very similar to the processus found in *Chelydra*. The distal end of the processus pterygoideus externus is a vertical plate as in most cryptodires. The pterygoids do not meet in the center, being separated by the basisphenoid for their whole length, as in *Mesochelys*, whereas the anterior edge of the pterygoid is a transverse suture with the palatine. There seems to be a short contact with

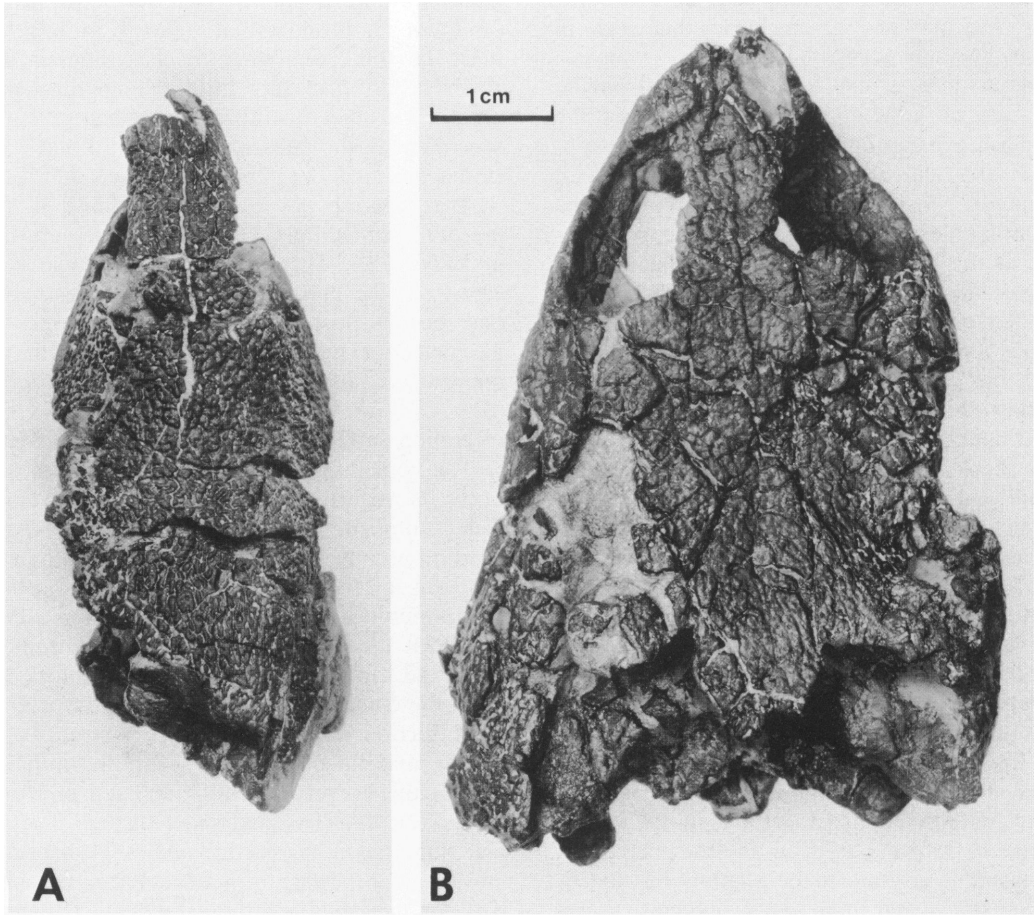


FIG. 12. *Glyptops plicatulus*, dorsal views of skulls. A. YPM 1784, Quarry Nine, Wyoming. B. AMNH 336, Bone Cabin Quarry, Wyoming. See figure 27 for restoration.

the jugal in YPM 1784 at the anterolateral limit of the processus pterygoideus externus. The same specimen shows the suture between the quadrate and the pterygoid, and it has the normal chelonian form. There is a small foramen within the pterygoid posterior to the carotid opening, and I have tentatively identified it (fig. 17) as the ventral opening of the foramen pro ramo nervi vidiani. Alternatively, it could be a nutrient foramen. The ventral surface of the pterygoid in AMNH 336 shows the attachment area of the pars ventralis of the *M. pterygoideus*. This area begins at the anterior edge of the fenestra subtemporalis medial to the

processus pterygoideus externus and continues posteromedially, curving around the fenestra subtemporalis.

One of the features I used in 1972 to argue that *Glyptops* was more primitive than baenids, is that in *Glyptops* the pterygoid incompletely floors the cavum acustico-jugulare. Since then, Evans and Kemp (1975) described *Mesochelys* which has a skull very similar to *Glyptops*; and I also had the opportunity to see more turtle skulls. I no longer think that the pterygoid condition in *Glyptops* is a satisfactory character. AMNH 336 has this region best preserved of the specimens of *Glyptops* and I think

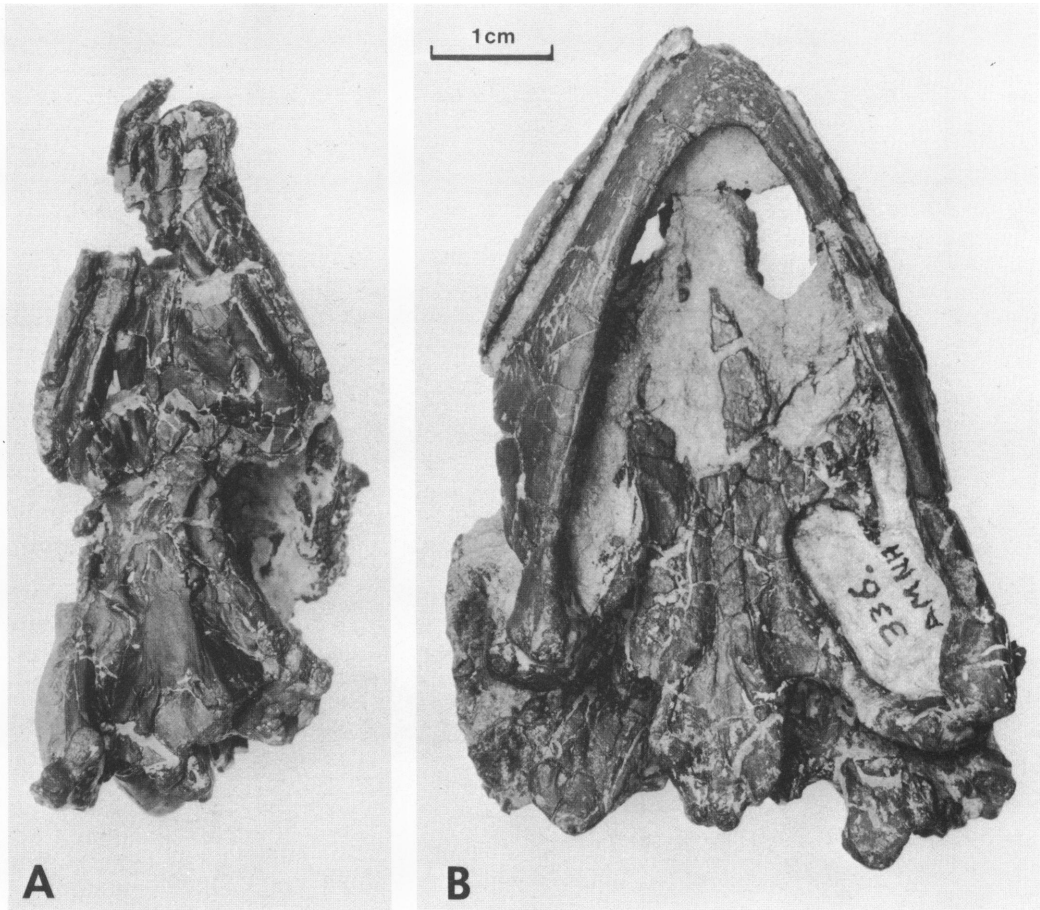


FIG. 13. *Glyptops plicatulus*, ventral views of skull. A. YPM 1784, Quarry Nine, Wyoming. B. AMNH 336, Bone Cabin Quarry, Wyoming. See figure 28 for restoration.

that it has been subject to crushing that has pushed the pterygoid anteriorly exposing more of the cavum acustico-jugulare (fig. 17). A comparison of *Mesochelys* with other cryptodires shows that many have a pterygoid that is no more extensive posteriorly than in *Glyptops* and *Mesochelys*.

BRAINCASE AND OTIC REGION (FIGS. 15-22)

The lateral wall of the braincase, although badly fractured, is visible in YPM 1784 (fig. 15). Baur (1891, p. 414) reported an epipterygoid in this specimen, and I can substantiate its presence. The suture between the crista pterygoideus and the processus inferior par-

ietalis is not visible on either side and the position of the presumed epipterygoid is similar to the position of the processus inferior parietalis in baenids. However, on the right side of YPM 1784 the epipterygoid is separated from the foramen nervi trigemini by a thin strip of bone which is the processus inferior parietalis. The epipterygoid seems relatively large but the dorsal limits are poorly preserved and it cannot be seen in its entirety.

