

THE SYSTEMATICS OF
THE NORTH AMERICAN FAMILY
BAENIDAE (REPTILIA, CRYPTODIRA)

EUGENE S. GAFFNEY

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ABSTRACT

A SYSTEMATIC REVISION of the North American family Baenidae has resulted in the following conclusions:

1) The family ranges from Albian, early Cretaceous, to Uintan, late Eocene, in age.

2) Definite members of the family are presently known only from North America.

3) Eight genera including nine species are soundly based on skull material: *Trinitichelys hiatti*, new genus and new species; *Hayemys latifrons* (Hay), new genus; *Plesiobaena antiqua* (Lambe), new genus; *Plesiobaena putorius*, new genus and new species; *Eubaena cephalica* (Hay); *Stygiochelys estesi* Gaffney and Hiatt; *Palatobaena bairdi*, new genus and new species; *Baena arenosa* Leidy; and *Chisternon undatum* (Leidy). Four more genera with one species each are known only from

shells: *Compsemys victa* Leidy; *Neurankylus eximius* Lambe; *Boremys pulchra* Lambe; and *Thescelus insiliens* Hay. The following are *nomina dubia*: *Polythorax missouriensis* Cope; "*Neurankylus*" *wyomingensis* Gilmore; "*Baena*" *hayi* Gilmore; "*Baena*" *nodosa* Gilmore; *Chisternon interpositum* Hay; "*Baena*" *ornata* Gilmore; and "*Baena*" *platyplastra* Gilmore.

4) The family Glyptopsidae has the nearest ancestor in common with the family Baenidae; together they constitute the superfamily Baenoidea. A classification based in part on degree of morphologic diversity but consistent with the phylogeny is developed. A strictly phylogenetic classification is also presented.

INTRODUCTION

CHELONIAN phylogeny is a rich field of inquiry for the historical biologist. In general, the turtles have a good fossil record, and because they are still living, many aspects of their biology can be determined with a high degree of validity, even for fossil forms. In addition, turtles are similar to birds in being morphologically uniform, in the sense that they have a restricted number of variations from a basic pattern (see Bock, 1963). Therefore, investigations of their phylogeny will yield information concerning evolutionary processes in such structurally uniform groups. However, more work has been done on the relationships of turtles to other vertebrates than on the phylogeny of turtles per se, and much of their history is unknown.

The attempted solutions of phylogenetic problems in the chelonians have been based mainly on the shell morphology. However, the most successful results have come from studies of the complete anatomy with emphasis on the skull and cervical vertebrae (for example: Walther, 1922; Nick, 1912; and Williams, 1950). Fossils have been largely ignored in these detailed studies (Zangerl, 1948, 1953, and 1960; Williams, 1950; and Parsons and Williams, 1961, are exceptions). Mesozoic turtles are an obviously important area for phylogenetic investigation, yet very little work has been done on them. The continental deposits of North America have provided a variety of Mesozoic

turtles, with excellent cranial material and a number of relatively complete skeletons available.

The present study is the first in a series of papers on the Baenoidea, a prominent group of Mesozoic turtles. The baenoids have usually been classified in the Amphichelydia, a group supposedly containing the ancestors of modern turtles. In fact, Romer (1956, p. 501) has suggested that a baenid, *Eubaena*, is "transitional" to modern cryptodires. An understanding of the relationships of the baenoids, then, might give some information concerning the relationships of cryptodires.

A study of the Baenoidea was submitted as a Ph.D. thesis at Columbia University in 1969 (Gaffney, ms). The original work is being published in several parts. The first major section consists of the systematics and relationships of the baenid genera. The cranial morphology and over-all relationships of the Baenoidea will follow. Smaller papers on *Glyptops*, baenid paleoecology, baenid lower jaws, and turtle skull terminology are also in preparation.

ACKNOWLEDGMENTS

I wish to express my gratitude to Dr. Edwin H. Colbert for his sponsorship of this project and for allowing me the use of specimens and facilities under his direction. I also thank Dr.

Bobb Schaeffer for providing facilities and a stimulating atmosphere for discussion of evolutionary problems. The encouragement and support of Drs. Colbert and Schaeffer have made this study possible.

Dr. Donald Baird of Princeton University was the first to interest me in turtles, and his friendship and guidance are warmly appreciated. Dr. Richard D. Estes brought together most of the North American baenid specimens, which he generously turned over to me. Dr. Malcolm C. McKenna and Dr. Donald Baird generously spent considerable time reading and offering constructive criticism of the original manuscript. Drs. Gareth J. Nelson and Niles Eldredge kindly read portions of the paper and discussed aspects of phylogenetic interpretation.

Many institutions and people provided facilities and lent specimens for this study. Universal help and generous sacrifice of time characterized these persons: Dr. Rainer Zangerl, Field Museum of Natural History; Dr. Bryan Patterson, Museum of Comparative Zoology; Dr. John Ostrom, Peabody Museum, Yale University; Dr. Glenn L. Jepsen, Princeton University; Dr. A. Gordon Edmund and Mr. Franklin Ross, Royal Ontario Museum; Dr. Dale A. Russell and Mr. Harold Shearman, National Museum of Canada; Keeper H. W. Ball, British Museum (Natural History); Dr. Joseph T. Gregory and Mr. Dennis Bramble, University of California, Museum of Paleontology, Berkeley; Dr. Robert E. Sloan, University of Minnesota; Dr. Craig C. Black and Dr. Mary R. Dawson, Carnegie Museum, Pittsburgh; Dr. Claude Hibbard, Museum of Paleontology, University of Michigan; Dr. Nicholas Hotton, III, United States National Museum, Smithsonian Institution; Dr. Horace Richards, Academy of Natural Sciences of Philadelphia; and Dr. Robert Hiatt, of Glendive, Montana.

The excellent stippled drawings are the work of Miss Jennifer Perrott of the Department of Vertebrate Paleontology, the American Museum of Natural History. Mrs. Susan Weeks and Miss Diane Sprungl deserve special thanks for art and editorial work. The photographs were taken by the Division of Photography, the American Museum of Natural History, and Mr. Chester Tarka of the Department of Vertebrate Paleontology, the American Museum of Natural History.

ABBREVIATIONS OF INSTITUTIONS

AMNH, the American Museum of Natural History
 ANSP, Academy of Natural Sciences of Philadelphia
 BM(NH), British Museum (Natural History)
 CM, Carnegie Museum
 FMNH, Field Museum of Natural History
 MCZ, Museum of Comparative Zoology, Harvard University
 NMC, National Museum of Canada
 PU, Princeton University
 ROM, Royal Ontario Museum
 UCMP, University of California, Museum of Paleontology
 UMMP, University of Michigan, Museum of Paleontology
 USNM, United States National Museum, Smithsonian Institution
 UNIV MINN, University of Minnesota
 YPM, Yale Peabody Museum

ABBREVIATIONS USED IN FIGURES

ant. postot., ANTRUM POSTOTICUM
 aper. nar. ext., APERTURA NARIUM EXTERNA
 aper. nar. int., APERTURA NARIUM INTERNA
 bo, basioccipital
 bs, basisphenoid
 cav. acust. jug., CAVUM ACUSTICO-JUGULARE
 cond. mand., CONDYLUS MANDIBULARIS
 cond. oc., CONDYLUS OCCIPITALIS
 ex, exoccipital
 fis. eth., FISSURA ETHMOIDALIS
 for. car. post., FORAMEN POSTERIOR CANALIS CAROTICI INTERNI
 for. mag., FORAMEN MAGNUM
 for. orb. nas., FORAMEN ORBITO-NASALE
 for. pal. post., FORAMEN PALATINUM POSTERIUS
 for. prepal., FORAMEN PRAEPALATINUM
 for. stap., FORAMEN STAPEDIO-TEMPORALE
 fos. cart. epi., FOSSA CARTILAGINIS EPIPTERYGOIDEI
 fos. temp., FOSSA TEMPORALIS
 fr, frontal
 inc. col. aur., INCISURA COLUMELLAE AURIS
 ju, jugal
 mx, maxilla
 na, nasal
 op, opisthotic
 pa, parietal
 pal, palatine
 pf, prefrontal
 pm, premaxilla
 po, postorbital
 pr, prootic
 proc. pter. ext., PROCESSUS PTERYGOIDEUS EXTERNUS
 proc. troch. otic., PROCESSUS TROCHLEARIS OTICUM
 pt, pterygoid
 qj, quadratojugal
 qu, quadrate
 so, supraoccipital

sq, squamosal

tub. bas., TUBERCULUM BASIOCCIPITALE

vo, vomer

HISTORY OF PREVIOUS WORK

Most of the work on North American baenoids was done before 1910. Leidy described the first baenoid, *Compsemys victus*, in 1856. The specimen, a shell fragment with characteristic ornamentation, is typical of the fragmentary material studied by workers from 1860 to 1880. During this period, specimens that extended from the Upper Jurassic into the Lower Tertiary were discovered in the western United States. The material was generally poor and little phylogenetic work was accomplished. In 1891, however, Baur described the skull of *Glyptops*, a Jurassic baenoid. He expressed the idea that this form was related to Lydekker's (1889) *Amphichelydia* and that it was structurally intermediate between living cryptodires and pleurodires. Hay's (1905a) further development of the *Amphichelydia* was based in large part on morphological features of the baenoids. His conclusions were similar to Baur's, namely that the baenoids then known were structurally

intermediate between cryptodires and pleurodires. Although Hay described skull material of North American baenoids in his paper, he based his phylogenetic statements on the shell morphology. "The Fossil Turtles of North America" (Hay, 1908) included the only complete revision of North American baenoids published to date. Hay included 10 genera and 22 species in the family Baenidae. The publication of his monograph marked the peak of activity on North American baenoids.

A few papers on baenoids were produced during the period from 1910 to 1935; almost all of them were by Gilmore (1915, 1916a, 1916b, 1916c, 1919a, 1919b, 1935). No broad analyses of relationships were attempted and the results were in the form of new species. Simpson, in 1938, presented a detailed description and discussion of affinities of the meiolaniid *Crossochelys* from Patagonia. He concluded that the meiolaniids were related to the *Amphichelydia* as typified by the North American Baenidae. Williams (1950) set up a superfamily Baenoidea within the suborder *Amphichelydia* to include meiolaniids and baenids in recognition of Simpson's work and his own studies of the cervical vertebrae.

SYSTEMATICS

MOST TAXONOMIC WORK on fossil turtles has been based on inadequate samples and incomplete specimens. A large number of fossil turtle species have been defined on single shells or parts of shells. Although shells are the commonest remains, their morphology is quite variable within a species and, without a large enough sample, it may be practically impossible to differentiate between interspecific and intraspecific variation. Furthermore, the shells are not generally so useful for phylogenetic studies as other parts of the anatomy, in particular the skull and vertebrae.

The classification presented herein is based

mostly on skull characters and will enable identification of skull material rather precisely, but shells can only be identified broadly, not even to genus in some cases. This is unfortunate for zoogeographic and stratigraphic work, as skulls are rather infrequent occurrences, compared to shells. However, I believe that a much more realistic classification has resulted.

In almost every case (the Uppsala specimens of Wiman, 1933, from the late Cretaceous of New Mexico are a major exception) the hypodigms and all the type specimens have been personally examined by the author.

A CLASSIFICATION OF THE NORTH AMERICAN BAENOIDEA

CLASS REPTILIA

ORDER TESTUDINES

SUBORDER CRYPTODIRA COPE (part), 1871

Superfamily BAENOIDEA (Cope, 1882) Williams, 1950

Family GLYPTOPSIDAE Marsh, 1890

Glyptops Marsh, 1890

G. plicatulus (Cope, 1877), Upper Jurassic; North America

Family BAENIDAE Cope, 1882

Subfamily TRINITICHELYINAE, new

Trinitichelys, new genus

T. hiatti, new species, Cretaceous; North America

Subfamily HAYEMYDINAE, new

Hayemys, new genus

H. latifrons (Hay, 1908), Upper Cretaceous; North America

Subfamily EUBAENINAE (Williams, 1950)

Plesiobaena, new genus

P. antiqua (Lambe, 1902), Upper Cretaceous; North America

P. putorius, new species, Paleocene; North America

Eubaena Hay, 1908

E. cephalica (Hay, 1904), Upper Cretaceous; North America

Stygiochelys Gaffney and Hiatt, 1971

S. estesi Gaffney and Hiatt, 1971, Upper Cretaceous; North America

Subfamily PALATобаENINAE, new

Palatobaena, new genus

P. bairdi, new species, Upper Cretaceous-Paleocene; North America

Subfamily BAENINAE (Cope, 1882), new rank

Baena Leidy, 1870

B. arenosa Leidy, 1870, Eocene; North America

Chisternon Leidy, 1872

C. undatum (Leidy, 1871b), Eocene; North America

Taxa within the family Baenidae but not assignable to subfamily:

Compsemys Leidy, 1856

C. victa Leidy, 1856, Cretaceous -Paleocene; North America

Neurankylus Lambe, 1902

N. eximius Lambe, 1902, Upper Cretaceous; North America

Boremys Lambe, 1906b

B. pulchra (Lambe, 1906a), Upper Cretaceous; North America

Thescelus Hay, 1908

T. insiliens Hay, 1908, Upper Cretaceous; North America

CLASS REPTILIA

ORDER TESTUDINES

SUBORDER CRYPTODIRA COPE (part), 1871

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 in its own canal traversing cranio-quadrate space; mandibular artery exiting from FORAMEN NERVI TRIGEMINI; epipterygoid usually present, when absent pterygoid cartilage persistent resulting in FOSSA CARTILAGINIS 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 cheloniids); FORAMEN SUPRAMAXILLARE present; descending process of prefrontal meeting vomer ventromedially; dentaries always united.

Head withdrawn by vertical flexure of neck in advanced forms with attendant development of widely spaced zygapophyses, reduced transverse process, and formed central articulations all 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.

DISCUSSION: The reasons for the classification of baenoids in the Cryptodira are given in a study (Gaffney, ms) of the relationships of the Baenoidea, where the characters summarized in this diagnosis are discussed in greater detail.

SUPERFAMILY BAENOIDEA (COPE, 1882) WILLIAMS, 1950

DIAGNOSIS: Cryptodiran turtles tending to

retain primitive features; skull with nasals; prefrontals not meeting on skull roof midline; FORAMEN POSTERIOR CANALIS CAROTICI INTERNI lying midway along length of basisphenoid-pterygoid suture; well-developed stapedia artery, reduced orbital and palatine arteries (inferred from preserved foramina); cervical vertebrae lacking well-developed retraction mechanism, early forms lacking formed central articulations; shell with mesoplastra and paired intergular scutes.

KNOWN DISTRIBUTION: Late Jurassic to late Eocene, North America.

DISCUSSION: A diagnosis of the Baenoidea is difficult to arrive at because the group consists of closely related lineages including primitive and advanced members with few characters in common, if end forms are examined. The inclusion of the Jurassic turtle *Glyptops* particularly causes practical problems with a diagnosis, but *Glyptops* is clearly related to the baenids. One of the unique derived or advanced characters found within the Baenoidea is the presence of the FORAMEN POSTERIOR CANALIS CAROTICI INTERNI about halfway along the length of the basisphenoid-pterygoid suture. In all other cryptodires the FORAMEN is near the posterior end of the pterygoid. The baenoid condition may be primitive for cryptodires but this is not substantiated by its presence in any other group of cryptodires. Baenoids also tend to have only the nasals, frontals, and parietals meeting on the skull roof with the prefrontals either absent from the dorsal surface (the usual condition) or restricted to small lappets (*Glyptops* and *Hayemys*). At present it appears that the baenoids did not develop fully retractile neck mechanisms, at least not to the extent seen in the living groups, and parallel evolution of formed central articulations took place within the Baenoidea.

Two families are here included in the superfamily Baenoidea: the Glyptopsidae, and the

		SKULLS	ASSOCIATED SHELL & SKULL	SHELLS
EOCENE	UINTAN	Baena arenosa Chisternon undatum		
	BRIDGERIAN	Baena arenosa Chisternon undatum		
	WASATCHIAN	Baena arenosa		
PALEOCENE	TIFFANIAN	Palatobaena bairdi Plesiobaena putorius		form-genus "Baena"
	TORREJONIAN			form-genus "Baena" Compsemys victa
	PUERCAN			Compsemys victa
CRETACEOUS	MAESTRICHTIAN	Hayemys latifrons Eubaena cephalica Stygiochelys estesi Palatobaena bairdi	Plesiobaena antiqua	Thescelus insiliens Neurankylus eximius form-genus "Baena" Compsemys victa
	CAMPANIAN		Plesiobaena antiqua	Boremys pulchra Thescelus insiliens Neurankylus eximius
	ALBIAN		Trinitichelys hiatti	
JUR.	PORTLANDIAN - KIMMERIDGIAN	Glyptops plicatulus		

FIG. 1. Geologic distribution of North American Baenoidea indicating known parts of the animals. Time dimension is not to scale (see fig. 46 for time distribution to scale).¹

Baenidae. The meiolaniids have been included in the Baenoidea (Williams, 1950; Romer, 1956) but pending further work on their rela-

tionships (Gaffney, in preparation) they will be excluded here because they lack certain definitive baenoid characters.

The Asian *Macrobaena* (Tatarinov, 1959) is apparently not a baenoid as it has prefrontals meeting in the midline, a carotid foramen entering the skull through or near the FENESTRA POSTOTICA, no mesoplastra, and formed centra with widely spaced zygapophyses. It is likely

¹*Palatobaena bairdi* and *Plesiobaena putorius* have been identified on the basis of skull material from Rock Bench Quarry of Torrejonian age. This material should be noted above. Furthermore, an associate skull and shell of *Plesiobaena* sp., Univ. of Wyoming 3348, has been found in the Tiffanian of Wyoming.

TABLE 1
A COMPARISON OF THE FAMILIES GLYPTOPSIDAE AND BAENIDAE

Character	Glyptopsidae	Baenidae
Skull shape	Very elongate, width much less than length	Width and length almost equal (except in <i>Trinitichelys</i>)
Prefrontal exposure on skull roof	Present	Present in most cases but (except in <i>Hayemys</i>) much more restricted than in <i>Glyptops</i>
Triturating surfaces	Narrow, no expanded areas developed	Varied, but always with medial expansions
Basisphenoid extending length of pterygoids	Yes	No
Epipterygoid	Probably present	Absent but a FOSSA CARTILAGINIS EPIPTERYGOIDEI always present
Pterygoid completely floors CAVUM ACUSTICO-JUGULARE	No	Yes
INCISURA COLUMELLAE AURIS	Widely open posteroventrally	Closed or almost closed posteroventrally, enclosing stapes and eustachian tube
Cervical vertebrae	Amphicoelous	Amphicoelous in early members, formed central articulations in later members
Last vertebral scute	Barely enclosed posteriorly by tapering marginal scutes	Either completely enclosed by rectangular marginal scutes or widely open posteriorly
Cervical (nuchal) scute	Small, rectangular	Variable, including condition in <i>Glyptops</i>

that *Macrobaena* is a testudinoid but further examination of the basicranium is necessary. Tatarinov (*ibid.*) also reported that *Baena* is found in the Mongolian Cretaceous but no material is described. *Chengyuchelys baenoides* (Young and Chow, 1953) has been reported as a possible baenid but the described material consists of shells that lack distinctive baenid features.