YPM 4717 (figs. 19-22) is a partial braincase which includes a disarticulated prootic, basi-sphenoid, basioccipital, and portions of the ex-occipital and pterygoid. This specimen is well preserved and provides useful braincase infor-

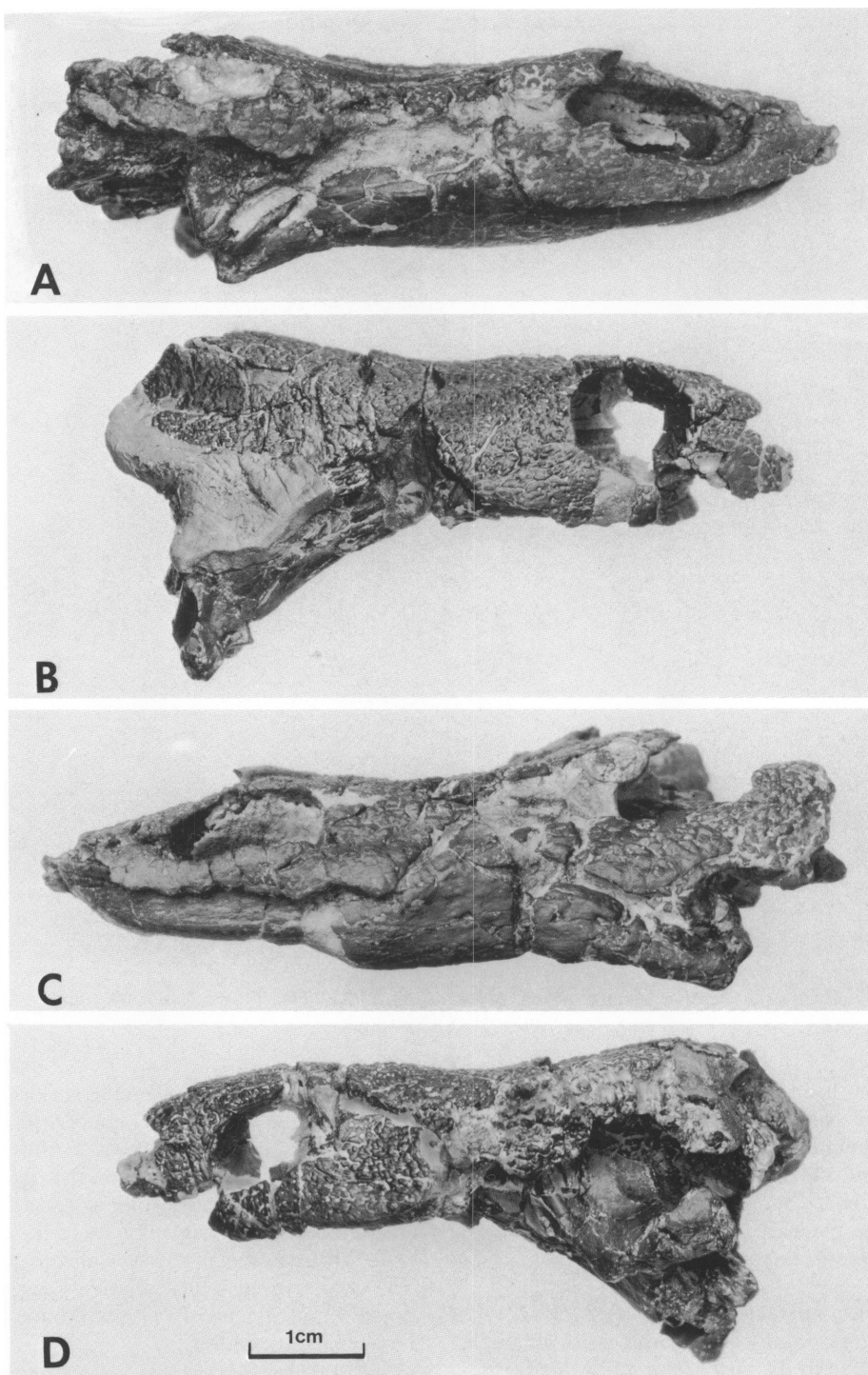


FIG. 14. *Glyptops plicatulus*, lateral views of skulls. A, C. AMNH 336, Bone Cabin Quarry, Wyoming. B, D. YPM 1784, Quarry Nine, Wyoming. See figure 26 for restoration.

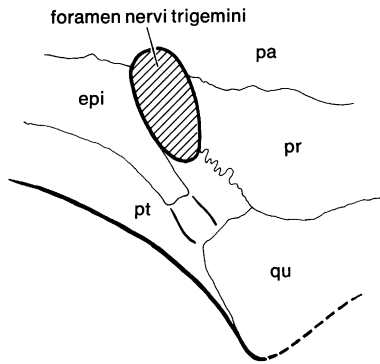


FIG. 15. *Glyptops plicatulus*, lateral view of left ethmoid region in YPM 1784.

mation. The basioccipital (see also fig. 18) is a roughly triangular element with a transverse contact anteriorly with the basisphenoid and lateral contacts with the exoccipitals. The pterygoids probably reach the anterolateral corners of the basioccipital but the contacts are small. The ventral surface is characterized by large, paired tubercula basioccipitalia that extend posteriorly as processes. A very shallow concavity lies between them. The condylus occipitalis is formed almost entirely by the basioccipital with slight contributions from the exoccipitals dorsolaterally. The condylus occipitalis has a concavity in its center for the ligamentum apicis dentis. The dorsal surface of the basioccipital shows a prominent basis tuberculi basalis. A W-shaped platform can be seen at the anterior end of the bone. An irregular tubercle in the middle of the dorsal surface may

represent a crista dorsalis basioccipitalis. The exoccipitals converge dorsally so the amount of dorsal exposure of the basioccipital is much less than the ventral amount.

The exoccipital can be seen in YPM 4717 internally, and in AMNH 336 externally. As in most turtles, there are two portions of the exoccipital: a ventromedial one and a dorsolateral one. The ventromedial portion borders the foramen jugulare posterius as seen in AMNH 336 (right side). The ventral edge of this portion has a broad contact with the basioccipital. The anterior area in the vicinity of the foramen jugulare posterius presumably articulates with the opisthotic but the area is broken and the relations cannot be determined. The two foramina nervi hypoglossi penetrate the exoccipital above the suture with the basioccipital. The posterior foramen is the larger and its internal opening, the exit from the braincase, is in the middle of a small concavity. The internal and external positions of the foramina can be seen on the left side of YPM 4717. Posteromedially, there is a curved area connecting the ventromedial and dorsolateral parts and forming the lateral margin of the foramen magnum. The dorsolateral portion meets the opisthotic laterally in a straight suture that can be followed posterolaterally out of the foramen jugulare posterius. The dorsal part of the exoccipital is preserved in YPM 4717, but its relations to the rest of the skull are not preserved. This portion seems to have a wide suture area, probably with the supraoccipital, but this cannot be determined.

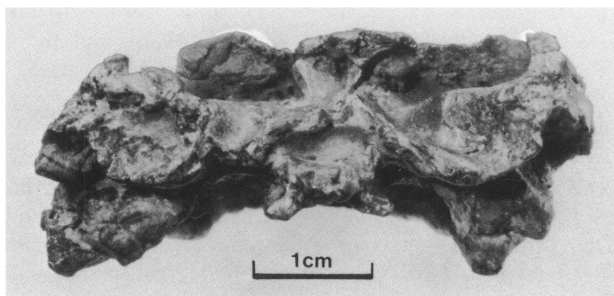


FIG. 16. *Glyptops plicatulus*, occipital view of AMNH 336.

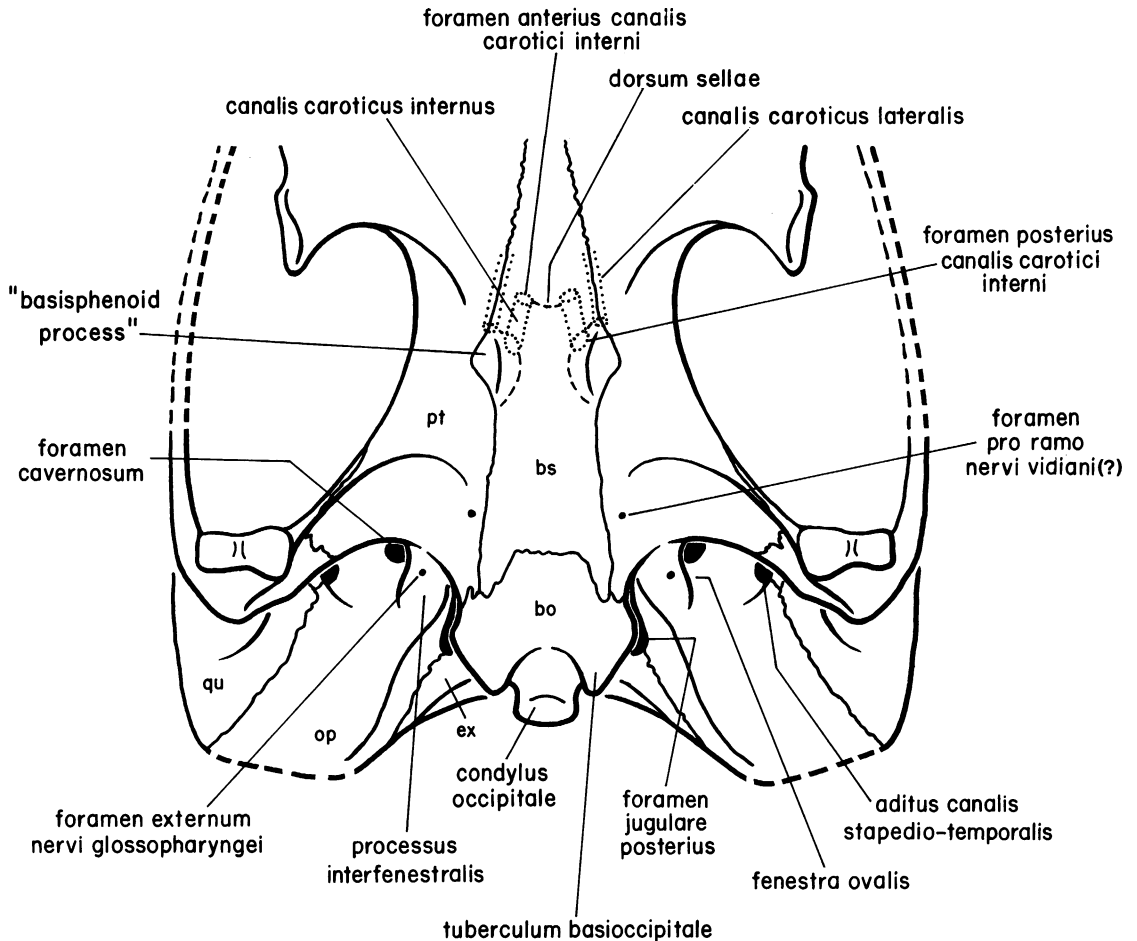


FIG. 17. Semidiagrammatic restoration of basicranial region in *Glyptops* with internal features dashed. Based on all three cranial specimens.

The supraoccipital is not recognizable as a distinct element, and the region in which it might be found is missing in most of the material. Therefore, the extent of the crista supraoccipitalis cannot be determined.

The main body of the opisthotic forms part of the posterior floor of the fossa temporalis superior. The posterior end of the bone forms a projection that continues past the level of the condylus occipitalis. The opisthotic sends a well-developed processus interfenestralis ventrally to the pterygoid. The processus has a small foramen externum nervi glossopharyngei

near its upper end. The processus interfenestralis forms the posterior half of the fenestra ovalis and the lateral wall of a small fenestra perilymphatica.

Both prootics are preserved in YPM 4717, but some of the internal anatomy is difficult to interpret due to breakage, the bone being so fragile in some areas that no more matrix can be removed to expose more bone. The prootics in the other two specimens cannot be distinguished readily. Dorsally, on the right otic chamber of AMNH 336, the foramen stapedio-temporale can be made out. The area is badly

broken, however, and the sutures are not distinguishable. The disarticulated prootics in YPM 4717 do not have enough of the edges involved preserved, and the position of the foramen stapedio-temporale is not certain in this specimen. The canalis stapedio-temporalis is not visible, but the aditus canalis stapedio-temporalis is preserved on the right side of AMNH 336 and is formed by the prootic and quadrate as in most turtles. The aditus is in the dorsolateral corner of the cavum acustico-jugulare. The canalis cavernosus lies below and internal to the aditus canalis stapedio-temporalis, and is walled dorsomedially by the prootic. YPM 4717 shows the posterior margin of the foramen nervi trigemini. The prootic contribution to the margin of this opening is in the posterodorsal area, above the pterygoid. The crista pterygoidea of the pterygoid forms the lower limits of the foramen nervi trigemini. A groove in the pterygoid below the foramen held the epipterygoid anteriorly and the epipterygoid process of the quadrate posteriorly. Dorsally, the parietal met the prootic at the dorsal margin of the foramen nervi trigemini, but although the parietal is now gone in YPM 4717, the suture area is preserved on the prootic. Just above the prootic-ptyergoid suture, in the same specimen, there is a low ridge beginning above the foramen nervi trigemini and extending postero-ventrally.

The internal anatomy of the prootic is mostly obscured, but some of the structures can be made out. The fossa acustico-facialis is a depression on the medial surface near the foramen nervi trigemini and houses at least two foramina; anteriorly, the foramen nervi facialis, and posteriorly, a foramen nervi acustici. The latter opening is incomplete posteriorly and another foramen could have followed it as in many modern turtles. The hiatus acusticus is broken so that its limits are in doubt. The anterior opening of the canalis cavernosus into the cavum cranii, the foramen cavernosum, is preserved on the right side of YPM 4717. It is formed dorsally by the prootic and ventrally by the pterygoid. The posterior area of the prootic consists mostly of the cavum labyrinthicum. This region is badly broken and most details

are obscured by matrix and broken bone. The canalis semicircularis horizontalis is seen in cross section at the surface facing the opisthotic. The prootic forms the anterior half of the fenestra ovalis.

The basisphenoid is a long element lying between the pterygoids and in front of the basioccipital as seen in palatal view. The prootic is sutured to the lateral edge of the basisphenoid dorsally. The ventral surface can be seen in all three specimens. Posterolateral processes of the basisphenoid seem to overlap the ventral surface of the basioccipital slightly, resulting in a curved suture line in ventral view even though the main part of the contact area is transverse, as seen in YPM 4717 (fig. 20).

The lateral morphology of the basisphenoid can be seen in YPM 4717. A wide suture area is present for the prootic dorsally and for the pterygoid ventrally, both bones attaching the length of the basisphenoid. The basisphenoid anterior to the canalis caroticus internus forms the medial wall for a canalis caroticus lateralis. However, as the pterygoid is not preserved on this side and as the opposite side is not determinable, the anterior opening of this canal is not known. The lateral surface of the basisphenoid is not well enough preserved to determine the presence or absence of a foramen pro ramo nervi vidiani.

Evans and Kemp (1975) have described a structure on the basisphenoid and pterygoid of *Mesochelys* as a remnant of a basiptyergoid articulation. Movable basiptyergoid articula-

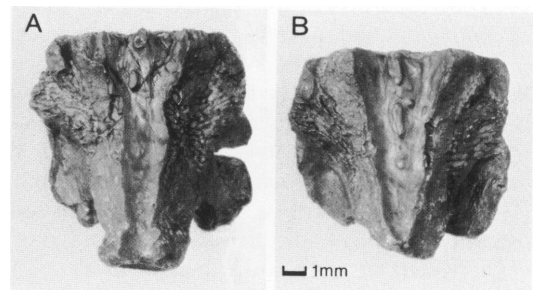


FIG. 18. *Glyptops plicatulus*, dorsal views of disarticulated basisphenoids, NMNH 26370 (A) and NMNH 26371 (B); Quarry Nine, Wyoming.

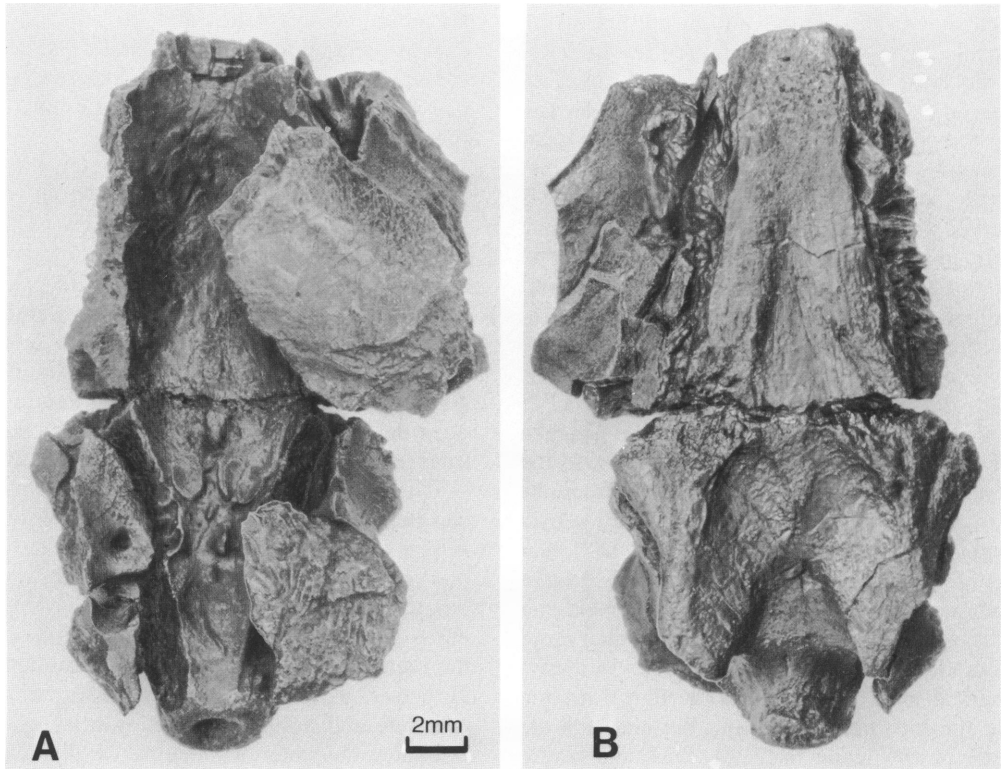


FIG. 19. *Glyptops plicatulus*, dorsal (A) and ventral (B) views of braincase. YPM 4717, Quarry Nine, Wyoming. See also figures 20-22.

tions are found in animals with kinetic skulls in which the pterygoid is movable with respect to the neurocranium. *Captorhinus* has such a condition and I have argued elsewhere (Gaffney, 1975) that the loss of this feature and the fusion of braincase and palatoquadrate are advanced features of turtles. The condition of the articulation is not completely known in *Proganochelys*, the sister taxon to all other turtles, but it is probably fused. It is certainly fused in all other turtles. In *Mesochelys* Evans and Kemp (1975, p. 30) described a "small lateral spur [on the basisphenoid], the basiptyergoid process, [which] fits into a distinct pit in the ventromedial edge of the pterygoid." Their figures show this structure quite clearly and an apparently identical structure is in the same area in *Glyptops* (YPM 4717, fig. 19).

The right pterygoid is separated off the basisphenoid showing a pit on the pterygoid and a small projection of the basisphenoid fitting into it. However, I do not think that this structure is homologous with the basiptyergoid articulation of kinetic animals. Elsewhere (Gaffney, 1975) I have suggested that turtles evolved from a kinetic ancestor and indicated changes that may have taken place in the morphology of the palatoquadrate and braincase. However, I did not discuss the fate of the basiptyergoid articulation per se and did not identify its possible homologue in an akinetic turtle. Developmental information on this area is available in *Chrysemys* (Kunkel, 1912) but it is not specific enough to allow identification of a structure or area in the adult.

A possible approach to this problem might

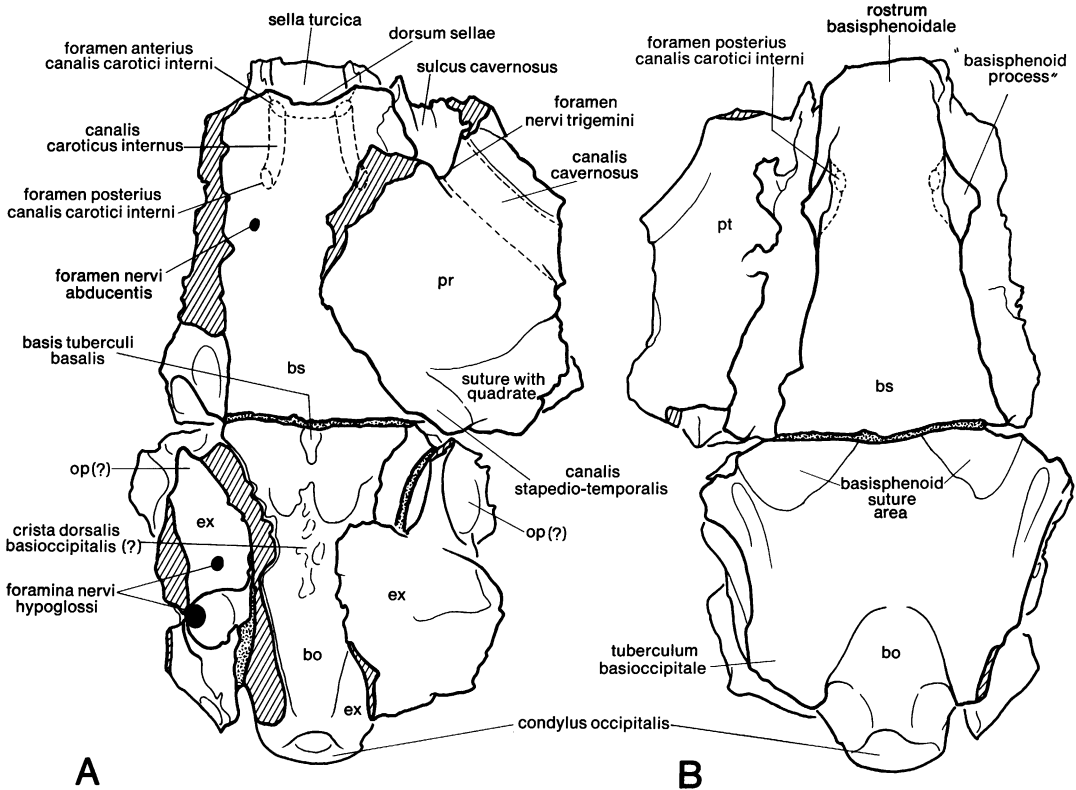


FIG. 20. Key for figure 19.

be made by a comparison of the basisphenoid in *Mesochelys* (the bone is more complete than in *Glyptops*) and a captorhinomorph. I am here assuming that the captorhinomorph morphology in this area is primitive with respect to Testudines but it must be kept in mind that this is not necessarily the case. In figure 23 the basisphenoid of *Mesochelys* is compared with the basisphenoid plus parasphenoid of *Captorhinus* (based on Price, 1935). The basisphenoid of turtles is presumed to be the fused basisphenoid plus parasphenoid of other reptiles. I have chosen the following structures as landmarks, i.e., as homologous features: dorsum sellae, foramen nervi abducentis, foramen anterius canalis carotici interni, and foramen posterius canalis carotici interni. The position of the basiptyergoid process in *Captorhinus* is dis-

tinctly anterior to most of the above structures and at the same level as the foramen anterius canalis carotici interni. In *Mesochelys*, however, the supposed process is posterior to all the landmark structures. The turtle basisphenoid does differ sharply from the *Captorhinus* basisphenoid in the compression of the region between the dorsum sellae and foramen anterius canalis carotici interni. This may have involved a posterior shift of the basiptyergoid process but, in my opinion, a comparison of *Mesochelys* and *Captorhinus* does not support the identification of a basiptyergoid process remnant in *Mesochelys* (and also in *Glyptops*).