FAMILY BAENIDAE COPE, 1882

Neurankylidae WILLIAMS, 1950.

Eubaenidae WILLIAMS, 1950.

TYPE: *Baena* Leidy, 1870.

KNOWN DISTRIBUTION: Albion to Uintan (early Cretaceous to late Eocene), North America (figs. 1, 46).

DIAGNOSIS: Baenoids with wedge-shaped skull (except in *Trinitichelys*); variable development of temporal and cheek emarginations; prefrontals with only slight dorsal exposure (except in *Hayemys*); triturating surfaces varied but invariably with some expansion, never narrow

as in *Glyptops*; basisphenoid shorter antero-posteriorly than pterygoids; pterygoid flooring CAVUM ACUSTICO-JUGULARE completely; epipterygoid absent but FOSSA CARTILAGINIS EPIPTERYGOIDEI present; CAVUM TYMPANI almost circular, INCISURA COLUMELLAE AURIS enclosing stapes and eustachian tube; well-developed ANTRUM POSTOTICUM; formed central articulations in cervical vertebrae of advanced forms; last vertebral scute either enclosed posteriorly by marginals or not enclosed posteriorly; cervical (nuchal) scute present but variably developed.

DISCUSSION: Williams in 1950 set up families within the Baenoidea primarily on the basis of vertebral characters. In light of the interpretation presented here, that the American forms are closely related, only one family is recognized for the American post-Jurassic baenoids.

Polythorax missouriensis Cope, 1876 (p. 258), was described on the basis of a carapace, plastron, and lower jaw. Published locality data consists of " . . . the Fort Union beds of Montana . . . "

TABLE 2
A COMPARISON OF THE SUBFAMILIES WITHIN THE BAENIDAE

Character	Trinitichelyinae	Hayemydinae	Eubaeninae	Palatobaeninae	Baeninae
Skull shape	Length greater than width, elongate compared to later baenids but not as elongate as <i>Glyptops</i>	Width and length equal	Width equal to or greater than length	Width greater than length, almost circular in outline	Width and length almost equal
Degree of temporal emargination relative to skull length	Shallow	Deep	Deep	Probably shallow (not completely preserved)	Shallow
Nasals expanded laterally	No	Yes	No	No	No
Exposure of prefrontals on skull roof	Slight	Well developed	Slight	Slight	Slight
Squamosal-parietal contact	Present but very limited	Absent	Absent	Indeterminate	Present, well developed
Parietal larger than frontal	Yes	No, parietals restricted laterally	Yes	Yes	Yes
Quadratojugal C-shaped with dorsal process	Yes	Yes	Yes	Indeterminate	No
Quadratojugal with broad anterior process	Yes	No	No	Indeterminate	No
Triturating surfaces	Expanded posteriorly, well-developed tomial ridge	Indeterminate	Variable (see table 3)	Widely expanded to form triangular crushing areas	Essentially as in <i>Trinitichelys</i> and <i>Plesiobaena</i> with slight differences
Jugal exposure in orbital margin	Present but limited	Yes	Variable (see table 3)	Yes	Yes

(Cope, 1876, p. 248) but the associated fossils (carnosaurs, ceratopsians, and hadrosaurs) indicate a Cretaceous age, assuming that the collection came from the same locality. However, there is no explanatory information of any sort in the original paper; it consists only of a list of new taxa diagnoses. Hay (1908, p. 100) indicated that the specimen came from "Judith River deposits," but there is no factual basis for this statement. The type was lost by Hay's time and no record of it has appeared since. The limited description of Cope's (1876, p. 258) suggests, as Hay noted (1908, p. 101), that the

specimen is similar to *Baena*. In fact, none of the described features permits its distinction. Since the specimen is unavailable and cannot be adequately diagnosed on the basis of published information, I am regarding it as a *nomen dubium*.

SUBFAMILY TRINITICHELYINAE, NEW

TYPE: *Trinitichelys*, new genus.

KNOWN DISTRIBUTION: Albian of Texas.

DIAGNOSIS: Baenids with elongate skull, width less than length, but not so elongate as in

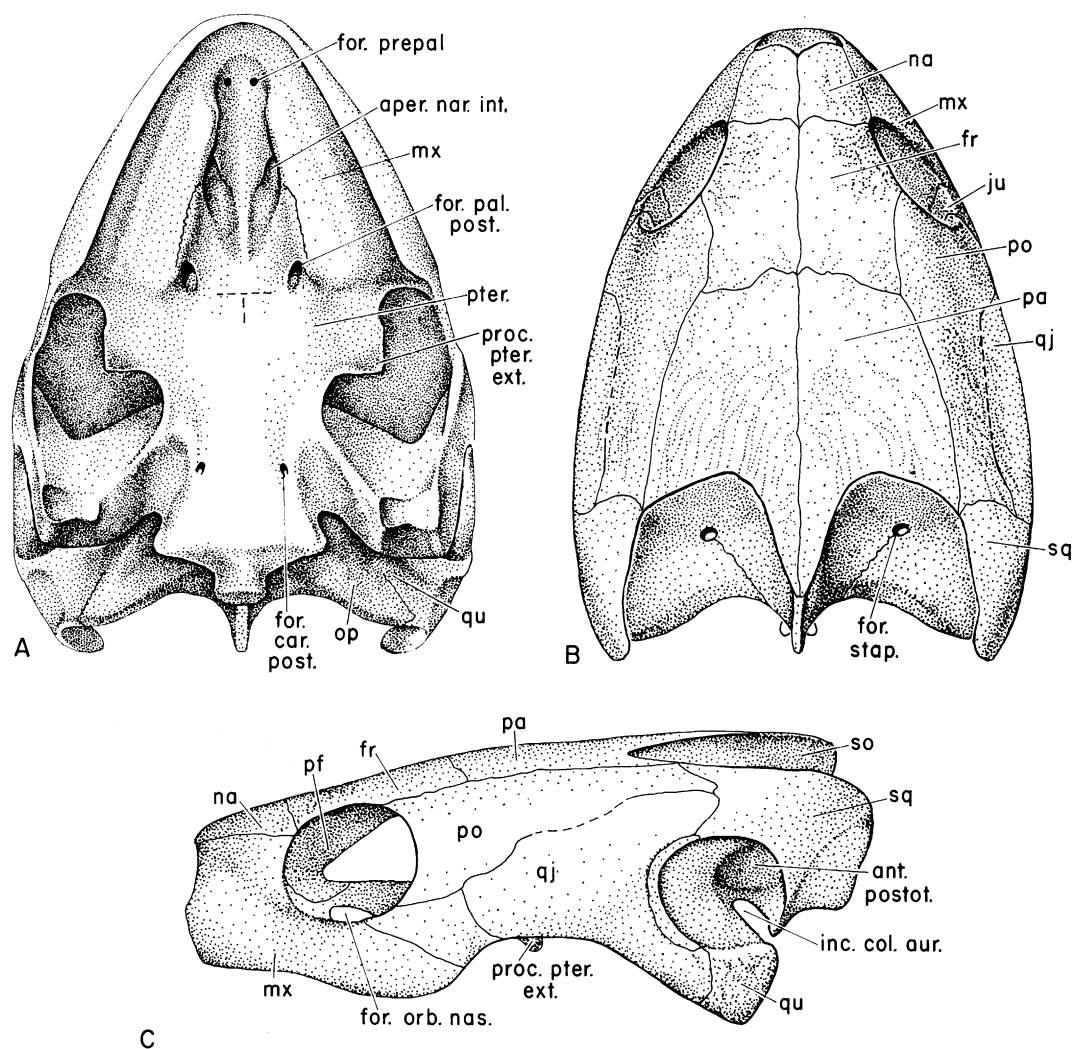


FIG. 2. *Trinitichelys hiatti*, new genus and new species. Restoration of skull based on type specimen MCZ 4070 from the early Cretaceous Trinity Formation of Texas. A. Ventral view. B. Dorsal view. C. Lateral view. See also figure 47. Condyle-premaxilla length 55 mm. Abbreviations on pages 246-247.

Glyptops; temporal emargination shallow compared to length of skull; nasals not expanded laterally; prefrontals without extensive dorsal exposure; parietal barely reaching squamosal; parietal larger than frontal; quadratojugal C-shaped with dorsal process and broad anterior extension; triturating surfaces expanded posteriorly, anteromedial ridge developed as in *Plesiobaena*; orbits open laterally; cervical vertebrae amphicoelous; shell oval in shape; shell and skull surface ornamentation similar to *Glyptops*; cervical (nuchal) scute small, rectangular; anterior of carapace without emargi-

nation; first vertebral scute rectangular without supracostal scutes; supramarginal scutes absent; xiphiplastral notch absent; paired intergulars present; gular scutes separated by intergulars (last vertebral scute, scalloping, and posterior edge of carapace indeterminate).

TRINITICHELYS,¹ NEW GENUS

TYPE SPECIES: *Trinitichelys hiatti*, new species.

KNOWN DISTRIBUTION: Albian of Texas.

DIAGNOSIS: Same as for subfamily.

DISCUSSION: See specific discussion.

¹ For the Trinity Formation.



***Trinitichelys hiatti*,¹ new species**

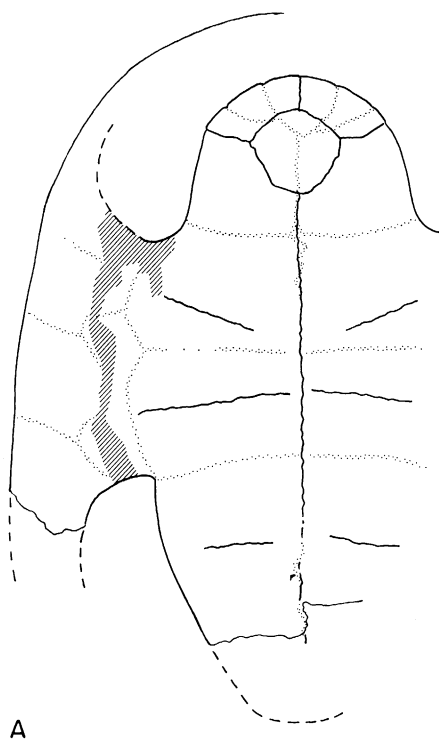
TYPE SPECIMEN (figs. 2-5, 47): MCZ 4070, an almost complete skeleton, lacking the lower jaw, caudal vertebrae, distal parts of the limbs, and posterior part of the shell.

LOCALITY: 1 mile from Hardee (Hardy, Harday) on road to Forestburg, Montague County, Texas. "Cross creek, then (into) ditch on right of road just above entrance from house; a small side gully comes in. Dirt wash must be scraped to find turtle layer" (from A. S. Romer's notebook entry for March 30, 1952. I am grateful to Prof. Bryan Patterson for these data).

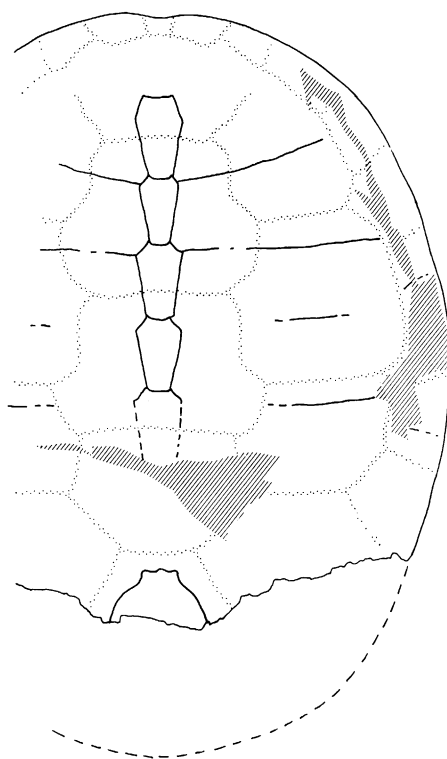
HORIZON: Trinity Sand of the Trinity Group, early Cretaceous. Probably early Albian in age (Stephenson et al. 1942).

¹ For Dr. Robert Hiatt of Glendive, Montana, who has generously lent many baenid specimens for this study.

FIG. 3. *Trinitichelys hiatti*, new genus and new species. Dorsal view of skull of type specimen, MCZ 4070, from the early Cretaceous Trinity Formation of Texas. Scale equals 1 cm.



A



B

FIG. 4. *Trinitichelys hiatti*, new genus and new species. MCZ 4070, partially restored shell of type specimen, from the early Cretaceous Trinity Formation of Texas. A. Ventral view. B. Dorsal view.

COLLECTORS: Alfred S. Romer, A. Witter, and party, March 30, 1952.

SPECIFIC DIAGNOSIS: As the genus is monotypic, there can be no delimiting of specific characters.

DISCUSSION: The type specimen was identified in the field as *Glyptops*, but a study of the skull shows it to be a distinct form, morphologically intermediate between *Glyptops* and the later baenids. The shell is nearly identical with those of *Glyptops* and *Neurankylus*. It differs from *Glyptops* in having the second and third vertebrals narrower anteriorly, as in *Neurankylus*. The shell differs from *Neurankylus* in having the sculpture pattern of *Glyptops* and in lacking keeled neurals (some *Neurankylus* specimens also lack keeled neurals). However, in the absence of skull material it would be difficult to differentiate among the three forms (as is discussed under *Neurankylus*).

Neurankylus wyomingensis Gilmore may prove to be referable to *Trititichelys*. The data are as follows:

TYPE SPECIMEN: USNM 7581, posterior half of shell (Gilmore, 1919a, pp. 113–115, pls. 29, 30).

LOCALITY: "Shoshone River, near Cody, Big Horn County, Wyoming" (*ibid.*).

HORIZON: "Colorado shale, Upper Cretaceous" (*ibid.*).

COLLECTOR: D. F. Hewett, 1912.

The incompleteness of the specimen of *Trititichelys* and the type of *N. wyomingensis* precludes a definite identification. *Trititichelys* lacks the posterior end of the carapace while in *N. wyomingensis* this is the part preserved. The ornamentation is the principal reason for Gilmore's separating this form from the other species of *Neurankylus*. The ornamentation, however, is also the main feature in which *N. wyomingensis* resembles *Trititichelys*. However, the ridges of *N. wyomingensis* are more broken up and nodular and not identical with the ornamentation of *Trititichelys*. Therefore, it seems best to consider *N. wyomingensis* a *nomen dubium* until better material is available.

SUBFAMILY HAYEMYDINAE, NEW

TYPE: *Hayemys*, new genus.

KNOWN DISTRIBUTION: Late Cretaceous, Wyoming.

DIAGNOSIS: Baenids with wedge-shaped skull, width approximately equal to length; temporal emargination deep compared to length of skull; nasals expanded laterally; prefrontal with

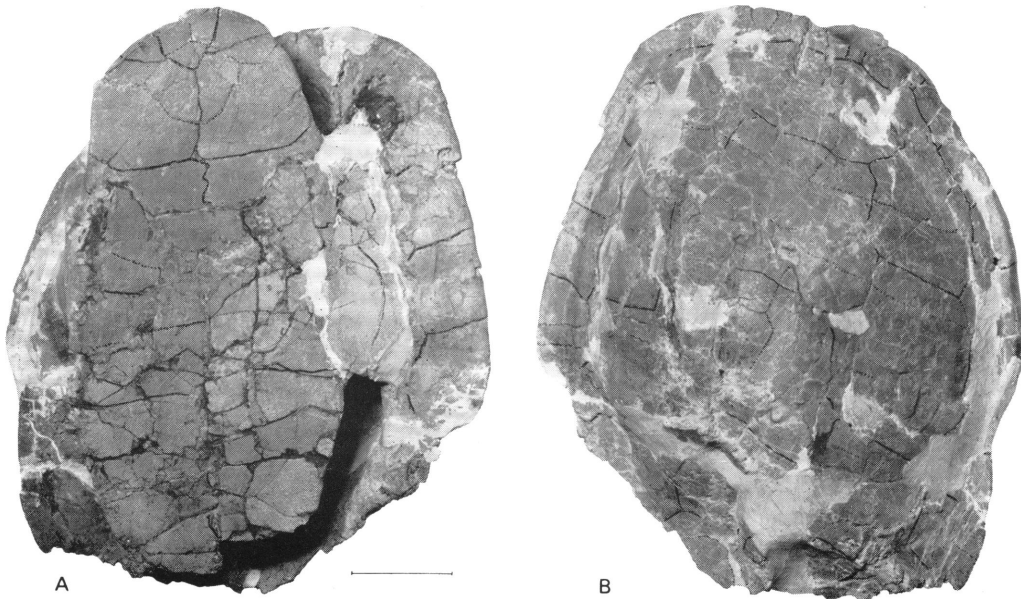


FIG. 5. *Trititichelys hiatti*, new genus and new species. MCZ 4070, shell of type specimen, from the early Cretaceous Trinity Formation of Texas. A. Ventral view. B. Dorsal view. Scale equals 5 cm.

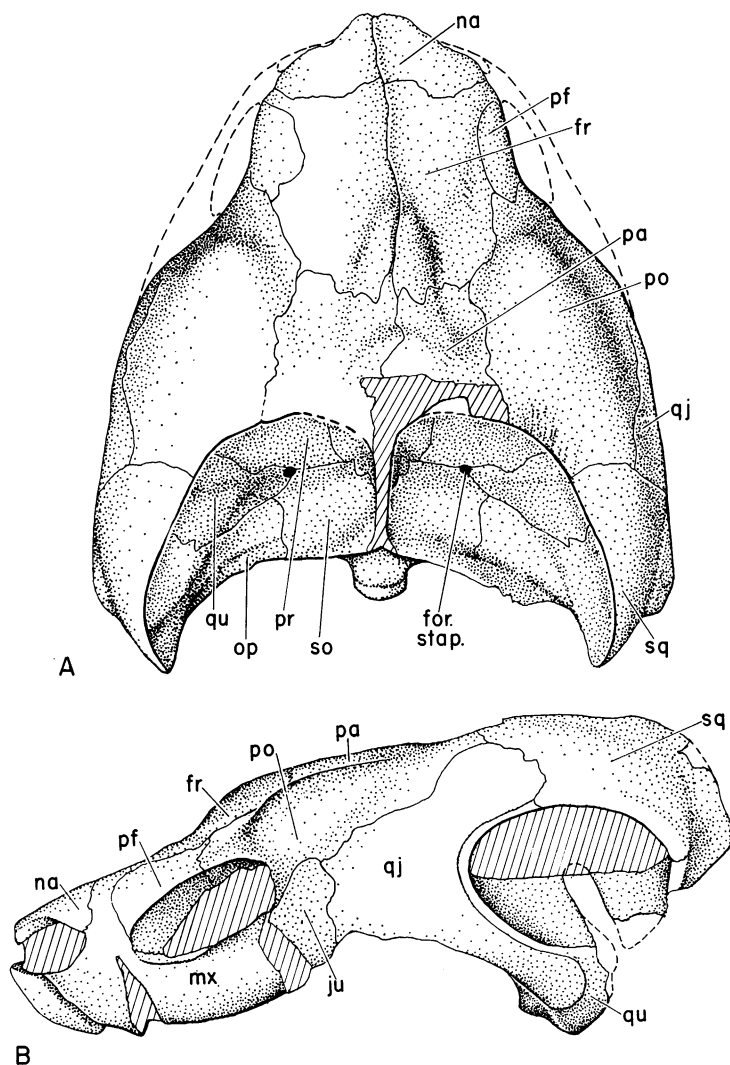


FIG. 6. *Hayemys latifrons* (Hay), new genus. Skull of type specimen, AMNH 6139, from the late Cretaceous Hell Creek Formation of Wyoming. A. Partially restored dorsal view. B. Lateral view without restoration, right side reversed. Hachured areas are broken or filled with matrix. Abbreviations on pages 246–247.

medially expanded dorsal lappet, not meeting in midline; no squamosal-parietal contact; frontal larger than parietal, parietals much restricted laterally; quadratojugal C-shaped with dorsal process but without anterior extension; triturating surfaces indeterminate; orbits open laterally; postcranium unknown.