What is this structure if it is not a basiptyergoid remnant? In both *Glyptops* and *Mesochelys* the ventral surface of the "process" forms a smooth-surfaced dorsal roof for a small

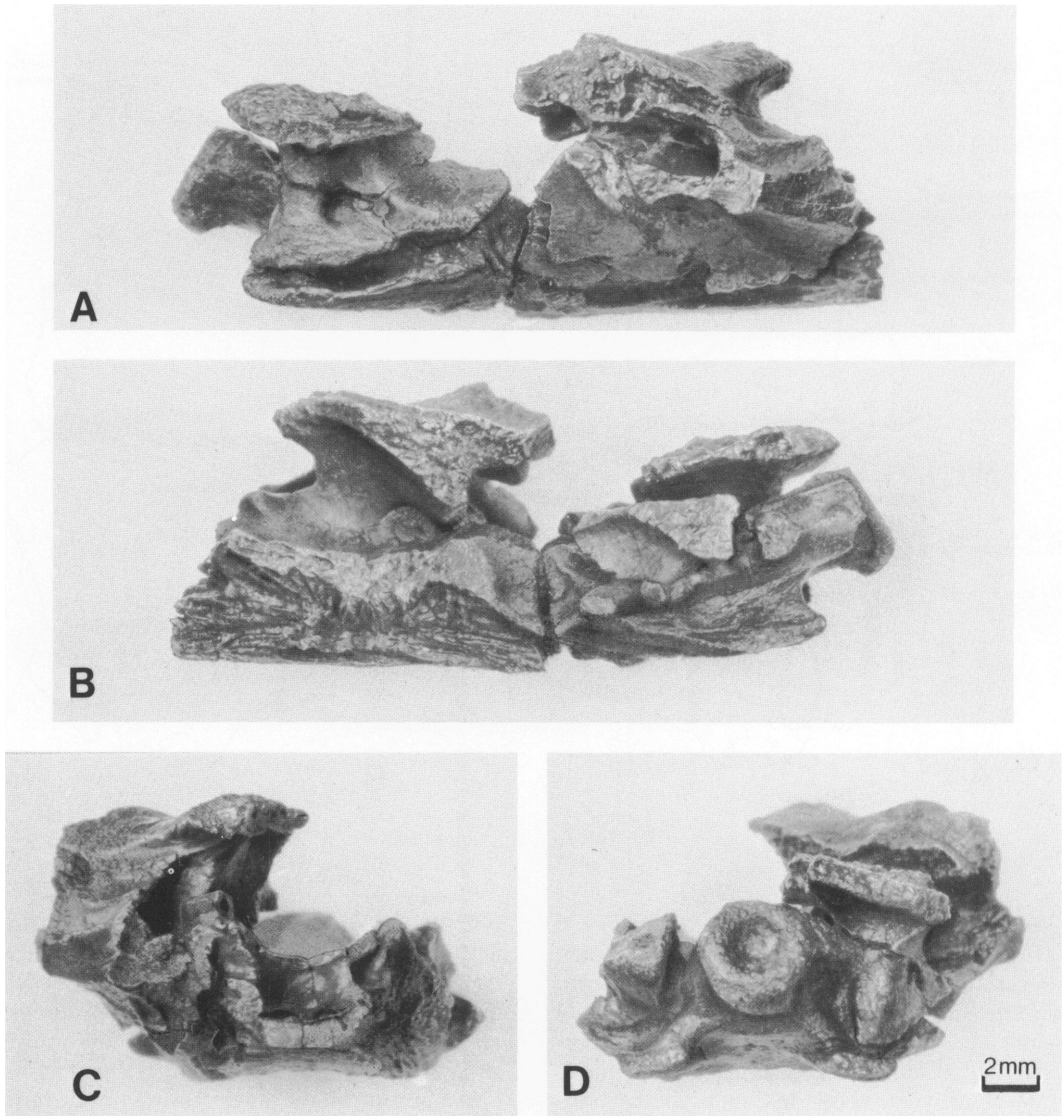


FIG. 21. *Glyptops plicatulus*, right lateral (A), left lateral (B), anterior (C), and occipital (D) views of braincase. YPM 4717, Quarry Nine, Wyoming. See also figures 19, 20, 22.

sinus just posterior and slightly lateral to the foramen posterius canalis carotici interni. This surface communicates with the foramen and can also be seen in YPM 1784. I have no idea what this sinus contained in life but the internal carotid artery must have passed through part of

it. The “basipterygoid process” seems to be due to the fact that the suture between basi-sphenoid and pterygoid jogs laterally at this point because of the presence of the sinus.

The foramen posterius canalis carotici interni in *Mesochelys* and *Glyptops* is formed entirely

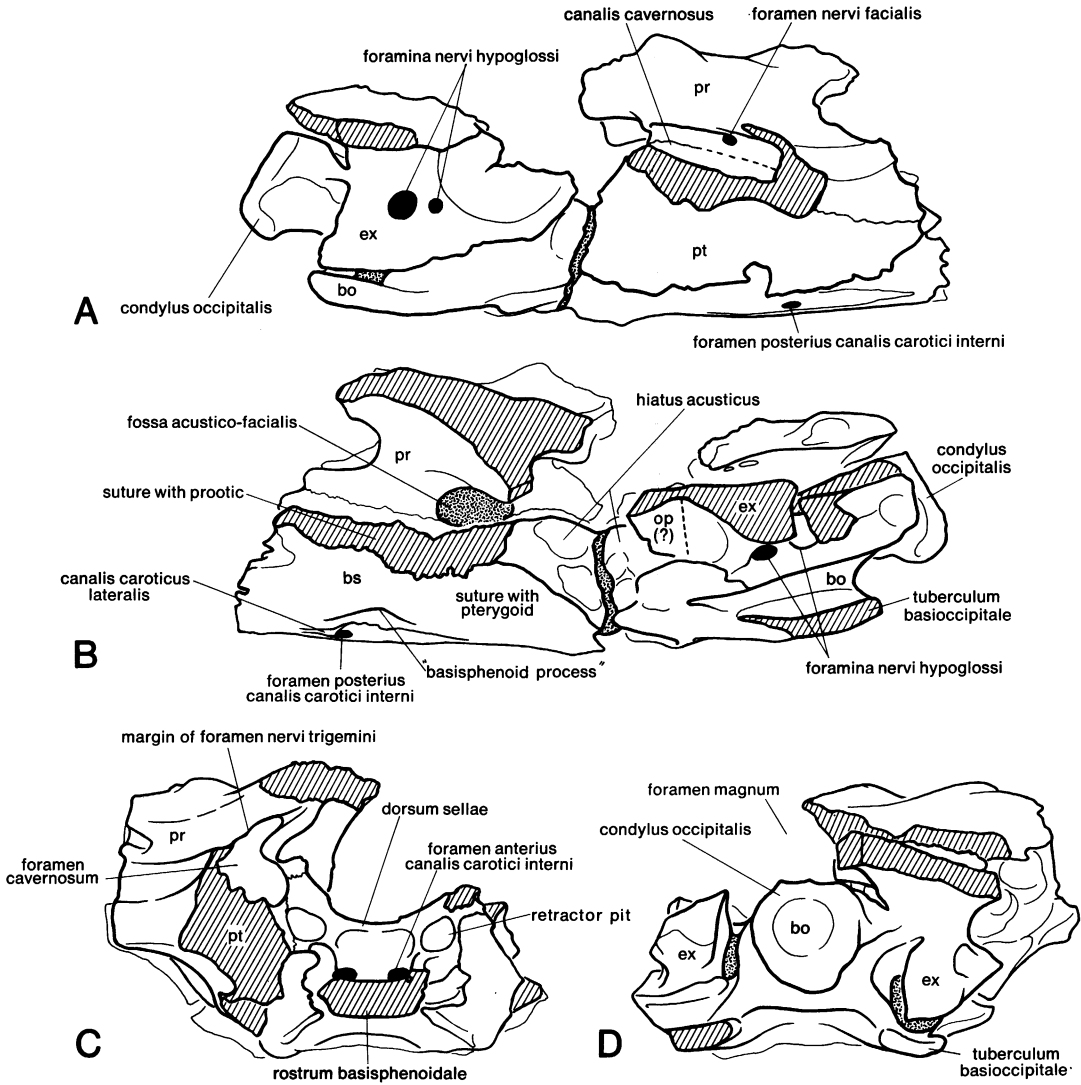


FIG. 22. Key for figure 21.

by the basisphenoid in contrast to all other turtles (condition unknown in *Proganochelys*) but in common with captorhinomorphs. In baenids the pterygoid almost always forms half of the foramen as well as a portion of the canalis caroticus internus (Gaffney, 1975, fig. 21), whereas in eucryptodires and pleurodires the basisphenoid rarely forms any of the foramen posterius canalis carotici interni. The con-

dition in *Glyptops* and *Mesochelys*, then, can be considered primitive for turtles.