HAYEMYS,¹ NEW GENUS

Eubaena HAY, 1908, p. 82 (in part).

¹ For Oliver Perry Hay.

TYPE SPECIES: *Eubaena latifrons* Hay, 1908, p. 83.

KNOWN DISTRIBUTION: Maestrichtian (Hell Creek Formation) of Wyoming.

DIAGNOSIS: Same as for subfamily.

DISCUSSION: See specific discussion.

Hayemys latifrons (Hay)

Figures 6, 7, 48

Eubaena latifrons HAY, 1908, pp. 83, 84.

TYPE SPECIMEN: AMNH 6139 (Hay, 1908,

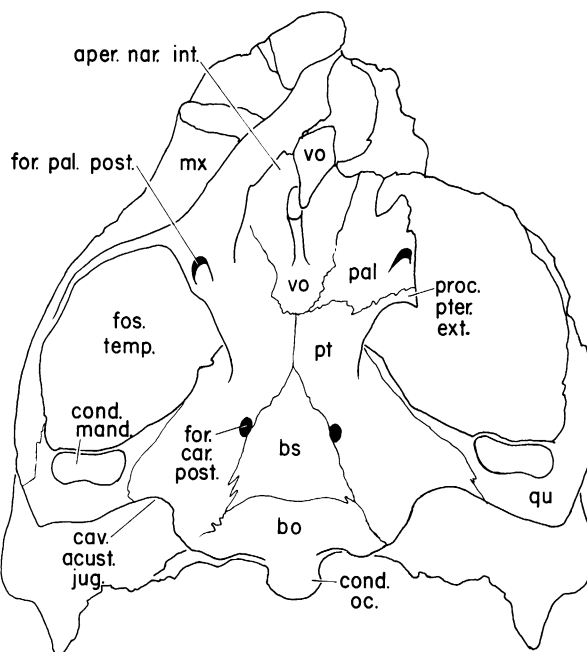
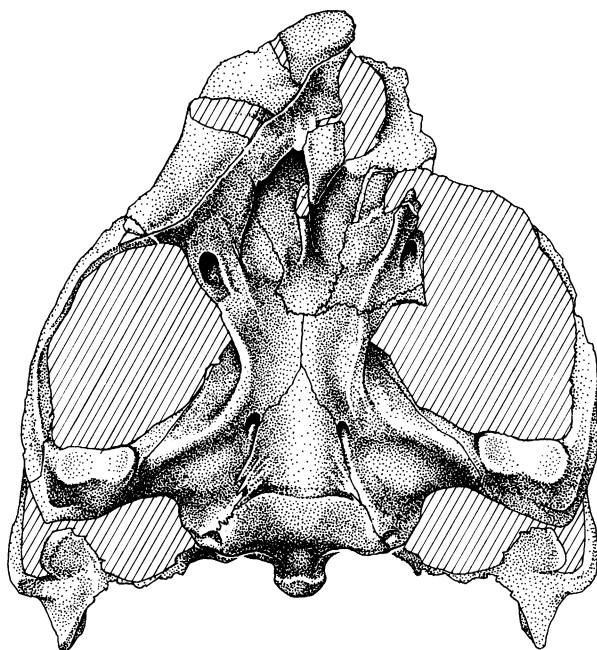


FIG. 7. *Hayemys latifrons* (Hay), new genus. Ventral view of skull of type specimen, AMNH 6139, from the late Cretaceous Hell Creek Formation of Wyoming. Left posterior area restored from right. See also figure 48. Condyle-premaxilla length 73 mm. uncorrected for distortion. Abbreviations on pages 246-247.

TABLE 3
A COMPARISON OF GENERA WITHIN THE EUBAENINAE

Character	<i>Stygiochelys</i>	<i>Eubaena</i>	<i>Plesiobaena</i>
Contacts of nasal	Frontal only	Frontal and maxilla	Probably frontal and maxilla
Frontal enters orbital margin	Yes	No	Yes
Length vs. width of parietals	Wider than long	Longer than wide	Probably subequal
Skull roof overlying CRISTA SUPRAOCCIPITALIS	Wide, not extending beyond FORAMEN MAGNUM	Narrow, extending over FORAMEN MAGNUM	Widest, extending over FORAMEN MAGNUM
Size of orbits	Large	Small	Small in <i>P. antiqua</i> , probably larger in <i>P. putorius</i>
Jugal enters orbital margin	Yes	No	Yes (may be variable)
Incipient secondary palate	No	Yes	No
Anterior portion of vomer	Wide	Narrow	Wide
Medial contact of pterygoids	Virtually absent due to contact of vomer and basisphenoid	Well developed	Well developed
Relative size of basisphenoid	Large	Small	Small
Length vs. width of skull	Width greater than length	Width and length about equal	Width and length about equal
Anterior part of skull developed into narrow snout	No	Yes	No
Triturating surfaces	Smoothly convex, without high tomial ridge	As in <i>Stygiochelys</i>	High tomial ridge followed by posterior medial expansion as in <i>Trinitichelys</i> and <i>Baena</i>

pp. 83, 84, figs. 69, 70), a crushed skull without lower jaws.

LOCALITY: "... Seven Mile Creek, Wyoming about 40 miles northwest of Edgemont, South Dakota" (*ibid.*).

HORIZON: "... Laramie deposits. . ." (*ibid.*). The specimen label reads "*Triceratops* zone." The locality is most probably in the outcrop area of what is called Hell Creek Formation on the Wyoming Geologic Map (Love, Weitz, and Hose, 1955).

COLLECTOR: Barnum Brown, 1900.

DISCUSSION: This genus is based on the type and only known specimen of *Eubaena latifrons* (Hay, 1908, p. 83). At the time of his description the sutures in the skull roof had not been determined. More recently, Richard D. Estes of

Boston University was able to make out the sutures and afterward generously turned the skull over to me for description. The development of a medially expanded prefrontal lappet, the comparatively great areal extent of the frontals, and the reduced parietals distinguish this form from the other known baenid genera. Knowledge of the triturating surfaces is incomplete because of crushing and bone loss, and precludes comparison of this taxonomically important area. No lower jaw has been associated with this form for the same reason. *Hayemys* is not clearly related to any of the other baenids and at present occupies a somewhat isolated position. No fragments or disarticulated elements have been recognized.

SUBFAMILY EUBAENINAE (WILLIAMS, 1950)

TYPE: *Eubaena* Hay, 1908.

KNOWN DISTRIBUTION: Campanian to Tiffanian, western North America.

DIAGNOSIS: Baenids with wedge-shaped skull, width equal or greater than length; temporal emargination deep; nasals not expanded laterally; prefrontals with small dorsal lappet; no squamosal-parietal contact; parietal larger than frontal; quadratojugal C-shaped with dorsal process but without anterior extension; triturating surfaces variable; orbits open laterally; (postcranium known only in *Plesiobaena*) cervical vertebrae with formed central articulations; shell oval in shape; shell surface smooth; cervical (nuchal) scute small, rectangular; anterior of carapace without emargination; first vertebral scute rectangular without supracostal scutes; supramarginal scutes absent; last vertebral scute opening posteriorly on edge of carapace, last marginal scutes triangular; posterior emargination indeterminate; scalloping absent; xiphiplastral notch absent; paired intergulars present or absent, when present meeting in midline, as do gulars.

***PLESIобаENA*,¹ NEW GENUS**

Baena LEIDY, 1870 (in part).

TYPE SPECIES: *Baena antiqua* Lambe, 1902, p. 44.

KNOWN DISTRIBUTION: Campanian of Alberta, Maestrichtian of Wyoming and Montana, Tiffanian of Wyoming.

DIAGNOSIS: Eubaenine with *Tritichelys*-like triturating surface, a high tomial ridge followed by a posterior expansion; no development of incipient secondary palate; preorbital skull length short compared with that of *Eubaena*; cheek emargination reaching beyond lower level of orbit; no lateral constriction of maxillae; skull roof portion overhanging CRISTA SUPRA-OCCIPITALIS more expanded than in other eubaenines; jugal exposed in orbital margin.

DISCUSSION: See specific discussion.

Plesiobaena antiqua (Lambe)

Figures 8–13, 49

Baena antiqua Lambe, 1902, p. 44.

TYPE SPECIMEN: NMC 1648 (Lambe, 1902,

¹ Greek *plesios*, near, close, and American Indian dialect *baena*, turtle; in allusion to the relationship between *Plesiobaena* and *Baena*.

fig. 10), the anterior lobe of the plastron and the anterior central area of the carapace.

LOCALITY: "... below the mouth of Berry Creek, Red Deer River ..." (*ibid.* p. 10). Alberta, Canada.

HORIZON: "Belly River series ..." (*ibid.*). Oldman Formation, Campanian (see Williams and Burke, 1964, for references), late Cretaceous.

COLLECTOR: L. M. Lambe, 1901.

DIAGNOSIS: A species of the genus *Plesiobaena*; skull narrower compared with that of *P. putorius* having less expanded triturating surfaces; lower jaws with symphyseal "hook"; low coronoid process; skull roof over CRISTA SUPRA-OCCIPITALIS ending in tapered projection, not expanded as in *Plesiobaena putorius*.

HYPODIGM: USNM 8801 (Gillmore, 1919a, pp. 116–119, figs. 1, 2, pls. 31, 32) an almost complete shell. Locality: "... 3 miles below Steveston on the Red Deer River, ... Alberta, Canada ..." (*ibid.*). Horizon: "... the Belly River Formation, Upper Cretaceous" (*ibid.*). Oldman Formation, Campanian, late Cretaceous. Collector: Bruce McKee, 1917.

NMC 8599 (Russell, 1934, pp. 105–107, pl. 4, fig. 1, pl. 5), a damaged shell, cervical and caudal vertebrae, limbs, mandible, and portions of both quadrates. Locality: "... south branch of Little Sandhill Creek, about 3 miles above the juncture with Red Deer River. The locality probably is in the northwest 1/4 of section 25, township 20, range 12, west of 4th meridian" (*ibid.*). See Geological Survey of Canada, 1950, for annotated map. Horizon: "... the Belly River beds ..." (*ibid.*). Oldman Formation, Campanian, late Cretaceous. Collector: C. M. Sternberg.

UMMP 20490 (Case, 1939, pp. 1–19, figs. 1–18), an almost complete skeleton. Locality: "... near Fort Peck, Montana ..." (*ibid.*). Horizon: "... Lance beds ..." (*ibid.*). Hell Creek Formation, Maestrichtian, late Cretaceous. Collectors: Ralph Nichols, UMMP party, 1938.

UCMP 49759 (referred by Estes, 1964, p. 97, to *Eubaena cephalica*), an almost complete skull with right ramus of lower jaw. Locality: UCMP V-5620, Lull 2 quarry. See Clemens, 1963, p. 23 with map; and Estes, 1964, for geology and ecology. Horizon: Lance Formation, Maestrichtian, late Cretaceous. Collector: UCMP party, 1956–1960.

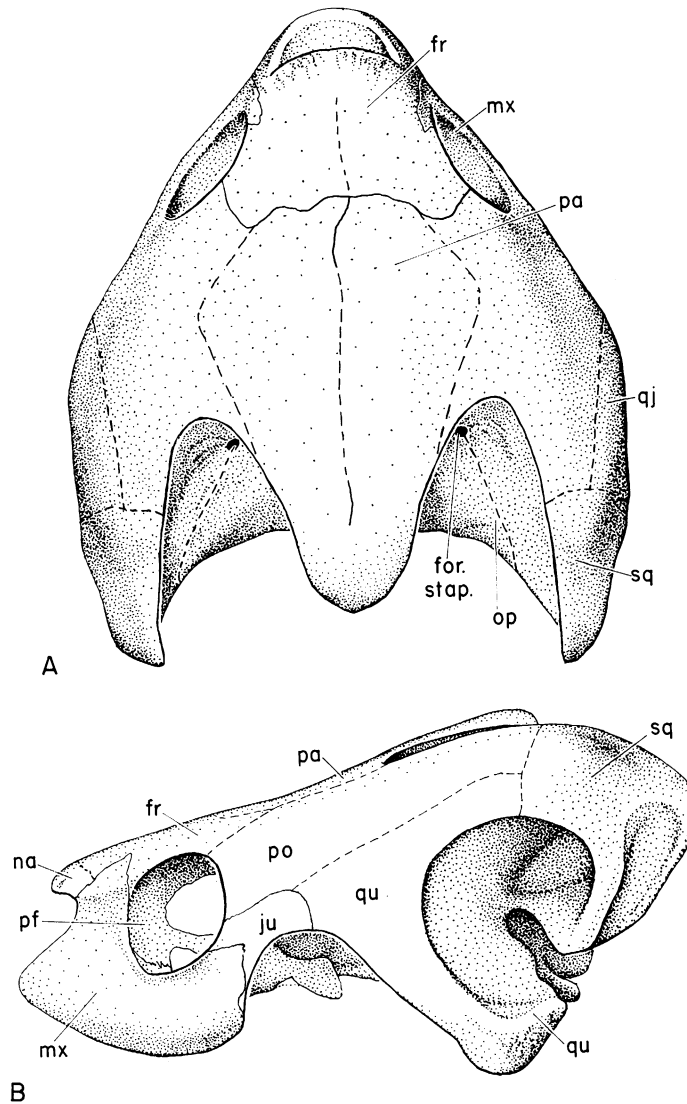


FIG. 8. *Plesiobaena antiqua* (Lambe), new genus. Restored skull based primarily on UCMP 49759 (condyle-premaxilla length 63 mm.) from the late Cretaceous Lance Formation of Wyoming. Dashed sutures from ROM 674 (fig. 10). A. Dorsal view. B. Lateral view. Abbreviations on pages 246-247.

DISCUSSION: This genus was originally recognized by Richard D. Estes after the publication of his Lance Formation lower vertebrate faunal paper (1964) in which he had referred a skull to *Eubaena cephalica*. A comparison of the skull with the type of *Eubaena cephalica* clearly shows that they are not the same genus. Estes graciously turned the specimen over to me for description. One of the most apparent differ-

ces between these genera is in the shape of the triturating surfaces. *Eubaena* (and *Stygiuchelys*) possess a very wide, broadly concave maxillary surface, whereas *Plesiobaena* has the primitive tomial ridge found in *Trinitichelys*.

Case (1939) described an almost complete skeleton (figs. 13, 49) of this genus and tentatively referred it to *Eubaena cephalica*. The statements in Williams (1950), Romer (1956),

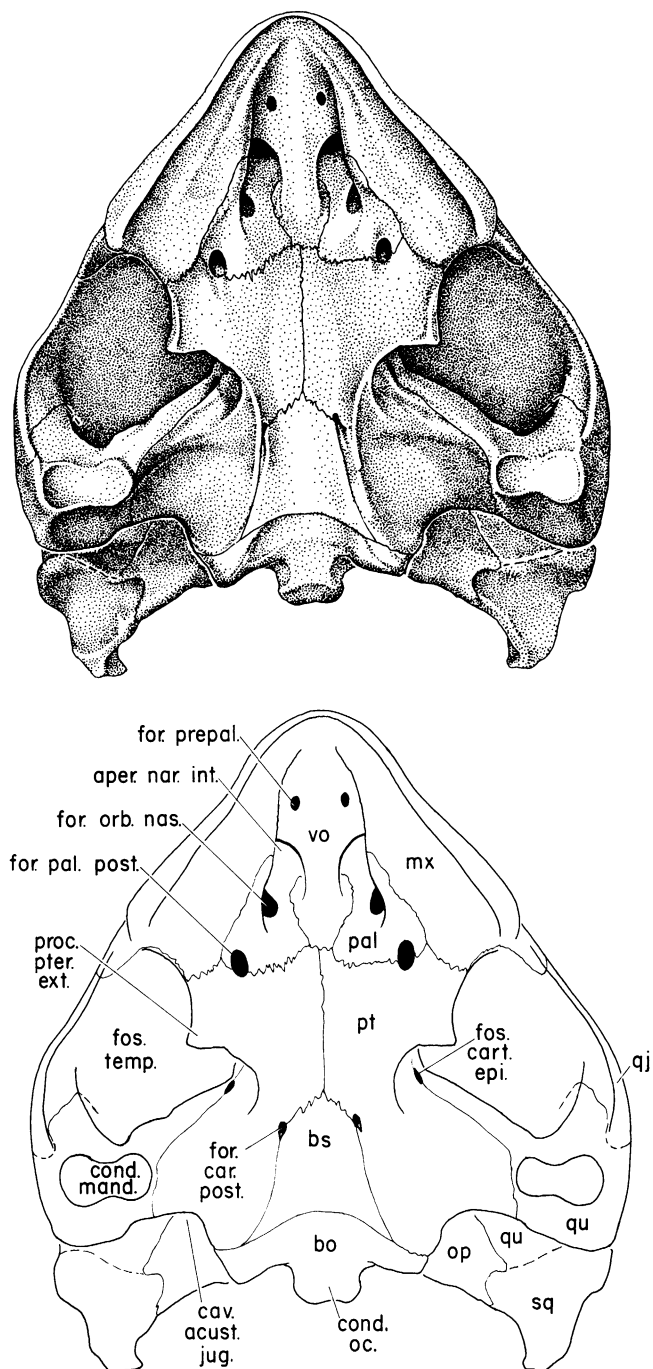


FIG. 9. *Plesiobaena antiqua* (Lambe), new genus. Restored ventral view of skull based primarily on UCMP 49759 from the late Cretaceous Lance Formation of Wyoming but with additions from ROM 674 and UMMP V20490. See also figure 49. Abbreviations on pages 246-247.



FIG. 10. *Plesiobaena antiqua* (Lambe), new genus. Dorsal view of skull, ROM 674, from the late Cretaceous Oldman Formation of Alberta, one of the few skulls known to be associated with a shell (fig. 12).

and Tatarinov (1959) about the postcranial features of *Eubaena* are all based on this specimen (UMMP 20490). The skull of the Case specimen and that of UCMP 49759 from Lance Creek are almost identical. The Case skull is not so well preserved as the Lance Creek skull, but some of the sutures are visible in the former, whereas almost none is visible in the Lance skull.

Another associated specimen (figs. 10, 11, 12) was found by the author in the collections of the Royal Ontario Museum (ROM 674). This specimen, apparently a young individual, has a somewhat broken skull with a number of open sutures. It agrees with the other two specimens in all the observable characters. The identity of the Lance-Hell Creek specimens with the Oldman type of "*Baena*" *antiqua* Lambe is established by this specimen.

A comparison of the shells (figs. 11, 12, 13) found associated with the skulls of *Plesiobaena antiqua* (UMMP 20490 and ROM 674) follows:

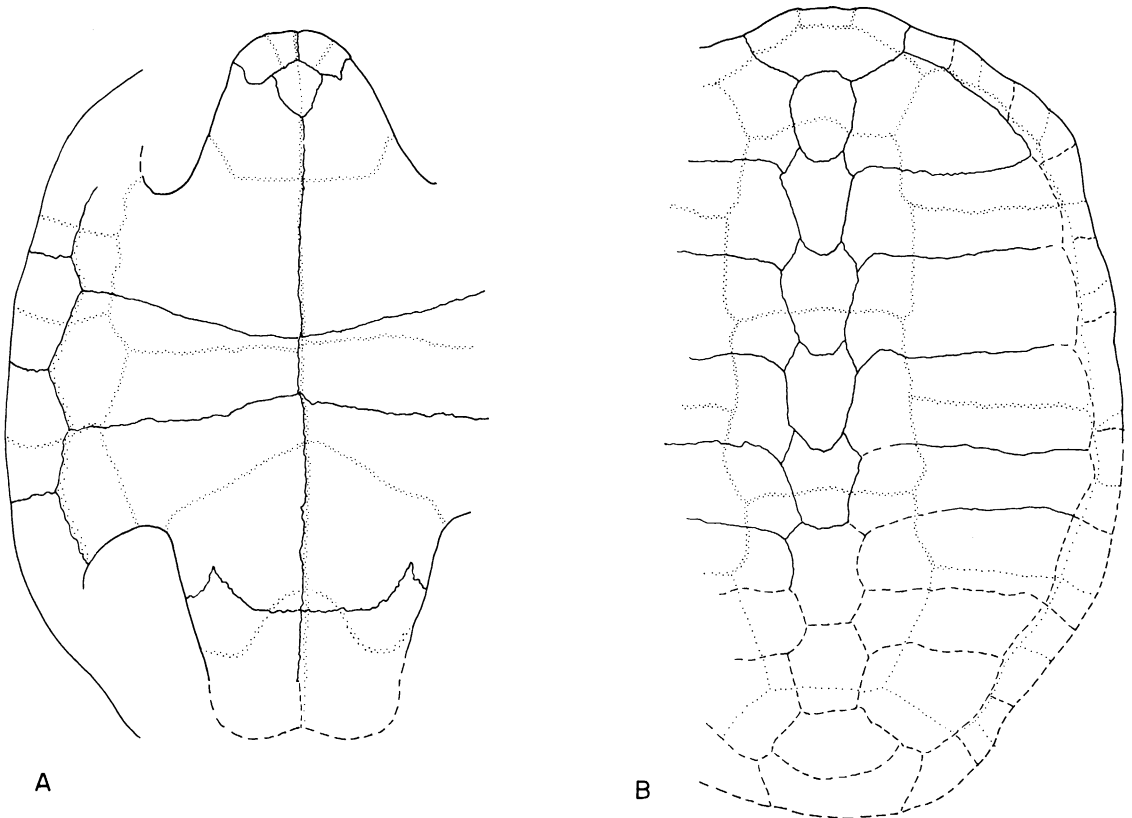


FIG. 11. *Plesiobaena antiqua* (Lambe), new genus. Composite shell based on ROM 674 and USNM 8801 (dashed lines, as figured in Gilmore, 1919a), both from the late Cretaceous Oldman Formation of Alberta.

The posterior parts of both carapaces are missing and nothing is known of the relations of the last marginals and the last vertebral. Both specimens are essentially the same as the type specimen of "*Baena*" *antiqua* Lambe, 1902, in the scute morphology of the anterior portion of the carapace. All three have a large first vertebral, lack "supernumerary" costal (pleural) scutes, and have small, rectangular cervical (nuchal) scutes. The only distinction among the carapaces of these individuals is that the second, third, and fourth vertebrals in ROM 674 are about as long as they are wide whereas, in the type of "*B.*" *antiqua* (NMC 1648) and UMMP 20490 they are wider than long (but just barely in NMC 1648). However, this may be due to the fact that ROM 674 is a smaller individual and the proportions of these scutes may vary with age (the length from anterior edge of the carapace to the posterior edge of the fifth neural in NMC 1648 is 18.5 cm., whereas the same distance in ROM 674 is 14.7 cm.).

The plastra of ROM 674 and UMMP 20490 are essentially identical. The gular scutes meet broadly in both forms and the anterior plastral lobes are narrow. In both of these characters they differ slightly from the type "*B.*" *antiqua*

(NMC 1648), as in that specimen the gulars meet for only a fraction of their length (much as in the type of "*B.*" *marshi* Hay, 1904, which has a different anterior vertebral scute pattern on the carapace) and the anterior plastral lobe seems to be fairly broad (this is not certain because only the anterior half is preserved).

Plesiobaena antiqua is the only late Cretaceous baenid with an associated skull and shell. It should be kept in mind that the two specimens on which this association is based are probably young individuals and adult shell morphology may differ somewhat.

***Plesiobaena putorius*,¹ new species**

Figures 14–17, 50

TYPE SPECIMEN: PU 14984, an almost complete skull, somewhat damaged.

LOCALITY: Cedar Point Quarry, SW 1/4, sect. 23, T. 55 N., R. 96 W., Bighorn Basin, Wyoming (label).

HORIZON: Fort Union Formation, early Tiffanian, Paleocene.

COLLECTOR: Princeton party, July 5, 1949.

DIAGNOSIS: A species of the genus *Plesiobaena*;

¹ *Putorius*, the European polecat, for Polecat Bench, the type locality.

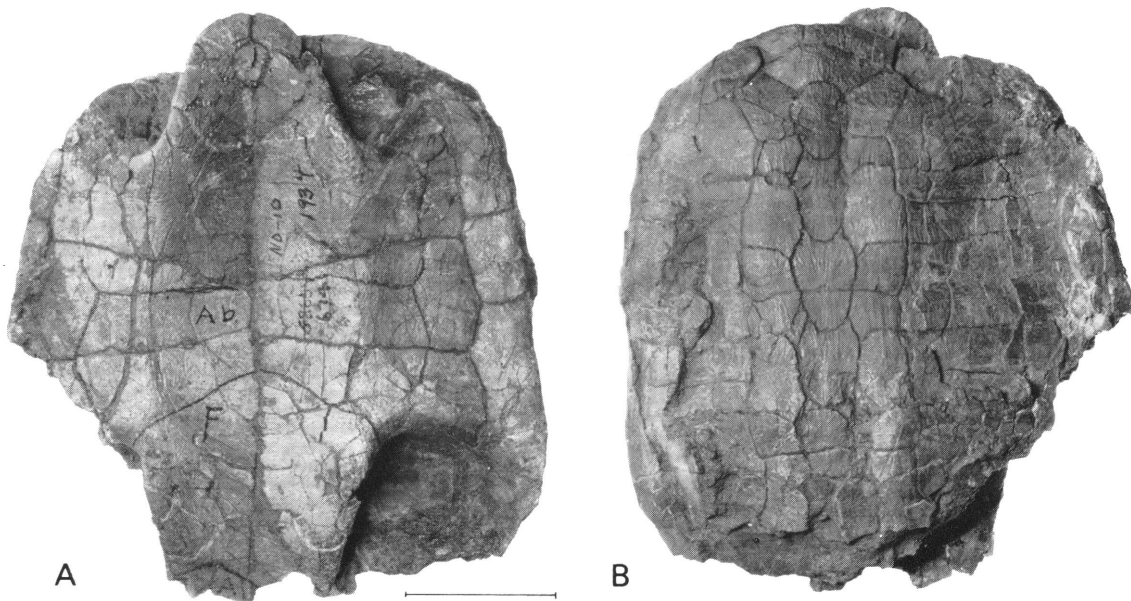


FIG. 12. *Plesiobaena antiqua* (Lambe), new genus. Shell of ROM 674 (see fig. 10 for skull associated with this specimen) from the late Cretaceous Oldman Formation of Alberta. Scale equals 5 cm. A. Ventral view. B. Dorsal view.

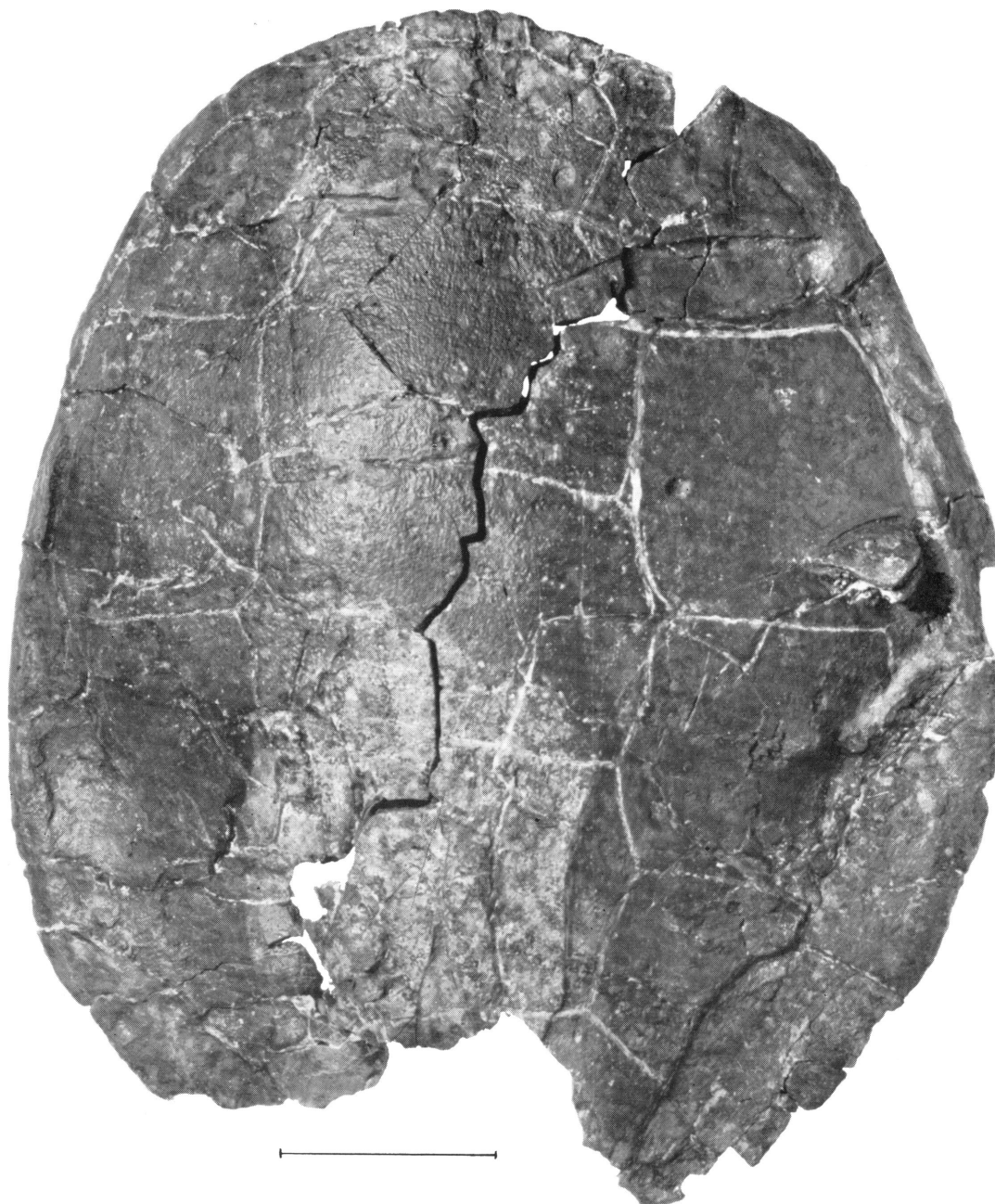


FIG. 13. *Plesiobaena antiqua* (Lambe), new genus. Carapace of UMMP V20490, shell and skull from the late Cretaceous Hell Creek Formation of Montana. Scale equals 5 cm.

skull wider than *P. antiqua*, with more expanded triturating surfaces; lower jaws without symphyseal "hook"; high coronoid process; skull roof over CRISTA SUPRAOCCIPITALIS ending in

characteristic semicircular projection.

HYPODIGM: PU 17108, complete lower jaws; 20741, posterior part of parietals. Locality: Quarry, sect. 36, T. 57 N., R. 99 W., Park

County, Wyoming (label). Horizon: Fort Union Formation, Rock Bench Quarry beds (label), Torrejonian, Paleocene (Van Valen and Sloan, 1966, p. 265). Collector: Princeton party.

PU 18011, posterior part of skull roof. Data: same as for PU 17108. Collector: Princeton party, 1947.

PU 14986a and b, parts of skull roof. Locality: Cedar Point Quarry, SW 1/4, sect. 23, T. 55 N., R. 96 W., Bighorn Basin, Wyoming (label). Horizon: Polecat Bench Formation, early Tiffanian, Paleocene (label). Collector: Princeton party, June 13, 1950.

AMNH 4950, anterior portion of skull roof; 4949, posterior portion of skull roof. Locality: Swain Quarry, SE 1/4, NE 1/4, sect. 3, T. 15 N., R. 92 W., Dad, Wyoming (label). Horizon: lower part of the Fort Union Formation, stratigraphically 487 feet above the contact with the Lance Formation, Torrejonian in age, Paleocene (Szalay, 1965, p. 1). Collector: AMNH party.

PU 16837, right side of skull. Locality: Elk Basin, SE 1/4, SW 1/4, sect. 7, T. 58 N., R. 99 W., Park County, Wyoming (label). Horizon: Paleocene, above Rock Bench level, sandstone forming ridge above Mantua sandstone (label). Collector: E. Lundelius, 1951.

PU 20600, skull. Locality: Cedar Point Quarries, SW 1/4, sect. 23, T. 55 N., R. 96 W., Bighorn County, Wyoming (label). Horizon: Fort Union Formation ("Polecat Bench" Formation), late Paleocene. Collectors: Taylor, PU party.

DISCUSSION: The skull on which this species is based is not well preserved and many features are obscured by powdery bone and preservatives. The sutures are fused in most areas and not determinable. Some sutures of the skull roof are visible on the underside of the bone. The skull is in two pieces, the upper half, consisting mostly of the skull roof; and the lower half, with palate and basicranium. A lower jaw, PU 17108, not found associated with this skull, is referred to this species because it fits very closely into the upper triturating surfaces. The type locality of *Plesiobaena putorius* also yielded the type of *Palatobaena bairdi* as well as baenid shell material.

A second good skull, PU 20600, from Cedar Point Quarries, has well-preserved triturating surfaces and skull roof but the basicranium is not preserved.

EUBAENA HAY, 1908

Baena LEIDY, 1870 (in part).

TYPE SPECIES: *Baena cephalica* Hay, 1904, p. 263.

KNOWN DISTRIBUTION: Late Cretaceous, Maestrichtian of Montana and Wyoming.

DIAGNOSIS: Eubaenine with expanded triturating surface, smoothly convex, no high tomial ridge, development of incipient secondary palate by medial extension of triturating surfaces; preorbital skull length long compared with that of *Plesiobaena*; cheek emargination not reaching lower level of orbit; lateral constriction of maxillae forming distinct "snout"; skull roof overlying CRISTA SUPRAOCCIPITALIS ending in blunt point; jugal prevented from exposure in orbital margin by meeting of maxilla and postorbital; fronto-parietal suture curved.

Eubaena cephalica (Hay)

Figures 18, 19, 57

Baena cephalica HAY, 1904, p. 263.

Eubaena cephalica Hay, 1908, p. 82.

TYPE SPECIMEN: YPM 1785 (accession number 2110) (Hay, 1904, pp. 263–265, pl. 12; Hay, 1908, pp. 82, 83, pl. 19 fig. 4, pl. 21 figs. 1, 2), an almost complete skull.

LOCALITY: "... Converse County, Wyoming ..." (*ibid.*). Probably now in Niobrara County.

HORIZON: "... Laramie deposits ..." (*ibid.*). Probably from the Lance Formation, Maestrichtian, late Cretaceous.

COLLECTOR: J. B. Hatcher for O. C. Marsh.

DIAGNOSIS: Same as for genus.

HYPODIGM: AMNH 2604, 2605, 2606, dentaries. Locality: 28 miles south of Lismas, Montana (label). An unsuccessful attempt to find this locality was made in 1970 by the author. Horizon: Hell Creek Formation, middle sandstone, Upper Cretaceous (label), Maestrichtian. Collector: Barnum Brown, 1908.

MCZ 3530, both parietals. Locality: Bug Creek Anthills, SW 1/4, sect. 9, T. 22 N., R. 43 E., McCone County, Montana (label). Horizon: Hell Creek Formation, Bug Creek Anthills level (see Sloan and Van Valen, 1965, fig. 1), Maestrichtian, late Cretaceous. Collectors: R. Sloan and party.

AMNH 4948, an almost complete skull, partially disarticulated. Data: same as for MCZ 3530.

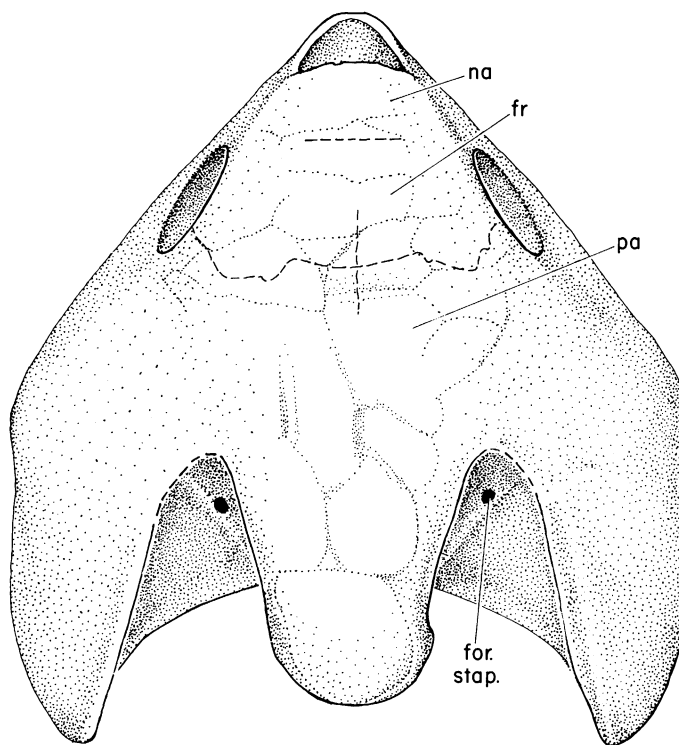


FIG. 14. *Plesiobaena putorius*, new genus and new species. Restoration of dorsal view of skull of type specimen, PU 14984, from the Paleocene Fort Union Formation of Wyoming. Dotted lines are sutures visible on ventral surface of skull roof. See also figure 17. Approximate condyle-premaxilla length 65 mm.