The canalis caroticus internus extends anteromedially through the basisphenoid to open at the posterolateral margin of the sella turcica, where it becomes the foramen anterius canalis carotici interni (figs. 17, 19). Just lateral to the foramen posterius canalis carotici interni lies the canalis caroticus lateralis (fig. 17). It ap-

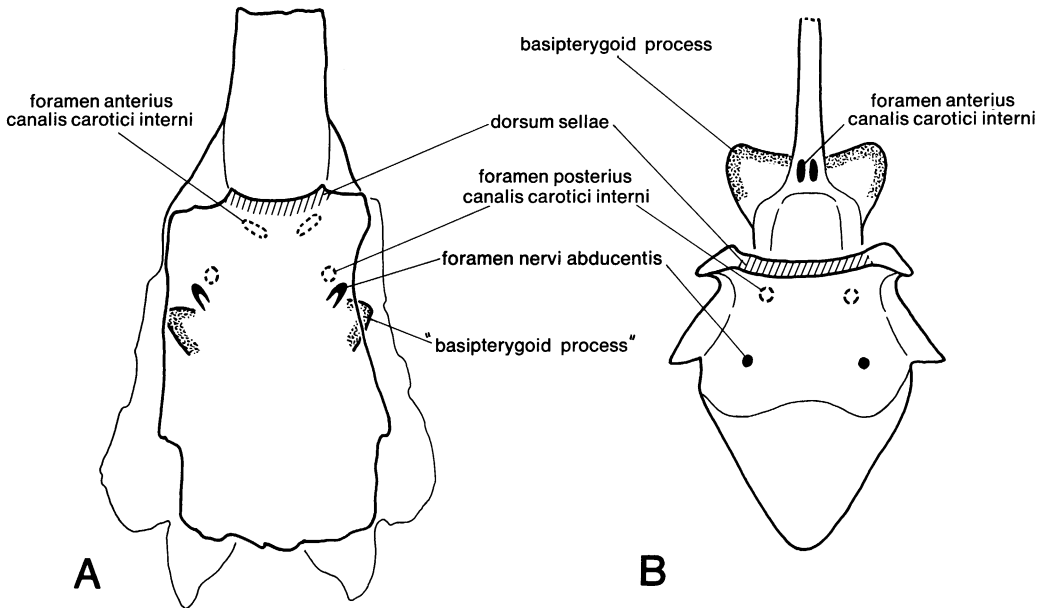


FIG. 23. Schematic dorsal views of the basisphenoid in *Mesochelys durlstonensis* (A, after Evans and Kemp, 1975) and *Captorhinus* (B, after Price, 1935, and specimens).

pears that the palatine artery (which would lie in the canalis caroticus lateralis) branches off the internal carotid artery within the basisphenoid sinus and before the carotid actually enters the foramen posterius canalis carotici interni. The canalis caroticus lateralis is distinctly smaller than the canalis caroticus internus, a condition primitive for all turtles. The foramen caroticum laterale is not preserved.

The basisphenoid of *Glyptops* and *Mesochelys* differs from nearly all turtles (with the important exception of *Proganochelys*) in extending the full length of the pterygoids and being exposed ventrally for its entire length. A comparison with other turtle basisphenoids (Siebenrock, 1897, figs. 28-31; Gaffney, 1976, figs. 26-31) shows that the basic morphology of the basisphenoid in *Glyptops* and *Mesochelys* is the same as in pleurodires and cryptodires. The proportions and shape of the rostrum basisphenoidale are the same in all Casichelydia (the monophyletic group of all turtles except *Proganochelys*, see Gaffney, 1975), and quite different from *Proganochelys*. The latter has an interpterygoid vacuity within which a cultriform process is visible, much as in *Captorhinus*.

Evans and Kemp (1975) suggested that *Mesochelys* is more primitive in this region than any other post-Triassic turtles in that the separation of the pterygoid by the basisphenoid is similar to the condition in *Proganochelys* rather than other Casichelydia. *Glyptops* is the same as *Mesochelys* in having the basisphenoid separating the pterygoids and being the same length as the pterygoids.

The quadrate is poorly preserved in *Glyptops*; YPM 1784 has the lower area and articular surface, whereas AMNH 336 has nearly all the areas present but badly fractured and distorted (fig. 14). Although I earlier believed that *Glyptops* lacked an antrum postoticum (Gaffney, ms.), I now think that the quadrate has no discernible differences from *Trinitichelys*. This is not to say that it is identical with *Trinitichelys*; the material is too poorly preserved to determine the shape of the incisura columellae auris, antrum postoticum, and cavum tympani.

LOWER JAW (FIGS. 13, 24, 25)

There are five lower jaw specimens belonging to turtles from the Morrison Formation.

The most complete is AMNH 336 (Bone Cabin Quarry, Wyoming), a shell, partial skeleton, and skull of *Glyptops*. Unfortunately, the lower jaws are tightly compressed into the skull (fig. 13B) and only the lower surfaces are visible, and the morphology described below comes primarily from the other specimens. This is doubly unfortunate because the other specimens are not associated with skull or shell material, and, although I identify them as *Glyptops*, the possibility remains that they belong to another taxon.

The dentary is best seen in YPM 5821 (fig. 24) in which parts of both rami are preserved. None of the medial elements are preserved in this specimen and the sulcus cartilaginis meckelii is exposed for its full length. The sulcus is relatively shallow, not deep and well-defined dorsally as in *Plesiochelys* and baenids. There is a large foramen alveolare inferius (the prominent foramen in fig. 24) just below the presumed sutural area for the coronoid bone.

Nearly all the triturating surface can be seen in YPM 5821 except the symphyseal area. The

lower jaws of *Glyptops* are distinctly long and narrow in contrast to most turtles, and the triturating surface is, as one would expect, also very narrow. The labial ridge is higher and much more acute than the lingual ridge. Both ridges are in parallel with a shallow trough between them. Although a narrow triturating surface would generally be presumed to be primitive for turtles, a comparison of *Glyptops* with Jaekel's (1916, fig. 61) *Proganochelys* (= "*Stegochelys*") shows that that form has distinctly broader triturating surfaces than *Glyptops*. I judge the narrow triturating surfaces of both skull and lower jaw as derived (autapomorphic) for *Glyptops* because of the absence of this feature in outgroups. The only turtles with comparable lower jaws are the Chelidae and just the advanced forms have thin triturating surfaces (Gaffney, 1977).

The symphysis is preserved only in AMNH 336. Both rami were fused as in most turtles, and there is a distinct dorsal projection of the labial ridge forming a symphyseal "hook."

The external surface of the lower jaw is

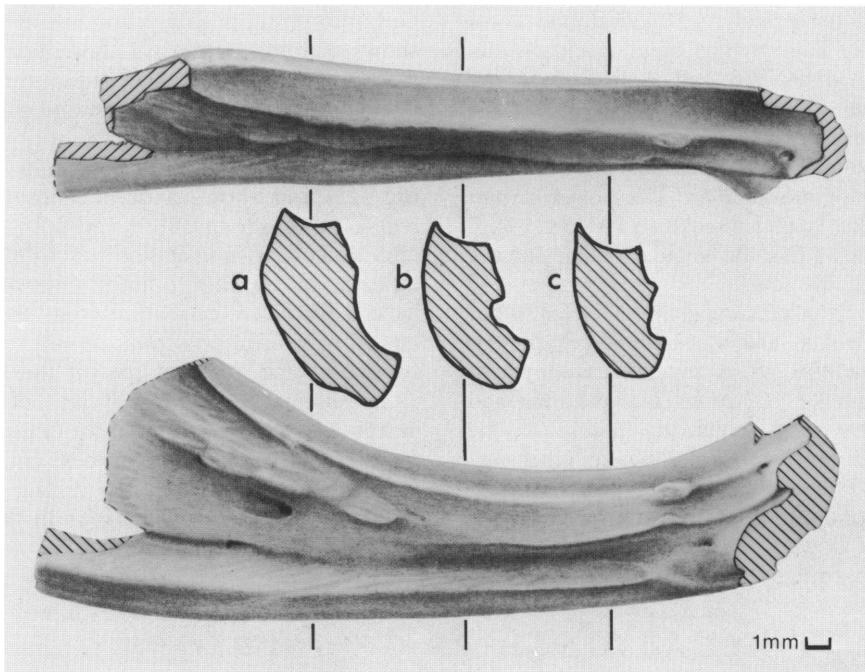


FIG. 24. *Glyptops plicatulus*, left dentary, YPM 5821, Quarry Nine, Wyoming.

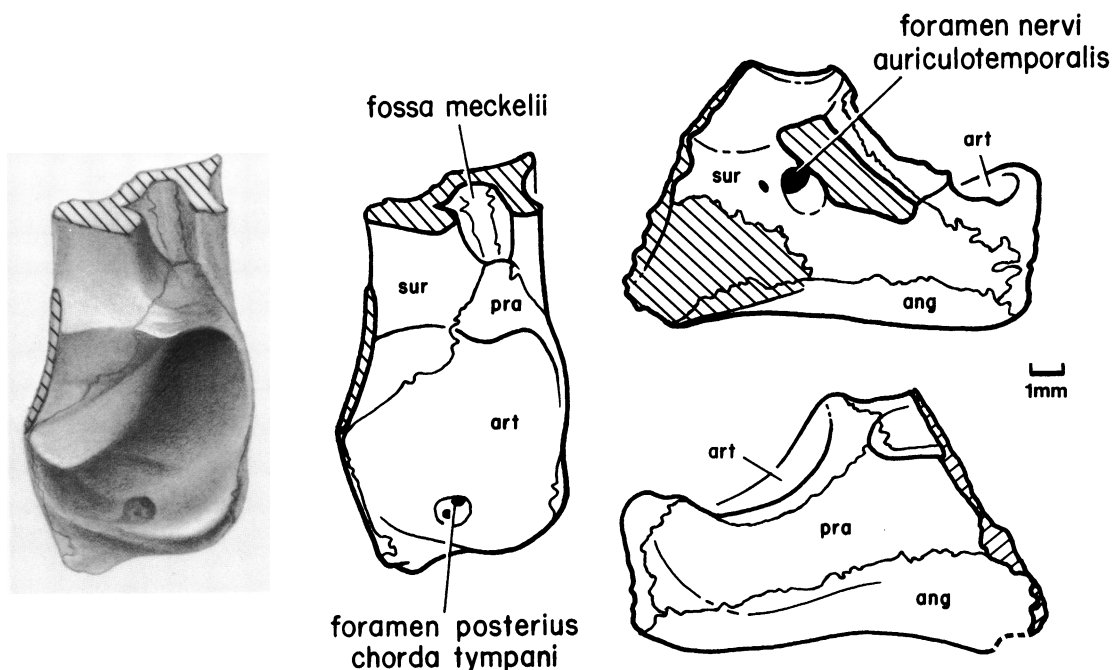


FIG. 25. *Glyptops plicatulus*, left articular region of lower jaw, YPM 5821, Quarry Nine, Wyoming.

preserved in a number of specimens but few sutures are visible. I cannot determine the dentary-surangular suture nor the limits of the coronoid bone. The right side of AMNH 336 (fig. 14) shows a moderately well developed coronoid process. The angular bone is clearly delimited in AMNH 336 and it lies along the posteroventral edge of the lower jaw as in most turtles. I cannot make out a foramen intermandibularis caudalis which is usually found on the medial edge of the angular. The posterior part of the angular is preserved in YPM 5821 (fig. 25) and it shows that the angular reaches nearly to the end of the jaw.