MCZ 3510, 3511, 3512, 3519, all maxillae. Data: same as for MCZ 3530.

MCZ 3525, right parietal. Data: same as for MCZ 3530.

DISCUSSION: Hay (1904) at first referred the type skull to *Baena* but erected a new genus in 1908 when he had better material of the Tertiary baenids, *Baena* and *Chisternon*. The triturating surfaces, snout shape, and skull roof morphology are the main regions that distinguish this genus from the other baenids.

As far as can be determined, *Eubaena* is restricted to the Maestrichtian of Wyoming but the subfamily extended into the Paleocene (*Plesiobaena putorius*).

The two known skulls are almost perfect and furnish very good information about the genus. The type specimen, YPM 1785, lacks only a small area around the right temporal margin. The AMNH Bug Creek specimen is lacking

more of the skull roof but it has been disarticulated and yields a great deal of information about the basicranium and braincase. Some of the right side of the basicranium is damaged but the left is mostly intact.

There are no shell "genera" that are restricted to the Maestrichtian of Wyoming, and *Eubaena* could belong to any of the late Cretaceous shells without skulls. It is likely, though, that it will prove to be associated with one of the species of the Cretaceous "*Baena*" as these are the commonest baenid shells in the Lance and Hell Creek formations.

*STYGIOCHELYS*¹ GAFFNEY AND HIATT, 1971

TYPE SPECIES: *Stygiuchelys estesi* Gaffney and Hiatt, 1971, pp. 1-9.

¹ For the River Styx, *Fluvius Stygius*, and *chelys*, Greek, turtle; in allusion to the type horizon, the Hell Creek Formation.

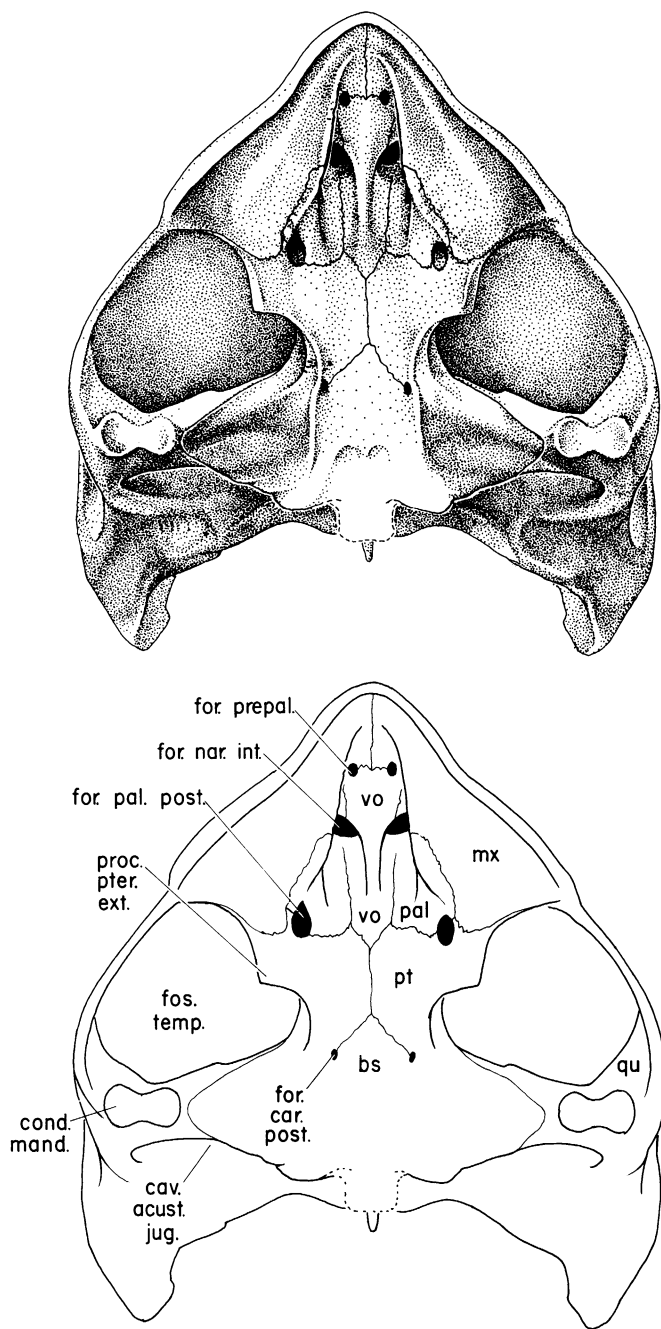


FIG. 15. *Plesiobaena putorius*, new genus and new species. Restored ventral view of skull based primarily on PU 20600 with additions from PU 14984, both from the Paleocene of Wyoming. See also figure 50. Abbreviations on pages 246–247.

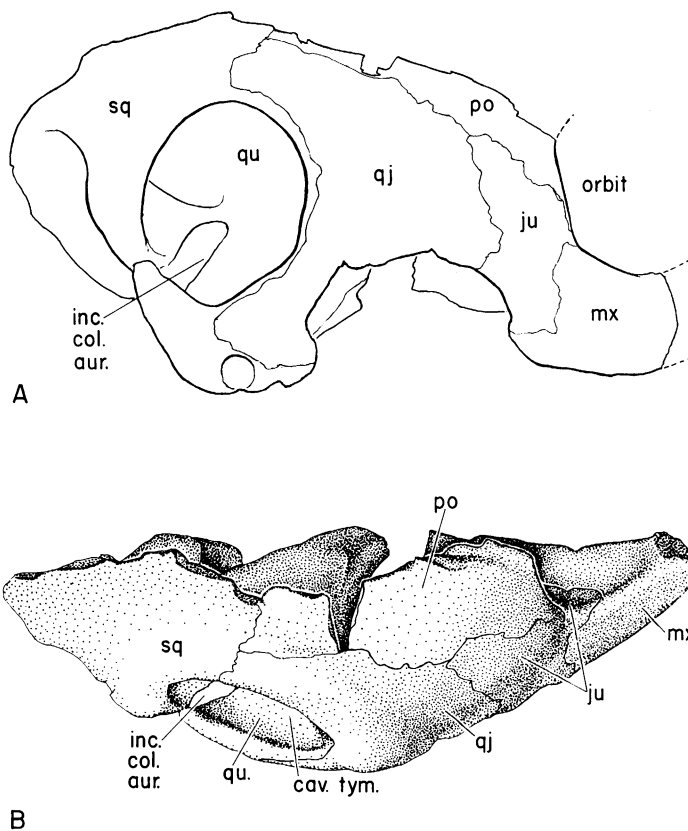


FIG. 16. *Plesiobaena putorius*, new genus and new species. PU 16837, right lateral portion of skull from the Paleocene Fort Union Formation of Wyoming. A. Lateral view. B. Dorsal view. Maximum length 58 mm. Abbreviations on pages 246–247.



KNOWN DISTRIBUTION: Maestrichtian of Montana.

DIAGNOSIS: Eubaenine with *Eubaena*-like triturating surface, smoothly convex, no high tomial ridge, but without development of incipient secondary palate as in *Eubaena*; preorbital skull length intermediate between *Eubaena* and *Plesiobaena*; cheek emargination not reaching lower level of orbit; lateral constriction of maxillae present; skull roof overlying CRISTA SUPRAOCCIPITALIS ending in point; jugal entering orbital margin; fronto-parietal suture tending to be curved.

FIG. 17. *Plesiobaena putorius*, new genus and new species. Dorsal view of skull, PU 20600, from the Paleocene Fort Union Formation of Wyoming. See figure 50 for ventral view. Scale equals 1 cm.

*Stygiochelys estes*¹ Gaffney and Hiatt, 1971

Figures 20, 21, 58

TYPE SPECIMEN: AMNH 2601, a partially damaged skull without lower jaws (*ibid.*, figs. 1, 2, 4, 6).

LOCALITY: SW 1/4, NW 1/4, sect. 1, T. 15 N., R. 55 E., near Glendive, Montana (data from Robert Hiatt).

HORIZON: Hell Creek Formation.

COLLECTOR: Robert Hiatt of Glendive, Montana.

DIAGNOSIS: Same as for genus.

DISCUSSION: *Stygiochelys* is probably closely related to *Eubaena* judging by the similar triturating surfaces. The over-all shape of the skull (width equal to length instead of being less than length as in *Eubaena*), large size of orbits, jugal entering orbital margin, and the skull roof ending over the CRISTA SUPRAOCCIPITALIS in a short, blunt point serve to distinguish *Stygiochelys* from *Eubaena*.

EUBAENINAE, GENUS INDETERMINATE

PU 16838, posterior half of skull, including ear, basicranium, and braincase.

LOCALITY: Southwest of Sage Point, NE 1/4, SE 1/4, sect. 2, T. 56 N., R. 99 W., Park Co., Wyo. (label).

HORIZON: Paleocene, approximately Rock Bench Quarry level (label), Torrejonian.

COLLECTOR: William Morris, July 1, 1951.

Unfortunately this specimen lacks the greater part of the skull roof and all the triturating surfaces, hence cannot be adequately identified. The CRISTA SUPRAOCCIPITALIS is higher than in other described Paleocene genera and indicates that the form may be new. The parietals are deeply emarginated and lack the posterior medial expansion that characterizes *Plesiobaena putorius*, but the deep emargination and pointed skull roof overlying the CRISTA SUPRAOCCIPITALIS are characteristic of *Eubaena*. However, in the absence of further information about the triturating surfaces and palate it would be premature to extend the range of *Eubaena* into the Paleocene.

The specimen is one of the best-preserved baenid braincases and furnishes significant information about the morphology of this region. The basicranium is free of the rest of the

skull and the sutures are open and easily determined.

SUBFAMILY PALATOBAENINAE, NEW

TYPE: *Palatobaena*, new genus.

KNOWN DISTRIBUTION: Maestrichtian of Montana, early Tiffanian or late Torrejonian of Montana, early Tiffanian of Wyoming.

DIAGNOSIS: Baenids with wide, almost circular skull, broadly curved in dorsal view; temporal emargination relatively shallow; nasals not expanded laterally but extended anteriorly into short shelf; prefrontal with limited dorsal exposure; parietal larger than frontal; quadratojugal morphology indeterminate; triturating surfaces widely expanded to form triangular crushing areas, surfaces flat, with low, blunt lingual ridge and vestigial tomial ridge; orbits open dorsolaterally, ridge separating orbital floor from cheek; postcranium unknown.

PALATOBAENA,² NEW GENUS

TYPE SPECIES: *Palatobaena bairdi*, new species.

KNOWN DISTRIBUTION: Maestrichtian of Montana, Paleocene of Wyoming and Montana.

DIAGNOSIS: Same as for subfamily.

Palatobaena bairdi,³ new species

Figures 22–25, 51

TYPE SPECIMEN: PU 16839, the right half of a skull, partially distorted.

LOCALITY: Cedar Point Quarry, SW 1/4, sect. 23, T. 55 N., R. 95 W., Bighorn Basin, Wyoming (label).

HORIZON: Fort Union Formation, early Tiffanian.

COLLECTOR: Princeton party, 1949.

DIAGNOSIS: Same as for genus.

HYPODIGM: FMNH PR 829, anterior part of skull. Locality: "Montana" (label). Horizon: "Cretaceous" (*ibid.*). Collector: David Dunkle (no further data available, personal commun.).

MCZ 3515, right maxilla. Locality: Bug Creek Anthills, SW 1/4, sect. 9, T. 22 N., R. 43 E., McCone County, Montana. Horizon: Hell Creek Formation, Bug Creek Anthills

² Latin *palatum*, palate, and *baena*, American Indian dialect for turtle.

³ For Dr. Donald Baird, Princeton University, in recognition of his unpublished work on this genus and chelonians in general.

¹ For Dr. Richard Estes of Boston University.

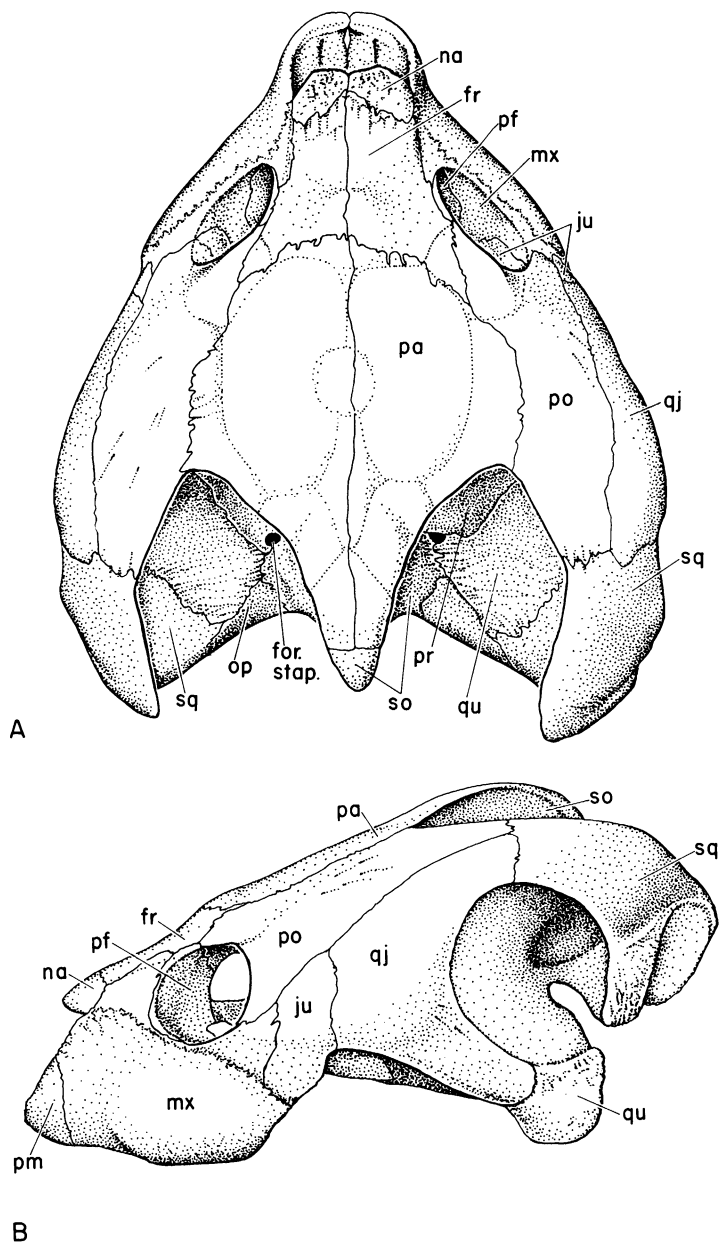


FIG. 18. *Eubaena cephalica* (Hay). Slightly restored skull of type specimen, YPM 1785, from the late Cretaceous Lance Formation of Wyoming. A. Dorsal view. B. Lateral view. Condyle-premaxilla length 66 mm. Abbreviations on pages 246-247.

level (see Sloan and Van Valen, 1965, fig. 1). Collectors: R. Sloan and party.

PU 16947, right maxilla. Locality: Mehling site, Medicine Rocks, T. 3 N., R. 58 E., Carter County, Montana (label). Horizon: Tongue

River Formation, Paleocene. Collector: Princeton party, 1958.

PU 17153, right maxilla. Locality: Quarry, sect. 36, T. 57 N., R. 99 W., Park County, Wyoming. Horizon: Rock Bench Quarry beds,

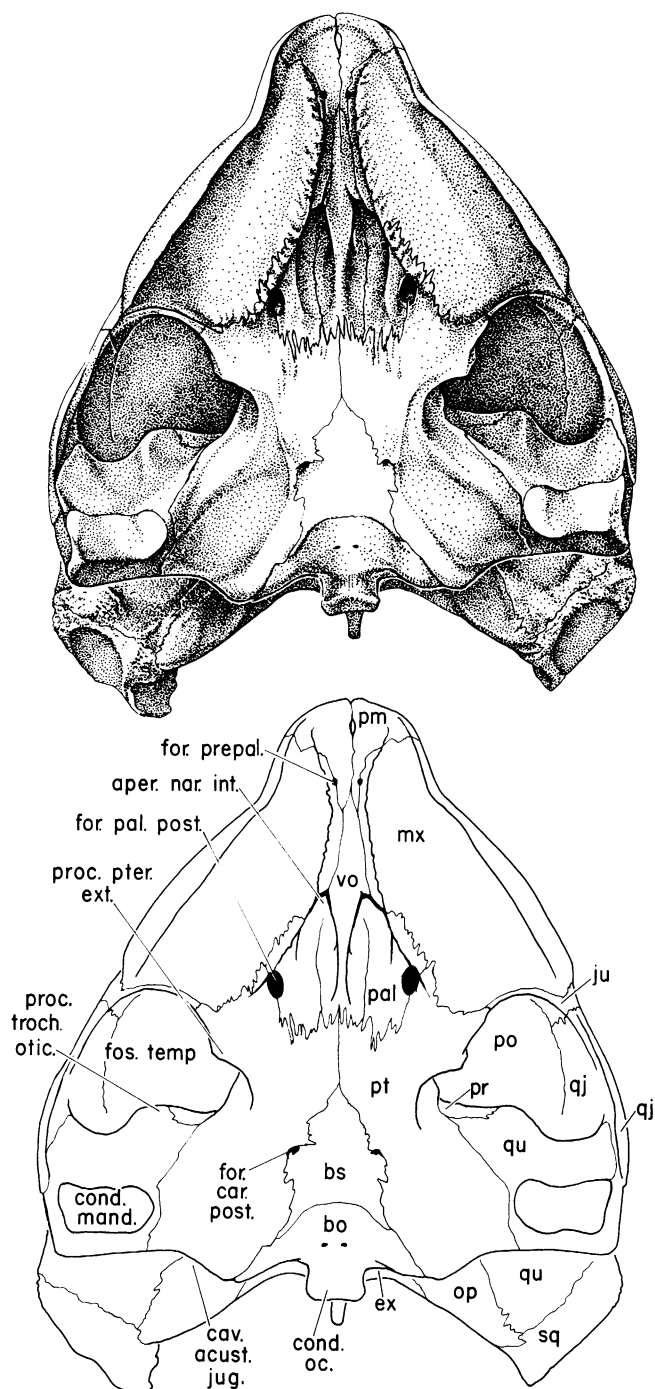


FIG. 19. *Eubaena cephalica* (Hay). Ventral view of type skull, YPM 1785, from the late Cretaceous Lance Formation of Wyoming. See also figure 57. Abbreviations on pages 246–247.

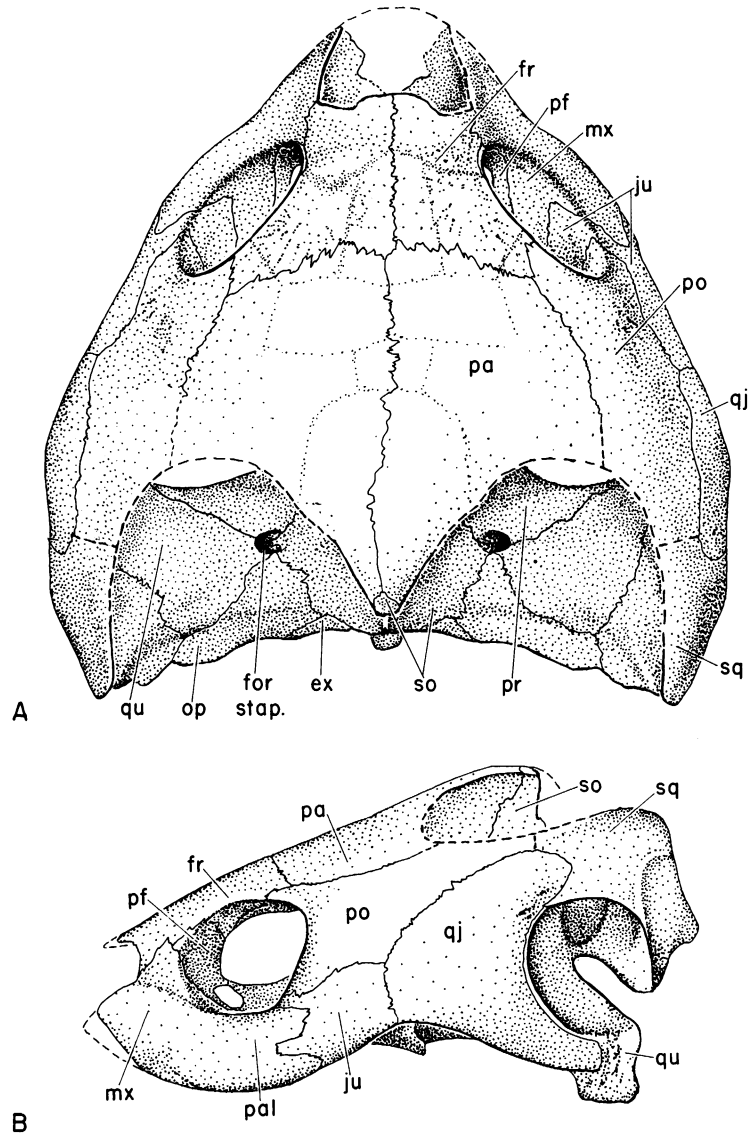


FIG. 20. *Stygiochelys estesi* Gaffney and Hiatt. Restored skull of type specimen, AMNH 2601, from the late Cretaceous Hell Creek Formation of Montana. A. Dorsal view. B. Lateral view. Condyle-premaxilla length about 63 mm. Abbreviations on pages 246–247.

Fort Union (“Polecat Bench”) Formation, Paleocene (label).

DISCUSSION: *Palatobaena* is based primarily on two partial skulls that are somewhat difficult to interpret. The restorations were made by finding the midline and determining the relations of other areas to it. The skull roof of the type specimen (fig. 24), however, has been distorted,

whereas the basicranium which is free of the skull roof, has not. Therefore, some discrepancies are present in the type specimen. In the restoration these inconsistencies have been worked out, but the result is still not entirely satisfactory. The interorbital distance seems to be too great, and the position of the orbits seems unnatural. Still, the restoration is con-

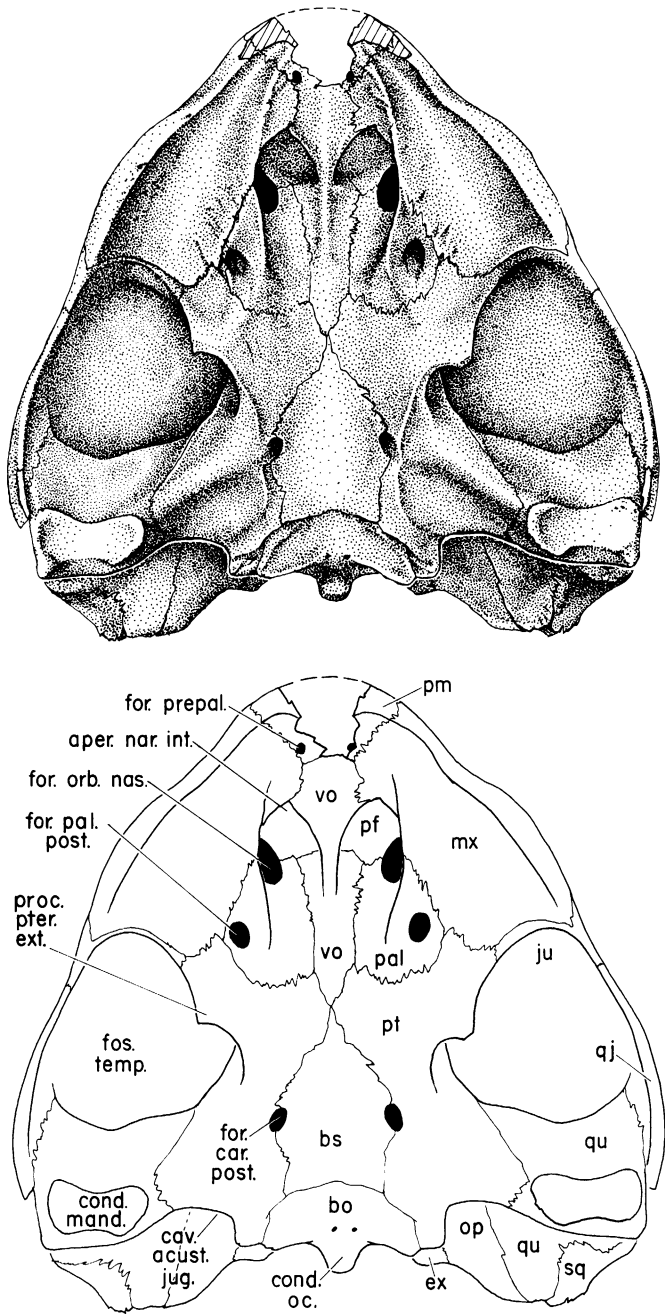


FIG. 21 *Stygiochelys estesi* Gaffney and Hiatt. Restored ventral view of skull based on type specimen, AMNH 2601, from the late Cretaceous Hell Creek Formation of Montana. See also figure 58. Abbreviations on pages 246–247.

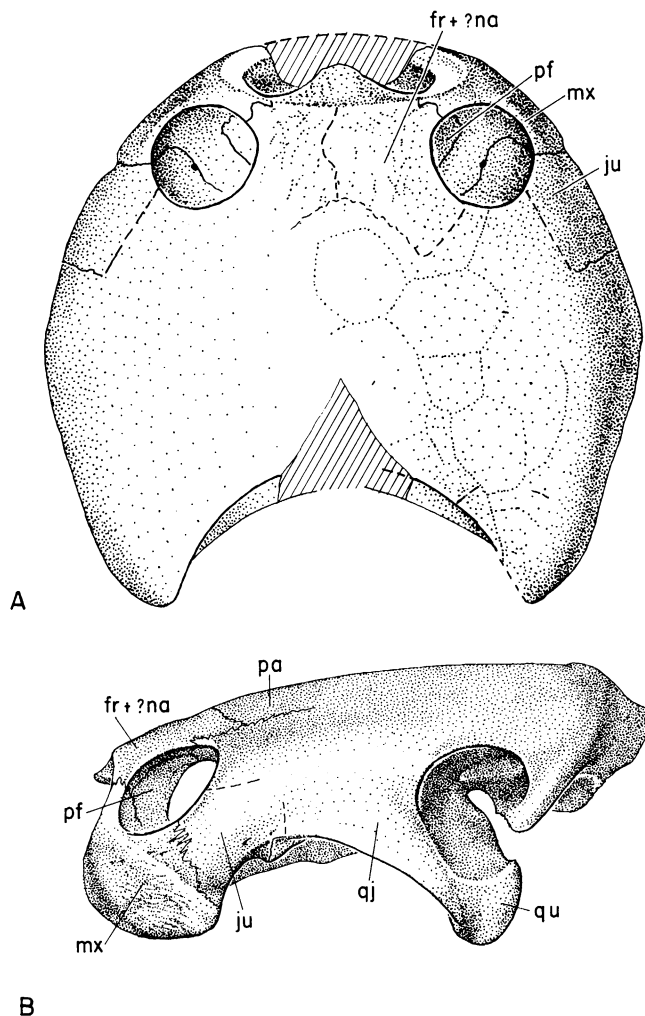


FIG. 22. *Palatobaena bairdi*, new genus and new species. Restored skull of type specimen, PU 16839, from the Paleocene Fort Union Formation of Wyoming. A. Dorsal view. B. Lateral view (some additions from FMNH PR829). Estimated condyle-premaxilla length 54 mm. Abbreviations on pages 246-247.

trolled in these areas and the Cretaceous specimen (fig. 25), which is undistorted, supports the restoration of the type.

This genus extends from the Maestrichtian into the Paleocene. It is quite possible that the lineage changed enough to call the Cretaceous specimens a different species from those of the Paleocene, but the specimens from the Cretaceous present few differences from those of the Paleocene.

SUBFAMILY BAENINAE (COPE, 1882) WILLIAMS
1950

TYPE: *Baena* Leidy, 1870.

KNOWN DISTRIBUTION: Wasatchian through Uintan, Wyoming and Utah.

DIAGNOSIS: Baenids with wedge-shaped skull in dorsal view; temporal emargination reduced; nasal not expanded laterally; prefrontals with little dorsal exposure; squamosal-parietal con-

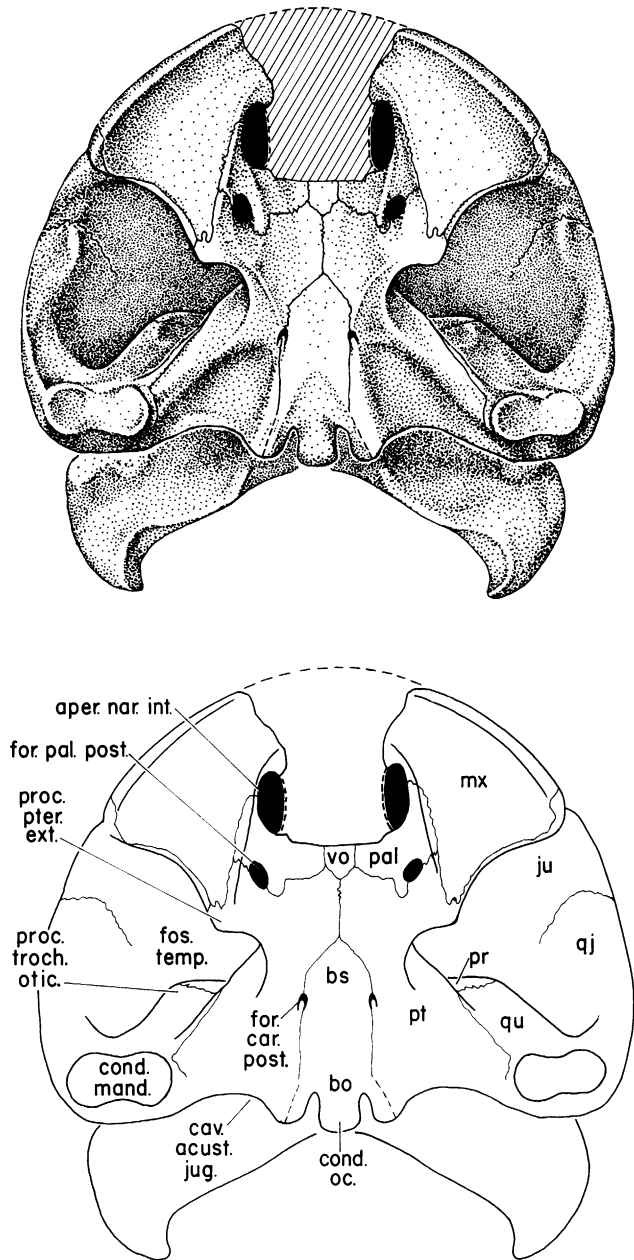


FIG. 23. *Palatobaena bairdi*, new genus and new species. Restored ventral view based on skull of type specimen, PU 16839, from the Paleocene Fort Union Formation of Wyoming. See also figure 51. Abbreviations on pages 246-247.

tact; parietal much larger than frontal; quadratojugal not C-shaped, lacking dorsal process; jugal widely exposed in orbital margin; triturating surfaces essentially as in *Plesiobaena*

with slight variations; orbits opening laterally; cervical vertebrae with formed central articulations; shell oval but usually pointed anteriorly; ornamentation highly varied; cervical



FIG. 24. *Palatobaena bairdi*, new genus and new species. Dorsal view of type specimen, PU 16839, from the Paleocene Fort Union Formation of Wyoming. Basicranium and ear region removed. Scale equals 1 cm.

(nuchal) scute small, sometimes double; anterior of carapace without emargination; first vertebral scute variable; supramarginal scutes absent; xiphiplastral notch absent; paired intergulars usually present; intergulars usually meeting in midline, but sometimes varying considerably; last vertebral scute opening on edge of carapace; posterior edge of carapace usually scalloped, usually emarginated to some extent.

*BAENA*¹ LEIDY, 1870

TYPE SPECIES: *Baena arenosa* Leidy, 1870, p. 123.

KNOWN DISTRIBUTION: Wasatchian to Uintan, Eocene of Wyoming and Utah.

¹ "For the genus I have adopted a name which, according to Prof. Hayden, is used by one of the Indian tribes of the Upper Missouri as that of a turtle" (Leidy, 1870, p. 124). Leidy's original spelling, *Baëna*, indicates the pronunciation.

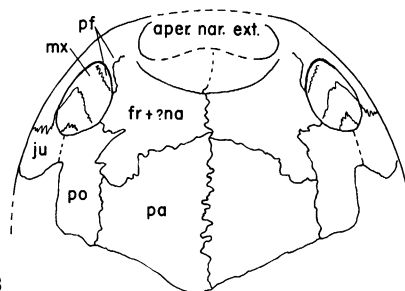
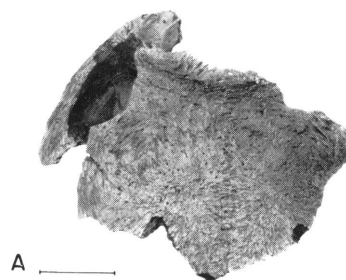


FIG. 25. *Palatobaena bairdi*, new genus and new species. Dorsal view of anterior skull fragment, FMNH PR829, from the late Cretaceous of Montana. A. Actual specimen. Scale equals 1 cm. B. Partial restoration made by transferring features from left to right. Abbreviations on page 246.

DIAGNOSIS: Baenines with slight temporal emargination; diameter of orbit and FORAMEN MAGNUM small relative to *Chisternon*; lateral maxillary constriction in some specimens; nasals fused to frontals, anterior margin of nasals with concavity facing anteriorly; posterior margin of skull roof without transverse ridge; basisphenoid small compared to *Chisternon*; preneural absent; first vertebral may be rectangular with no supracostal scutes or it may be triangular with supracostal scutes.

DISCUSSION: See specific discussion.

Baena arenosa Leidy, 1870

Figures 26–33, 52–54

Baena affinis LEIDY, 1871a, p. 367.

Baena sima HAY, 1908, p. 71.

Baena clara HAY, 1908, p. 74.

Baena riparia HAY, 1908, p. 76.

Baena emilae HAY, 1908, p. 80.

Baena inflata GILMORE, 1915, p. 112.

TYPE SPECIMEN: USNM 103 (Leidy, 1873, pl. 13 figs. 1, 2), a partial shell.

LOCALITY: "... the junction of the Big Sandy and Green Rivers, Wyoming, ... " (Leidy, 1873, p. 161).

HORIZON: "... the lowermost of the Bridger Formation" (Hay, 1908, p. 67).

COLLECTOR: Hayden, 1870.

DIAGNOSIS: Same as for genus.

HYPODIGM: ANSP 10055 (type specimen of *Baena affinis* Leidy, 1871a, p. 367; Leidy, 1873, p. 163, pl. 13 fig. 3), a shell. Locality: Church Buttes on Black's Fork of Green River, 3 miles north of Fort Bridger, Wyoming (Leidy, 1873, p. 163). Horizon: Bridger Formation. Collector: J. Van A. Carter.

AMNH 1111 (Cope, 1884 [1885], pl. 19 figs. 3–5, last two captions should be reversed), plastron and portion of carapace. Locality: Black's Fork, Wyoming (*ibid.*). Horizon: Bridger Formation. Collector: E. D. Cope, 1872.

AMNH 1112 (Cope, 1884 [1885], pl. 17 figs. 1, 2; specimen is figured upside down). Locality: Ham's Fork, N. of Bridger Basin, Wyoming (*ibid.*, p. 148). Horizon: Bridger Formation, *Orohippus* zone (label). Collector: E. D. Cope, 1872.

AMNH 1115 (Hay, 1908, figs. 49–51), shell, portion of pelvis. Locality: Laclede Meadows, SW of Bitter Creek station and W. of Haystack Mountain, SW Wyoming (label). Horizon: Washakie Formation (label). Collector: AMNH Expedition, 1893.

AMNH 1675 (*ibid.*, figs. 57, 58; pl. 16 figs. 1, 2, type of *Baena clara* Hay, 1908), shell. Data: Bridger Formation, Wyoming, "exact level and locality not known" (*ibid.*, p. 74). Collector: AMNH Expedition, 1893.

AMNH 1816, shell. Locality: 45 feet south of Bitter Creek, Wyoming (label). Horizon: Bridger Formation (possibly Wasatch Formation).

AMNH 1851, shell. Locality: White River, Utah (label). Horizon: Uinta Formation, top of B (label). Collector: O. A. Peterson, April, 1895 (label), 1905 (catalogue).

AMNH 1925 (type of *Baena emiliae* Hay, 1908, figs. 67, 68, pl. 20 figs. 1, 2), shell. Locality: White River, Utah (label). Horizon: Level B, Uinta Formation (label). Collector: O. A. Peterson, 1894.

AMNH 3932 (figured as *Chisternon undatum*, in Hay, 1908, fig. 71), shell. Locality: SW Wyoming, Bridger Basin. Horizon: Bridger beds (label). Collector: AMNH Expedition of 1893.