The splenial is preserved in AMNH 336 but it is badly broken and the splenial-prearticular suture is doubtful. It is nonetheless apparent that the splenial of *Glyptops* is quite long and narrow and extends anteriorly nearly to the symphysis, a condition unknown in other turtles except *Proganochelys* (Jaekel, 1916, p. 189). This condition is presumably primitive for Casichelydia as well as in Testudines. The posterior limits of the splenial are dubious and the

position of the foramen intermandibularis medius not visible.

The prearticular and surangular are poorly delimited in the available material of *Glyptops*. Only the posterior jaw fragment of YPM 5821 shows definite portions of those bones as well as the posterior margin of the fossa meckelii. Other information on the size and shape of the fossa is lacking.

The articular is well preserved in YPM 5821 (fig. 25) and shows a deep concavity for the reception of the quadrate. Almost all of the area articularis mandibularis is formed by the articular in contrast to most other turtles that have a distinct contribution from the surangular. A foramen posterius chorda tympani is formed by the posterior part of the articular.

In summary, the lower jaw of *Glyptops* agrees with cryptodires in most features. It differs from nearly all turtles except chelids in the narrowness of the triturating surface and from all turtles except *Proganochelys* in the extreme length of the splenial.

RELATIONSHIPS OF *GLYPTOPS*

Although a number of systematically important areas in the skull of *Glyptops* (particularly

the posterior portion of the skull roof, and the anterior part of the palate) are not sufficiently

well preserved to allow comparison with other taxa, some hypotheses of relationships involving *Glyptops* can be tested. The earliest assessment of relationships for *Glyptops* was made by Baur (1891). On the basis of shell features Baur placed *Glyptops*, *Helochelys* (Cretaceous, Europe), and *Pleurosternon* (Jurassic, Europe) in the same family, the Pleurosternidae. He also said "*Compsemys* [= *Glyptops*] is very nearly related to the Tertiary genus *Baena*, which has probably to be considered as its direct suc-

cessor" (1891, p. 425). And again (*ibid.*, p. 414), "the skull as a whole shows characters which we expect to find in the ancestors of Cryptodira and Pleurodira." I have discussed this last idea and the development of the "Amphichelydian" concept elsewhere (Gaffney, 1975, p. 402). Other than Hay (1905, 1908a) referred to in Gaffney (*op. cit.*), very little appeared on the relationships of *Glyptops* until my revision of the Baenidae (1972). In that paper I developed a hypothesis that *Glyptops*

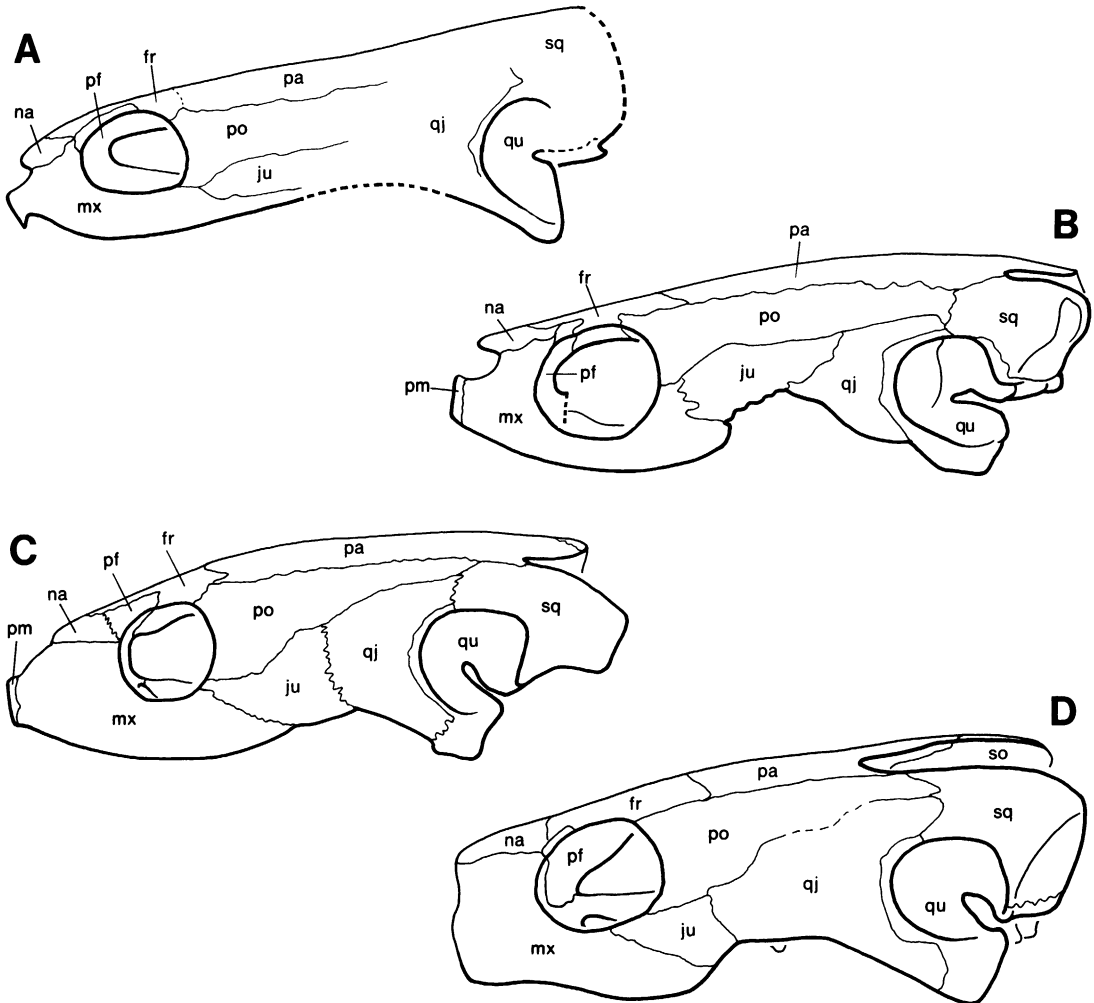


FIG. 26. Lateral views of A. *Glyptops plicatulus*, Late Jurassic, United States; B. *Mesochelys durlstonensis*, Early Cretaceous, Britain (after Evans and Kemp, 1975); C. *Dorsetochelys delairi*, Early Cretaceous, Britain (after Evans and Kemp, 1967); D. *Trinitichelys hiatti*, Early Cretaceous, United States (modified from Gaffney, 1972).

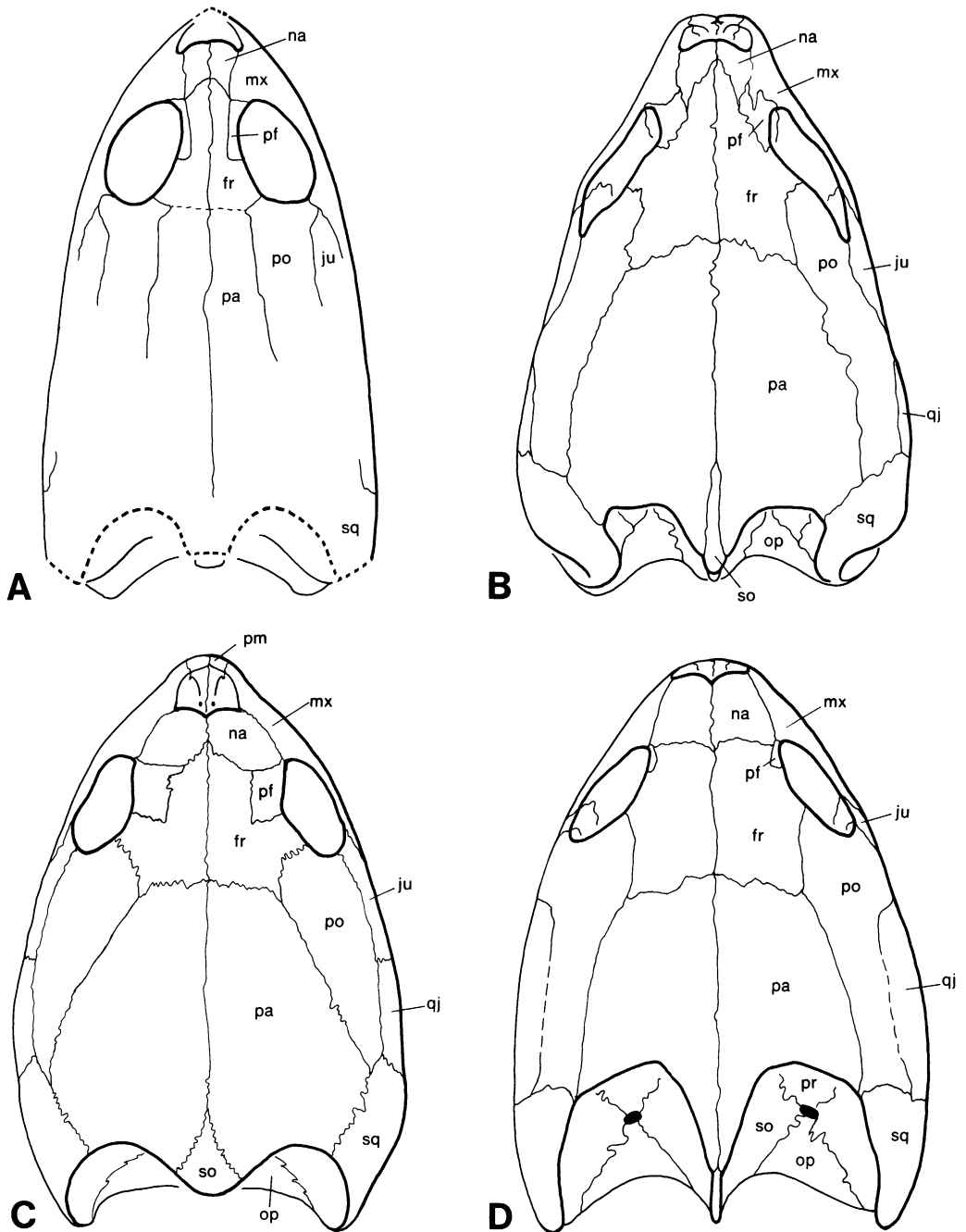


FIG. 27. Dorsal views of A. *Glyptops plicatulus*, Late Jurassic, United States; B. *Mesochelys durlstonensis*, Early Cretaceous, Britain (after Evans and Kemp, 1975); C. *Dorsetochelys delairi*, Early Cretaceous, Britain (after Evans and Kemp, 1976); D. *Trinitichelys hiatti*, Early Cretaceous, United States (modified from Gaffney, 1972).