AMNH 5900, shell. Locality: Grizzly Buttes East, Wyoming. Horizon: Bridger B. Collectors: W. Granger, O. P. Hay.

AMNH 5906, shell. Locality: Grizzly Buttes West, Wyoming. Horizon: Bridger B. Collector: O. P. Hay, July, 1903.

AMNH 5921, shell. Locality: Grizzly Buttes East, Wyoming. Horizon: Bridger B. Collectors: O. P. Hay, A. Thompson.

AMNH 5922, shell. Locality: Grizzly Buttes West, Wyoming. Horizon: Bridger B, "middle beds." Collector: A. Thompson, June 26, 1903.

AMNH 5935, shell. Locality: Grizzly Buttes East, Wyoming. Horizon: Bridger B. Collector: O. P. Hay, July 20, 1903.

AMNH 5952, shell, skull, limbs. Locality: Grizzly Buttes West, Wyoming. Horizon: Bridger B. Collector: O. P. Hay, 1903.

AMNH 5957, shell (Hay, 1908, p. 76). Locality: Grizzly Buttes West, Wyoming. Horizon: Bridger B. Collector: A. Thompson, July 11, 1903.

AMNH 5965, shell (*ibid.*, pl. 15). Locality: Grizzly Buttes West, Wyoming. Horizon: Bridger B. Collector: A. Thompson, July 11, 1903.

AMNH 5970, shell. Locality: Leavitt Creek, Fort Bridger, Wyoming. Horizon: Bridger Fm., "lower beds" (label). Collector: A. Thompson, July 12, 1903.

AMNH 5971 (type of *Baena sima* Hay, 1908, figs. 52, 53, pl. 13 figs. 1, 2, pl. 14 fig. 4), skull, shell, postcranium. Locality: Little Dry Creek, South of Fort Bridger (see Wheeler, 1961, pl. 2). Horizon: Bridger B, "from lower brown ss" (label). Collector: Albert Thompson, June 1, 1903.

AMNH 5973 (Hay, 1908, figs. 44–48, pl. 12), skull, shell, postcranium. Locality: Grizzly Buttes West, Wyoming (label). Horizon: Bridger Formation (probably B). Collector: O. P. Hay, 1903.

AMNH 5977 (type of *Baena riparia* Hay, 1908, figs. 59–66, pls. 17, 18, 19 figs. 1–3), an almost complete skeleton. Locality: Grizzly Buttes West, 15 miles southeast of Fort Bridger, Wyoming (*ibid.*, and label). Horizon: Bridger Formation, B level (label). Collector: Albert Thompson, July 11, 1903.

AMNH 5984, shell, lower jaws, limb. Locality: Grizzly Buttes East, Wyoming. Horizon: Bridger B. Collectors: W. Granger, O. P. Hay, July 22, 1903.

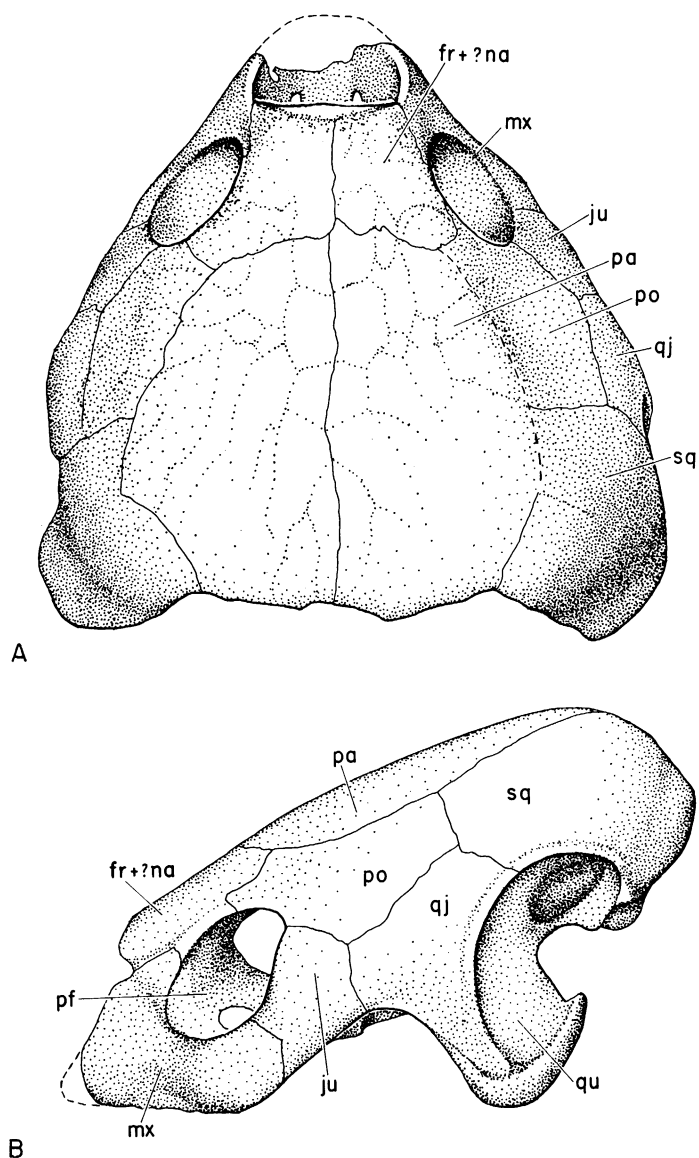


FIG. 26. *Baena arenosa* Leidy. Skull of MCZ 4072 from the Eocene Willwood Formation of Wyoming. A. Dorsal view. B. Lateral view (partially restored from right side). Approximate condyle-premaxilla length 54 mm. Abbreviations on pages 246–247.

AMNH 5985, shell. Locality: Grizzly Buttes West, Wyoming. Horizon: Bridger B. Collector: O. P. Hay, July, 1903.

AMNH 5986, shell. Locality: Grizzly Buttes East, Wyoming. Horizon: Bridger B. Collector: A. Thompson, July 31, 1903.

AMNH 5990, shell. Locality: Grizzly Buttes

East, Wyoming. Horizon: Bridger B. Collector: O. P. Hay, July 20, 1903.

AMNH 6144, shell. Locality: Haystack Mountain, Wyoming. Horizon: "35 (or 3?) feet below pink layer," Washakie Formation. Collector: AMNH Expedition, September 13, 1906.

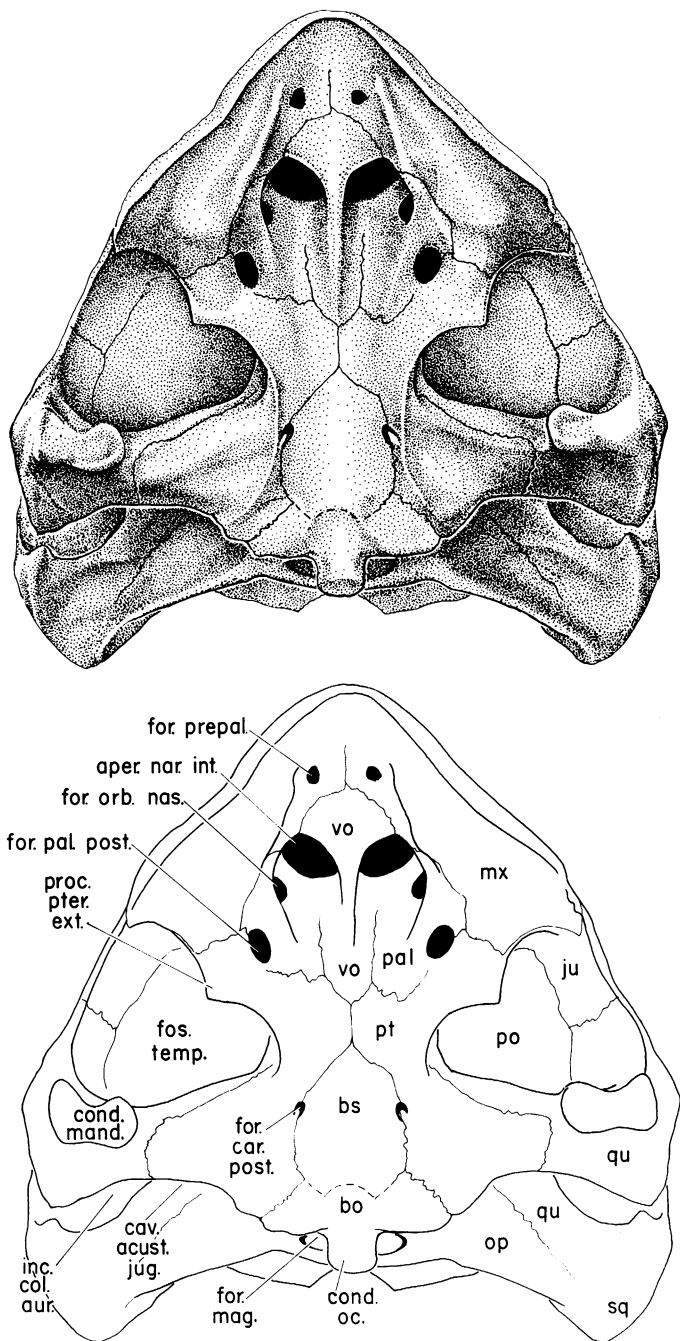


FIG. 27. *Baena arenosa* Leidy. Partially restored ventral view of skull of MCZ 4072 from the Eocene Willwood Formation of Wyoming. See also figures 52-54. Abbreviations on pages 246-247.

TABLE 4
A COMPARISON OF THE GENERA WITHIN THE BAENINAE

Character	<i>Baena</i>	<i>Chisternon</i>
Temporal emargination relative to <i>Eubaena</i>	Greatly reduced	Somewhat reduced
Diameter of orbit and FORAMEN MAGNUM	Small	Large
Nasals and frontals fused	Probably	No
Anterior margin of nasals with concavity facing anteriorly	Yes	No
Posterior margin of skull roof with transverse shelf	No	Yes
Relative size of basisphenoid	Small	Large
Preneural	Absent	Present
First vertebral scute	Rectangular with no supracostal scutes or triangular with supracostal scutes	Forms posterior half of hourglass-shaped sulcus pattern occupying nuchal area, supracostal scutes present laterally

MCZ 4072, skull. Locality: 1 mile northwest of land marker for the mutual corner of sections 23, 24, 25, and 26, T. 48 N., R. 96 W., in channel sandstone, weathered outcrop, 17 miles east of Squaw Nipple Buttes, Buffalo Basin, Wyoming (field notes). Horizon: Willwood Formation (see Van Houten, 1944). Collectors: Lewis and party, August 13, 1952 (I am grateful to Prof. Patterson for these data).

All the following are mentioned by Gilmore (1915).

CM 2956, skull. Locality: White River, near Ouray, Utah (label). Horizon: Uinta C. Collector: O. A. Peterson.

CM 2356 (*ibid.*, pl. 18 fig. 1), shell. Locality: East of Dragon-Vernal Road between White and Green rivers, Uinta Basin, Uinta County, Utah. Horizon: Uinta B. Collectors: Earl Douglass and party, June 18, 1908.

CM 3443, shell. Locality: Wagon-hound Bend, White River, Uinta County, Utah. Horizon: lower part of Uinta B. Collector: Earl Douglass, 1915.

CM 3253, shell. Locality: 2 or 3 miles west of Well No. 2, Uinta County, Utah. Horizon: Uinta C. Collector: Earl Douglass.

CM 2159, shell. Locality: Devil's Playground, Uinta Basin, Uinta County, Utah. Horizon: top of Uinta B or bottom of Uinta C. Collector: Earl Douglass, 1908.

CM 3243, shell. Locality: 1 mile northeast of Well No. 2, "near first gap," Uinta County,

Utah. Horizon: Uinta B. Collectors: Earl Douglass and J. T. Goetschius, October 2, 1908.

CM 3406 (type of *Baena inflata* Gilmore, 1915, figs. 2, 3, pl. 19), shell. Locality: McCook Canyon, White River, Uinta County, Utah. Horizon: Uinta A (near top). Collector: O. A. Peterson, 1912.

CM 3227 (type of *Baena platyplastra* Gilmore, 1915, fig. 8, pl. 18 fig. 2), plastron. Locality: northeast of Well No. 2, Uinta Basin, Uinta County, Utah. Horizon: Uinta B. Collectors: Earl Douglass and J. F. Goetschius, August 5, 1908.

USNM 18102, skull. Locality: Grizzly Buttes, Little Dry Creek, Bridger Basin, Wyo. (label). Horizon: Bridger B, Eocene (label). Collector: G. F. Sternberg, September 2, 1947.

DISCUSSION: On the basis of skull and shell material there appear to be only two baenid genera in the American Eocene. The principal differentiation between these taxa is in the skull morphology. The shells may be distinguished only when the anterior part of the carapace is present, the rest of the shell being identical in both genera. The two names available for these taxa are *Baena* Leidy, 1870, and *Chisternon* Leidy, 1872. The problem discussed here is the fact that the type species of both genera are represented by shells lacking the diagnostic anterior end of the carapace.

In 1870, Leidy (pp. 123–124) named *Baena arenosa*. His description was brief and lacked

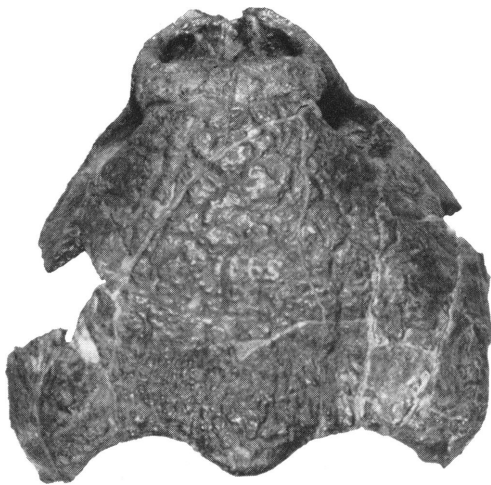


FIG. 28. *Baena arenosa* Leidy. Dorsal view of skull of AMNH 5971 from the Eocene Bridger Formation of Wyoming. Surface rugosities apparent in this specimen are not present in all members of this species. See figure 53 for ventral view. Scale equals 2 cm.

figures. In 1871 (1871a, p. 367), Leidy summarized the genus and named a new species, *B. affinis*. No figures were given. It is important to note that the type and only known specimen of *B. affinis* has enough of the anterior part of the carapace to place it in one of the two Eocene taxa. In 1873, Leidy (pp. 160–169) redescribed the above two specimens in much greater detail along with new material. The first figures of the specimens also appeared at this time (*ibid.*, plates 13, 15, 16). *Baena affinis* was synonymized with *B. arenosa*. Even though the type specimen of *Baena arenosa* is, strictly speaking, indeterminate, it can still be identified by using the referred specimen, the type of *B. affinis*, to supplement it. Thus, in the interest of a more stable nomenclature, the genus *Baena* can be retained.

The oldest (Willwood Formation, figs. 26, 27) and the youngest (Uinta Formation, fig. 52) *Baena* skulls are illustrated for the first time. The Uinta skull is rather poorly preserved, but the triturating surfaces can be readily compared with a Bridger *Baena* (figs. 53, 54). Most of the differences between the Uinta and Bridger skulls are probably attributable to crushing and breakage in the Uinta specimen, nonetheless, the characteristic triturating surfaces can be

seen. The Willwood skull presents some definite proportional differences from Bridger material but (see below under Skull and Jaws) I believe these are attributable to the juvenile nature of the Willwood skull. Figures 27, 52–54 show the limited variation in triturating surfaces, whereas figures 26, 28, and 29 illustrate the greater variation in skull roof emargination.

The four species of this genus recognized by

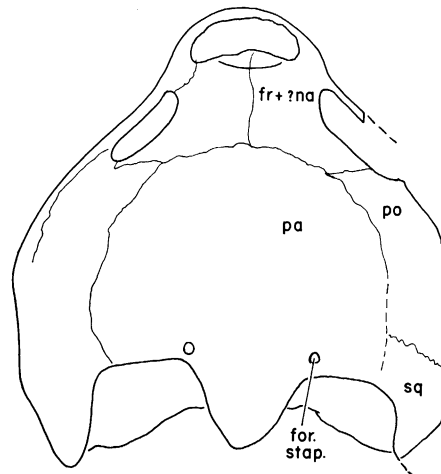


FIG. 29. *Baena arenosa* Leidy. Dorsal view of skull, USNM 18102, from the Eocene Bridger Formation of Wyoming. Compare relative degree of temporal emargination in this specimen with figures 26 and 28. Position of FORAMEN STAPEDIO-TEMPORALE on otic chamber is indicated for a landmark. Maximum length on midline 75 mm. Abbreviations on pages 246–247.



FIG. 30. *Baena arenosa* Leidy. Anterolateral view of AMNH 5971 from the Eocene Bridger Formation of Wyoming. Narial morphology is characteristic of this species. Same specimen as in figures 28 and 53.

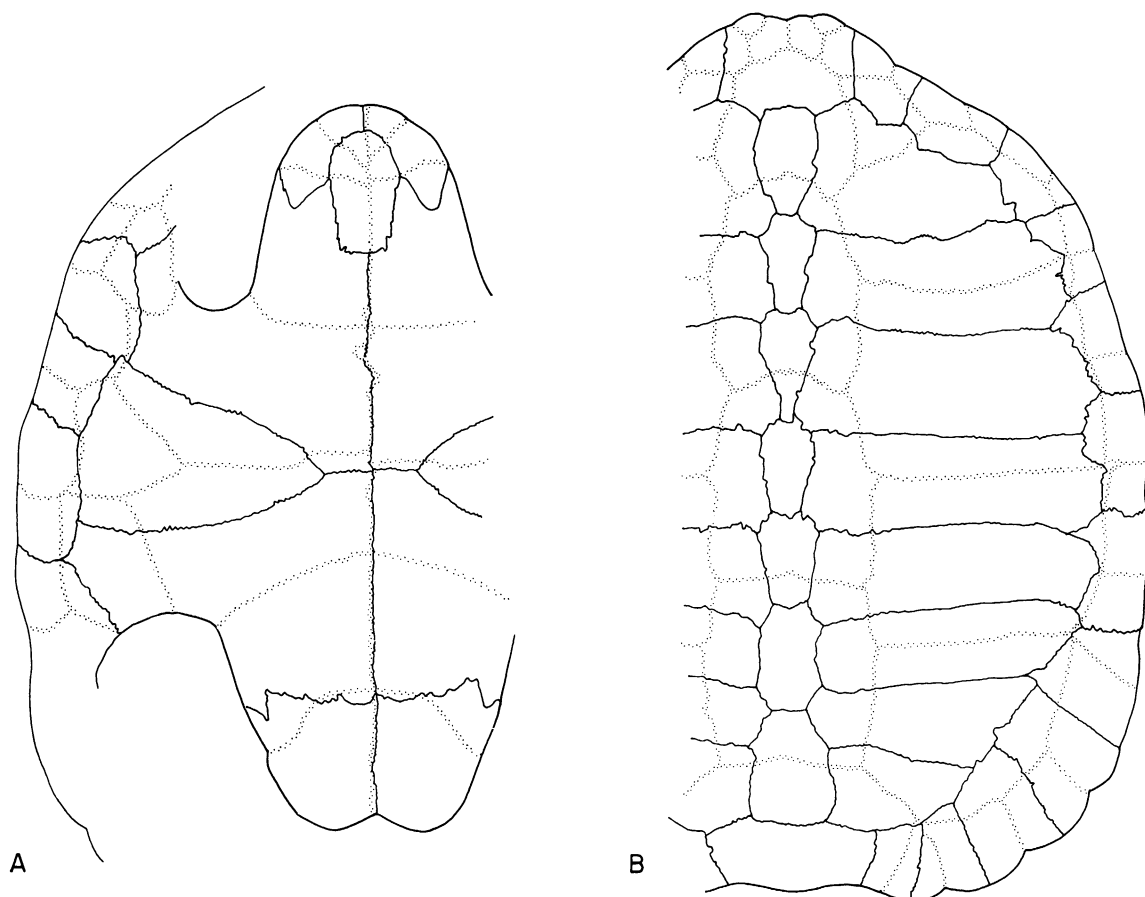


FIG. 31. *Baena arenosa* Leidy. Partially restored shell of AMNH 5977, a probable juvenile from the Eocene Bridger Formation of Wyoming. Sutures are best seen in this specimen but mesoplastra meet in midline in all other known *B. arenosa* shells. A. Ventral view. B. Dorsal view. Straight midline length about 315 mm. After Hay, 1908.