and the Baenidae form a monophyletic group, the Baenoidea (I also suggested that *Glyptops* could be hypothesized as the ancestor of the Baenidae, but I would rather consider that a *lapsus calami*). Later in Gaffney (1975) I developed a theory of relationships for the higher categories of turtles and repeated the argument that the Baenoidea (including *Glyptops*) is a monophyletic group and the sister group of the remaining cryptodires (the Eucryptodira). At about the same time Evans and Kemp (1975) described a relatively well-preserved skull from the Purbeckian (Early Cretaceous) of Dorset, *Mesochelys*, and argued that it was a glyptopsid on the following characters:

1. Basisphenoid separates pterygoids for their entire length
2. Foramen posterius canalis carotici interni is about half-way down the length of the basisphenoid

3. Pterygoid incompletely floors cavum acustico-jugulare

Evans and Kemp (1975, 1976) argued that these features were primitive for all turtles and that *Mesochelys* also had a remnant of the basiptyergoid articulation, another primitive feature.

These phylogenetic views were more fully articulated in the 1976 paper in which Evans and Kemp used a cladistic approach to analyze the above characters and to develop a cladogram of cryptodiran turtles. When I argued that the Glyptopsidae plus the Baenidae form a strictly monophyletic group (Baenoidea), the shared derived character I used was the position of the foramen posterius canalis carotici interni. Evans and Kemp (1976) asserted that this character was primitive for turtles in general and that the Baenoidea are not demonstrably monophyletic. The alternative phylogeny they pro-

TABLE 4
Cranial Comparison of *Glyptops* and Other Turtles

	<i>Glyptops</i>	<i>Mesochelys</i>	<i>Dorsetochelys</i>	Baenidae	Eucryptodira	Pleurodira
Basisphenoid extending length of pterygoids and preventing their midline contact	yes	yes	no	no	no	no
Foramen posterius canalis carotici interni lying midway along the length of the basisphenoid	yes	yes	yes	yes	no	no
Dorsal prefrontal lappets	well developed but not meeting medially	as in <i>Glyptops</i>	as in <i>Glyptops</i>	small or absent (except in <i>Hayemys</i>)	large and meeting medially (except in <i>Rhinochelys</i> and <i>Desmatochelys</i>) ¹	as in <i>Glyptops</i> in Chelidae; as in Eucryptodira in Pelomedusidae
Posterior temporal emargination well developed so that parietal-squamosal contact is small or absent	indeterminant but probably no	no	no	yes in primitive members	yes in primitive members	no in Chelidae; yes in most Pelomedusidae
Well developed pterygoid-basioccipital contact	no	no	no	yes	variable, primitively no	no

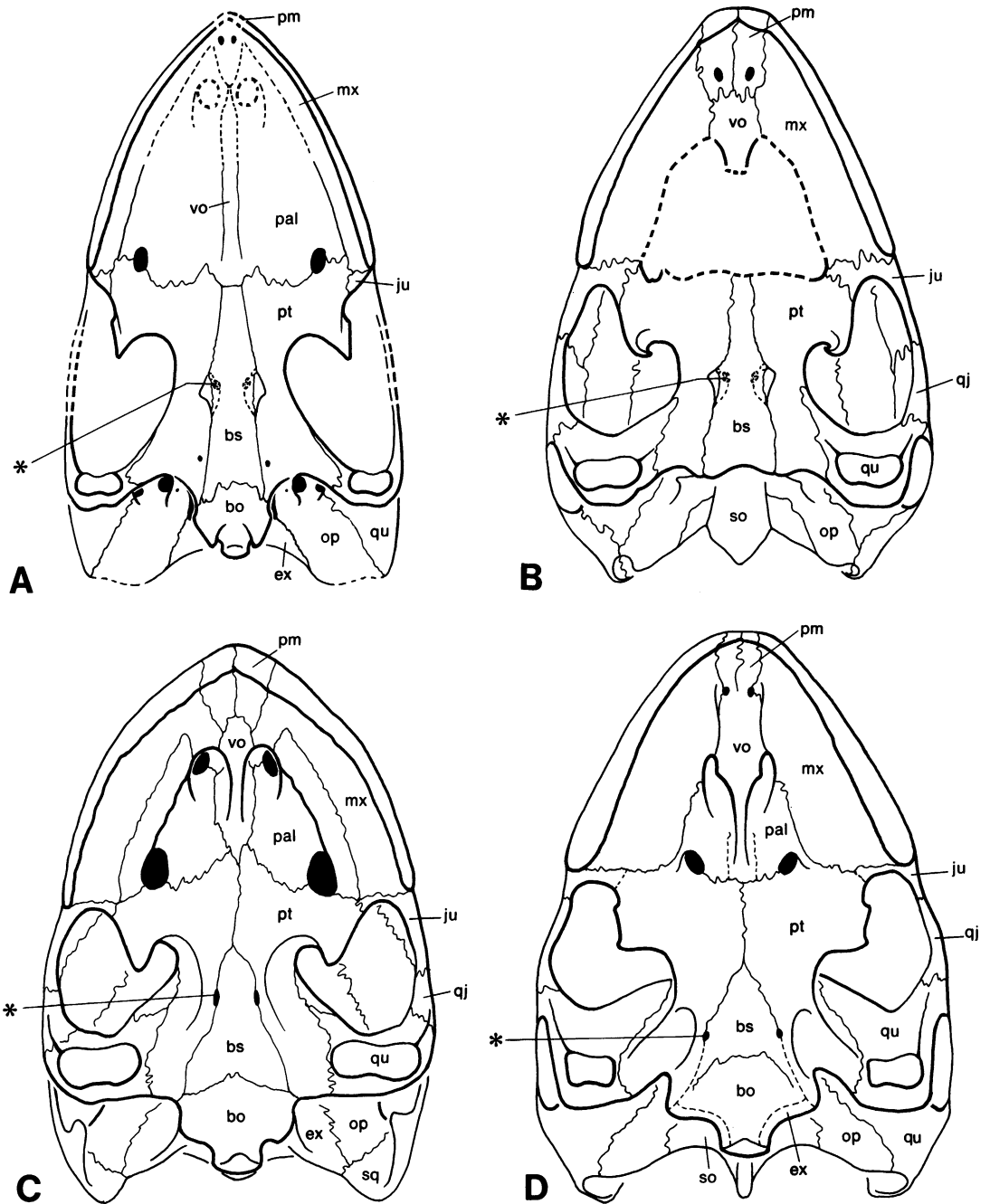


FIG. 28. Ventral views of A, *Glyptops plicatulus*, Late Jurassic, United States; B, *Mesochelys durlstonensis*, Early Cretaceous, Britain (after Evans and Kemp, 1975); C, *Dorsetochelys delairi*, Early Cretaceous, Britain (after Evans and Kemp, 1976); D, *Trinitichelys hiatti*, Early Cretaceous, United States (modified from Gaffney, 1972). Asterisk points to foramen posterius canalis carotici interni.

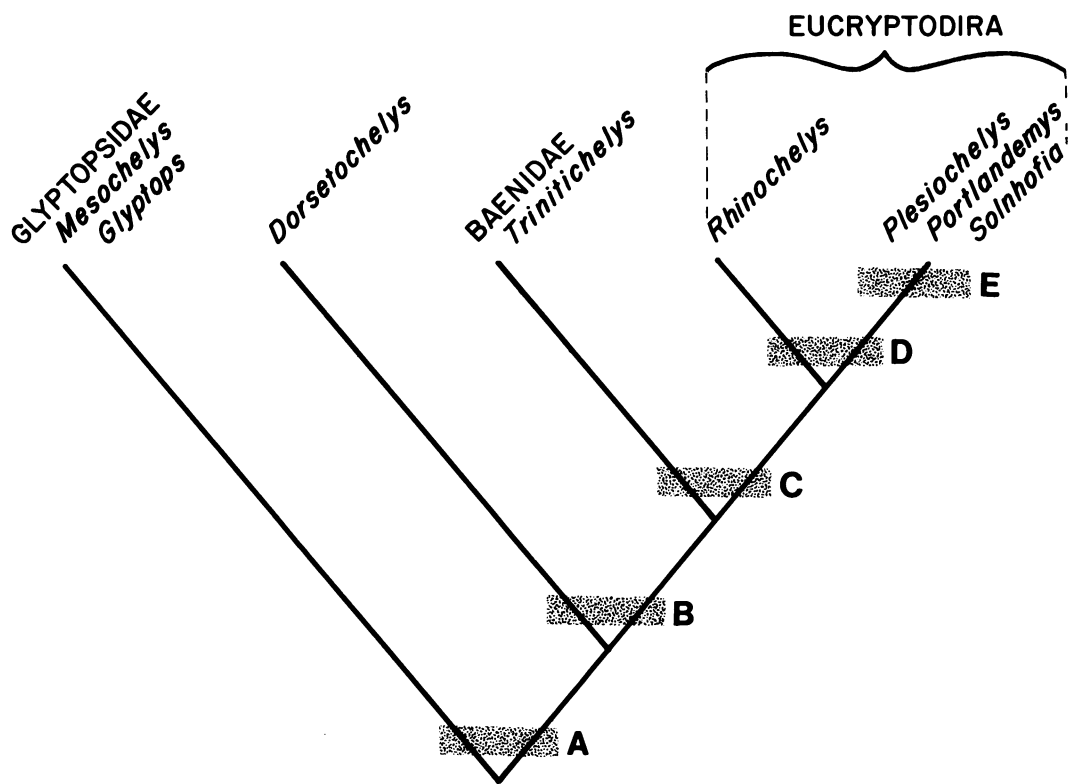


FIG. 29. Cladogram redrawn from Evans and Kemp (1976). Letters refer to character distributions discussed in text.

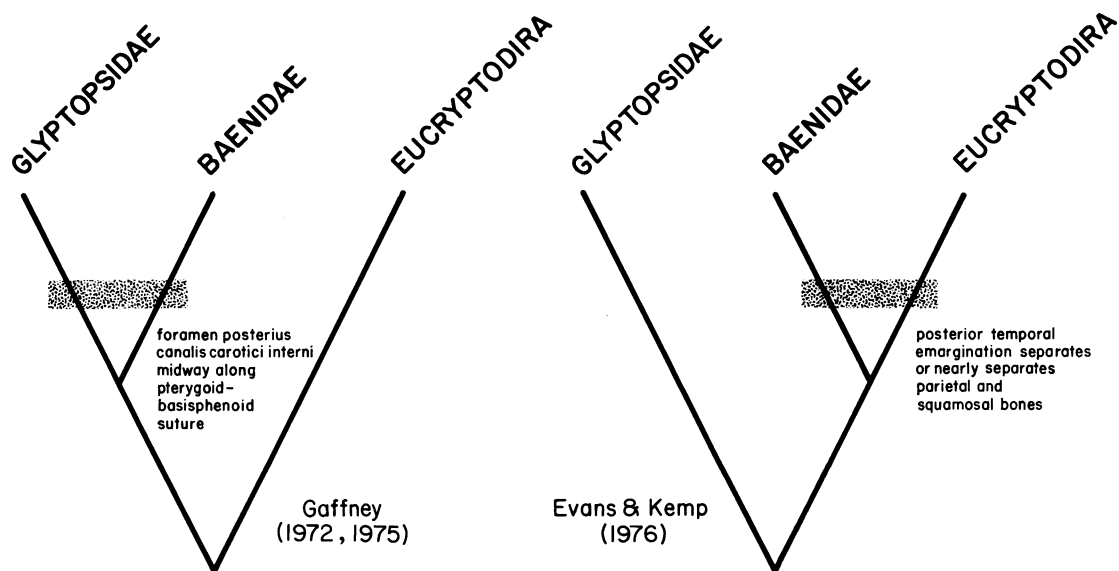


FIG. 30. Contradictory three-taxon statements concerning Glyptopsidae. See text.

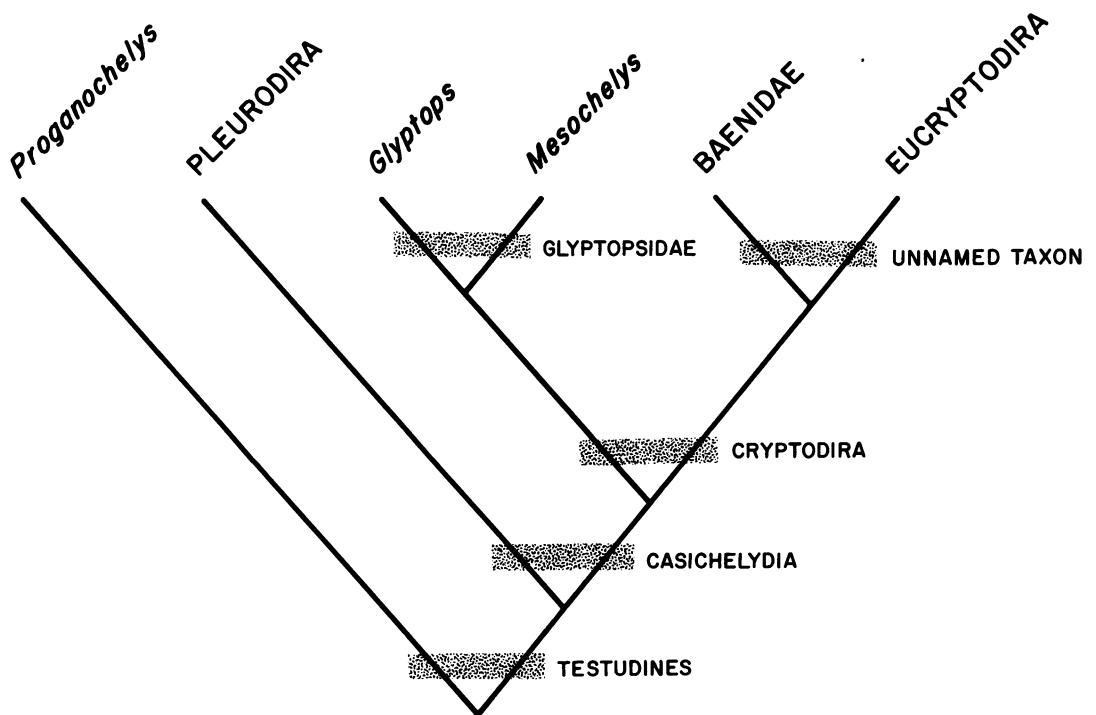


FIG. 31. Cladogram of major turtle taxa showing relationship of Glyptopsidae favored by author. Diagnoses of Testudines, Casichelydia, Pleurodira, Cryptodira, and Eucryptodira can be found in Gaffney (1975), for Glyptopsidae and Baenidae see text.

posed utilizes a series of characters that they argued were derived for each group as indicated in figure 29. The following letters refer to the character distributions indicated in figure 29:

- A. This character suite is the Cryptodira as diagnosed in Gaffney (1972 and 1975).
- B. Evans and Kemp (1976) argue that *Mesochelys* and *Glyptops* are the sister group for all other cryptodires on the following characters:
 1. A remnant of the basipterygoid articulation is absent in all cryptodires except *Mesochelys* and *Glyptops*. I have suggested above in the section on the basisphenoid that the identification of a basipterygoid articulation remnant in *Glyptops* and *Mesochelys* is incorrect. Therefore, the absence of this feature cannot be used as a derived character.
 2. In 1972 I suggested that a rela-

tively small, wedge-shaped basisphenoid (in ventral view) is derived for cryptodires while an elongate one, that is the same length as, and completely separates the pterygoids, is primitive. The latter condition is found in *Glyptops* and *Mesochelys*, whereas the former characterizes baenids and eucryptodires. Evans and Kemp substantiate this idea by comparison with *Proganochelys* and other reptiles in order to show that an elongate basisphenoid separating the pterygoids was primitive for turtles. Both analyses, however, are in error. I was strongly influenced by the age and generally plesiomorphic morphology of *Glyptops*. Neither study made comparisons with the appropriate group which is not *Proganochelys* or captorhinomorphs but the sister group of cryptodires, the pleurodires (see fig. 31). A comparison of the

basisphenoid in cryptodires and pleurodires (see figs. 4-9 in Gaffney, 1975) indicates that the common ancestor of those groups (in other words the morphotype of Casichelydia) would have a basisphenoid with the following features: it would be roughly triangular with the rostrum basisphenoidale covered ventrally by pterygoids that meet in the midline for about half their length. The condition in *Glyptops* and *Mesochelys* is then interpreted as a synapomorphy for those two taxa.¹

3. Previously (1972) I suggested that *Glyptops* was primitive because the pterygoid fails to completely floor the cavum acustico-jugulare as in most other cryptodires. Evans and Kemp (1975, 1976) also reported this condition in *Mesochelys* and used the complete flooring of the cavum acustico-jugulare as a derived character for baenids and eucryptodires. As discussed above, I now believe that I was mistaken about this feature and that *Glyptops* (and also *Mesochelys*) does not differ significantly from other cryptodires in this area.

- C. Evans and Kemp (1976) suggested that baenids and eucryptodires are a monophyletic group that is tested by the common presence of temporal emargination that separates or nearly separates the parietal and squamosal. This appears to be a good character at this level. Some eucryptodires (e.g., cheloniids, *Dermochelys*) do have a well-developed parietal-squamosal contact but I would interpret this as secondary and postulate that the primitive eucryptodire temporal condition was like that seen in *Trinitichelys*. I would also interpret the well-developed parietal-squamosal contact in some baenids (e.g., *Baena*) as secondary on the basis of the cladogram of the Baenidae in Gaffney (1972). The broad

squamosal-parietal contact in chelids I would consider primitive for Casichelydia and Pleurodira with the reduced contact derived within Pelomedusidae independently of Cryptodira.

- D. This group is essentially the Eucryptodira of Gaffney (1975) and Evans and Kemp use the same character and arguments as in that paper.
- E. In contrast to my hypothesis (Gaffney, 1975, 1976) of using basicranial features to unite the Chelonioidea, Evans and Kemp (1976) separated *Rhinochelys* (a chelonoid), *Portlandemys* (a chelonoid), and *Solnhofia* (a non-chelonoid). The last three taxa are related by Evans and Kemp on the presence of medially meeting prefrontals, a condition absent in *Rhinochelys*, baenids and glyptopsids. *Desmatochelys* (Zangerl and Sloan, 1960) and chelids (Gaffney, 1977) also do not have medially meeting prefrontals. Medially meeting prefrontals do certainly characterize pelomedusids and most eucryptodires but within the eucryptodires I would hesitate to ascribe the complex basicranial features in common between *Rhinochelys*, *Desmatochelys*, and other chelonoids to convergence.

In summary, we may compare the basic elements of the Evans and Kemp hypothesis and my earlier one. If we disregard *Dorsetochelys* temporarily, we can see that there are two alternative three-taxon statements (fig. 30). Evans and Kemp have presented four characters [B(1), B(2), B(3), and C, in the above list] that falsify my hypothesis, whereas I have presented only one character to falsify their hypothesis. However, I argue above that three of their characters are inadequate for the intended purpose. We are left with two hypotheses each falsified once. At the present time I believe that the Evans and Kemp hypothesis is to be preferred because of the distinct possibility that the carotid character I proposed is plesiomorphic at this level. In 1975 (p. 416) I discussed the possibility that both conditions were not synapomorphies: "An alternative hypothesis is to consider one of the known carotid positions

¹Although trionychids also have pterygoids that do not meet in the midline, this condition is due more to the large size of the palatines rather than an unusually elongate basisphenoid.

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 posterius 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." I still believe that the hypothesis of a monophyletic Baenoidea cannot be ignored but I do prefer the alternative suggested by Evans and Kemp. Neither hypothesis has been satisfactorily tested and a search for more characters should continue.

In conclusion, *Glyptops* has a synapomorphy in common with *Mesochelys*, namely an elongate basisphenoid extending the full length of and completely separating the pterygoids. Together these taxa form the Glyptopsidae. This family would be the sister group of Baenidae plus Eucryptodira.

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