Hay with his principal criteria are as follows (1908, p. 60):

- “1. Shell broad behind and deeply scallopt [*sic*]; strongly sculptured on back.....*arenosa*
2. Not so strongly sculptured; a broad groove along the back.....*riparia*
3. Shell oval, thin; the sculpture broken up into wrinkles; no median groove.....*sima*
4. Shell oval; rounded behind; nearly smooth.....*clara*”

The following is a discussion of the characters used by Hay to separate Bridger *Baena* species. In this discussion names refer to type specimens only.

Shell Shape: Of the four type specimens, only that of *Baena clara*, AMNH 1675, is pre-

served in a relatively undistorted condition; in fact, it is one of the few baenid specimens known that still seems to exhibit the original cross section. *Baena sima* (AMNH 5971) and *B. clara* are distinguished by Hay (*ibid.*) as having an oval shell, implying that the others do not. *Baena arenosa* is crushed dorsoventrally and *B. riparia* is damaged posteriorly, but they both agree with the other specimens as far as the preserved outlines are concerned. The outline of *B. arenosa* is more angular than in *B. clara* or *B. sima* but I believe this is owing to the dorsoventral crushing of *B. arenosa*. The broad groove along the back (Hay, 1908, p. 60) of *B. riparia* also seems to be owing to crushing.

Ornamentation: Hay seems to have given this character slightly more weight than the others

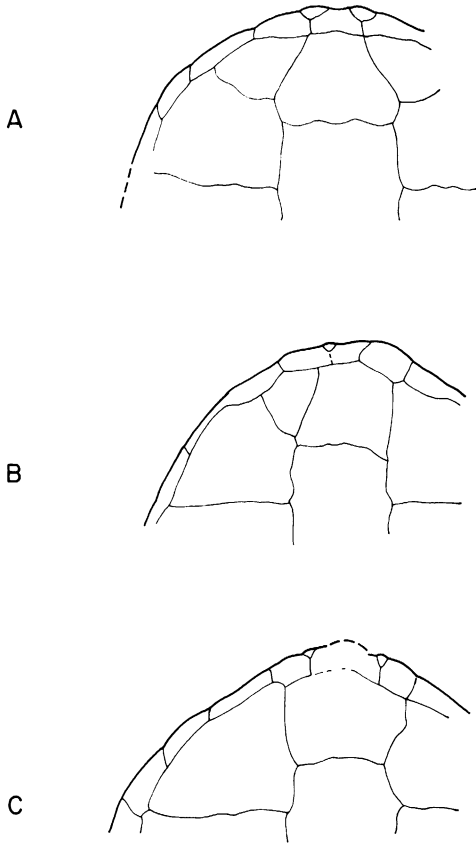


FIG. 32. *Baena arenosa* Leidy. Variation in sulci on dorsal surface of anterior area of carapace. A. AMNH 5900. B. AMNH 3932. C. AMNH 5971.

as many of the specimens identified by him in the American Museum of Natural History collections differ from the type in all characters except the ornamentation. This character, however, is broadly gradational, and although two particular specimens may look quite distinct intermediates can be found among the specimens from Grizzly Buttes (East and West).

Scute Pattern: Although Hay did not emphasize scute morphology in defining these species, distinct differences are present among the type specimens. There are two areas where these scute distinctions are present (figs. 32, 33): (1) the presence or absence of a pair of scutes between the first pleural (costal scute) and the first vertebral (neural scute); and (2) whether the sulcus between the anal and femoral scutes is sigmoid or straight. Almost all the Bridger *Baena* specimens have the small lateral scutes

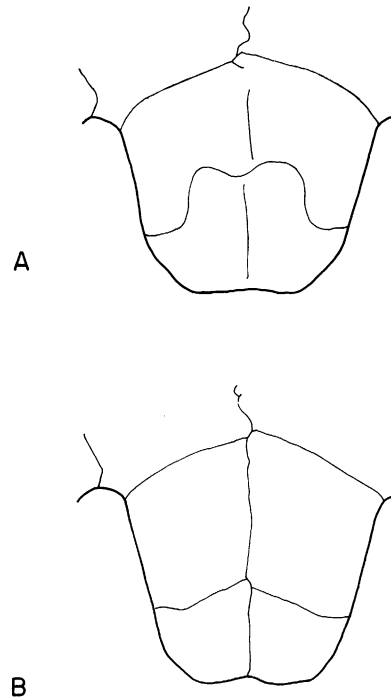


FIG. 33. *Baena arenosa* Leidy. Variation in sulci on ventral surface of posterior plastral lobe. A. Femoro-anal sulcus has sharp anterior lobe. B. Femoro-anal sulcus is relatively straight.

between the first vertebral and first pleural and have a sigmoid sulcus between the femoral and anal scutes. However, the types of *B. clara* (AMNH 1675) and *B. sima* (AMNH 5971) lack the lateral scutes, and *B. clara* has a straight femoral-anal sulcus. The anterodorsal scute morphology of the type of *B. arenosa* cannot be determined. There are two other specimens (AMNH 5907 and 5952) in addition to the types of *B. clara* and *B. sima* which lack these scutes. Both of these specimens have sigmoid femoral-anal scutes. One other specimen (AMNH 1112) has a straight femoral-anal sulcus as in *B. clara* but this specimen has lateral scutes between the first vertebral and first pleural (in fact it has three, two are present on the left side). Furthermore, AMNH 3932 (fig. 32B) has the lateral scute present on the left side but not on the right. The differences in scute morphology, then, seem to be best interpreted as individual variation.

Skull and Jaws: The types of *Baena riparia* (AMNH 5977) and *Baena sima* (AMNH 5971)

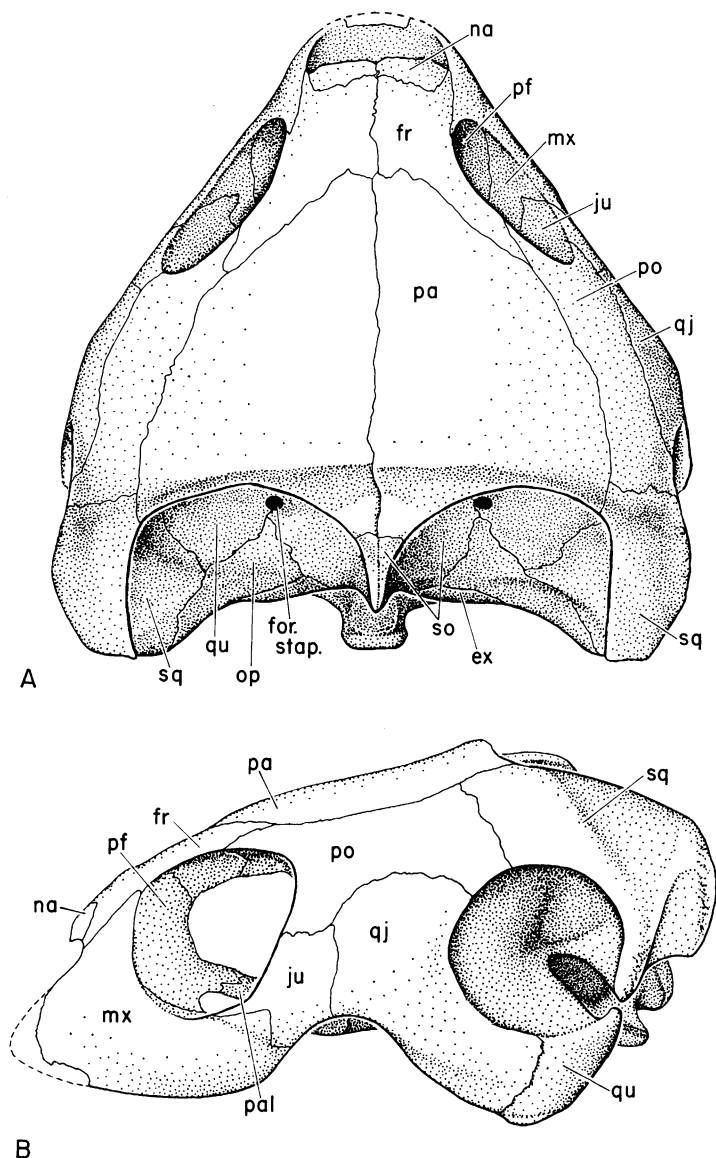


FIG. 34. *Chisternon undatum* (Leidy). Partially restored skull of AMNH 5961 (with additions from other specimens) from the Eocene Bridger Formation of Wyoming. A. Dorsal view. B. Lateral view. Condyle-premaxilla length about 68 mm. Abbreviations on pages 246-247.

include cranial material. *Baena sima* (figs. 28, 30, 53) has an almost complete skull and lower jaws. *Baena riparia* (Hay, 1908, pl. 19) has a fragmentary skull with almost complete lower jaws. The two skulls are different in that *B. riparia* has thinner bones and a less robust construction than *B. sima* but both are essentially the same in the features preserved. The

lower jaws, however, are rather different. The jaw of *B. sima* is more massive, has wider triturating surfaces, and has a deeper cavity for the M. adductor mandibulae superficialis on the lateral side of the jaw. Although the shell of *B. riparia* is about 10 per cent smaller than *B. sima* (median plastral length in *B. riparia* is 262 mm., and in *B. sima* it is 320 mm.), the

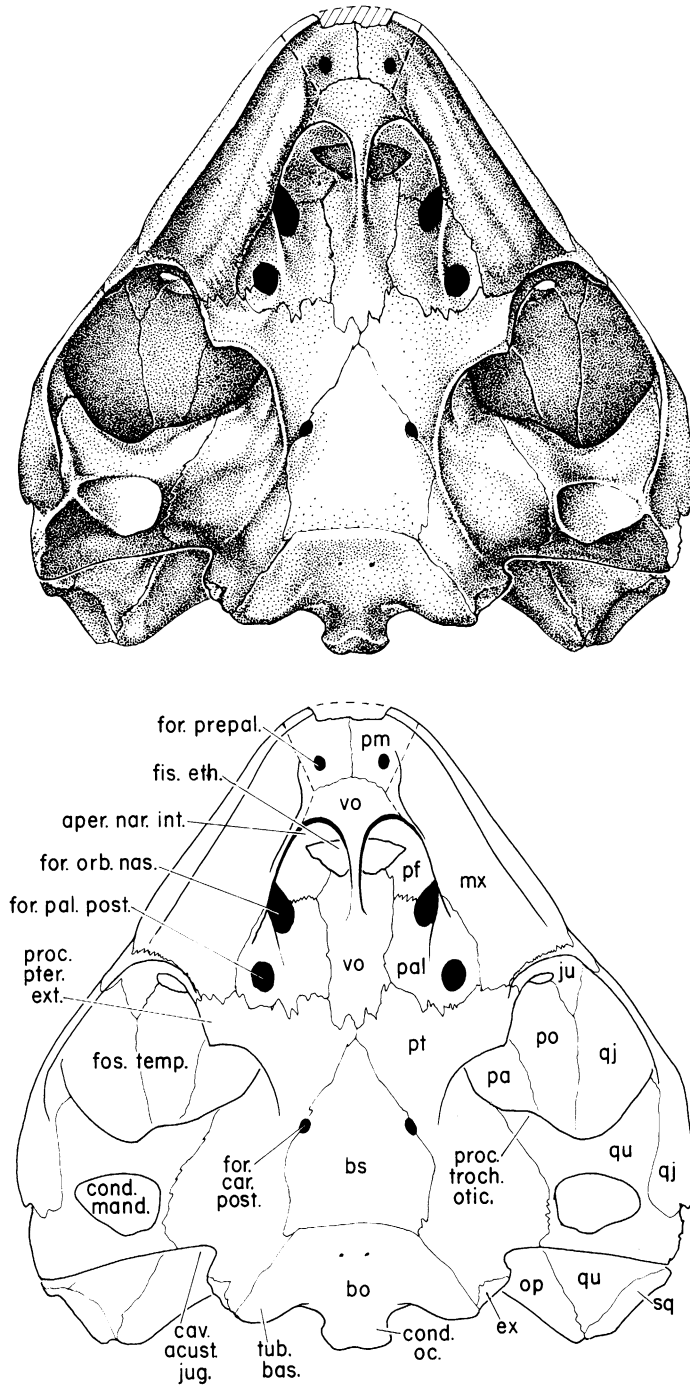


FIG. 35. *Chisternon undatum* (Leidy). Partially restored ventral view of skull of AMNH 5961 from the Eocene Bridger Formation of Wyoming. See also figure 55. Abbreviations on pages 246–247.

lower jaw of *B. sima* is only slightly larger (the actual specimens are nearly the same in length but a portion of the articulation is missing in *B. sima*). Nevertheless, I believe that the differences between the jaws are due mainly to differences in age and development. Living trionychids are known to exhibit considerable changes in lower jaw and skull morphology within a single population because of age and sex (Stejneger, 1944, p. 9).

The skull (MCZ 4072) on which the main illustrations of *Baena* (figs. 26, 27) are based also differs somewhat from most other specimens. This is probably due to the fact that this specimen is a juvenile, but as the MCZ skull is also stratigraphically older (Willwood Formation) than the other skulls seen in this study it may reflect genetic differences. However, owing to the juvenile nature of this individual almost all the sutures are open and much easier to determine than in older individuals and for this reason it is figured. The triturating ridges are much less pronounced in this specimen than in most others (compare fig. 27 and fig. 54). The posterior edge of the skull roof is less emarginated in the Willwood specimen. Figure 28 illustrates the commoner condition.

The type of *Baena sima* (AMNH 5971) has a very rugose sulcus pattern on the dorsal surface of the skull (fig. 28), but this seems to be an intensification of the scale pattern in a juvenile (fig. 26).

Other species referred to *Baena*: *Baena emiliae* Hay, 1908. Gilmore (1915, pp. 109–112) discussed six additional specimens from the Uinta Formation of Utah and referred by him to *B. emiliae*. Examination of these specimens and the type (AMNH 1925) suggests that all seven specimens may be referred to *B. arenosa*.

Baena inflata Gilmore, 1915 (pp. 112–116). Gilmore based this species on CM 3406 from the Uinta Formation of Utah and referred two other specimens to the taxon. One of these specimens, CM 3442, lacks the “inflation” of the costals which seems to be the only definitive character of the species and was referred to it by Gilmore because “In size, general contour, and the dimensions of the dermal scutes, the specimen closely resembles the type” (Gilmore, 1915, p. 115). I can find no character on which to distinguish this nominal species from *B. arenosa*.

Baena gigantea Gilmore, 1915. On the basis

of the anterior scute pattern of the carapace (CM 3441), this species from the Uinta Formation of Utah is referred to *Chisternon undatum*.

Baena platyplastra Gilmore, 1915. The type (CM 3227), Uinta Formation, Utah, is a plastron lacking the anterior portion of the anterior lobe. Because there is no carapace, and Gilmore referred none to it, this species must be considered a *nomen dubium*.

CHISTERNON¹ LEIDY, 1872

Baena LEIDY, 1870 (in part).

TYPE SPECIES: *Baena undata* Leidy, 1871b, p. 228.

KNOWN DISTRIBUTION: Bridgerian-Uintan Eocene of Wyoming and Utah.

DIAGNOSIS: Baenines with temporal emargination greater than in *Baena* but less than in *Eubaena*; diameter of orbit and FORAMEN MAGNUM large relative to *Baena*; lateral maxillary constriction absent; nasal separate from frontals, lacking concavity and tapering in thickness anteriorly; posterior margin of skull roof with transverse ridge; basisphenoid large relative to that in *Baena*; preneural present; first vertebral forms posterior half of hourglass-shaped sulcus pattern occupying nuchal area, supracostal scutes present laterally in “waist” of hourglass.

Chisternon undatum (Leidy)

Figures 34–36, 55, 56

Baena undata LEIDY, 1871b, p. 228.

Baena hebraica COPE, 1872, p. 463.

Chisternon undatum (LEIDY), 1872, p. 162.

Chisternon hebraicum (COPE), new combination of Hay, 1908, p. 87.

Baena gigantea GILMORE, 1915, p. 116.

TYPE SPECIMEN: ANSP 10040 (Leidy, 1873, pl. 14), a partial shell.

LOCALITY: “. . . a few miles from Fort Bridger . . .” (Leidy, 1873, p. 169). “. . . a range of buttes a few miles from Fort Bridger” (Hay, 1908, p. 85).

HORIZON: Probably from the Bridger Formation.

COLLECTOR: J. Van A. Carter, (possibly) 1871.

DIAGNOSIS: Same as for genus.

¹ *Chi* in allusion to the shape of that letter, *sternon* in reference to the *chi*-shaped sternal plates of the plastron.

HYPODGM: AMNH 5904, a shell, skull, vertebrae, and limb elements (referred to *Chisternon hebraicum* by Hay, 1908, pp. 89–91, figs. 82–87). Locality: Grizzly Buttes East, Bridger Basin, Wyoming (see Wheeler, 1961, pl. 2, for map and stratigraphic data about the Bridger Formation). Horizon: Bridger Formation, probably Bridger B, Eocene. Collectors: Walter Granger and Oliver P. Hay, July 28, 1903.

AMNH 5959 (Hay, 1908, p. 86, fig. 72), a partial shell. Locality: Grizzly Buttes West, Bridger Basin, Wyoming (see Wheeler, 1961, pl. 2, for map). Horizon: Bridger Formation, "in sandstone, lower beds of the locality" (label), probably Bridger B, Eocene. Collector: O. P. Hay, 1903.

AMNH 5961 (referred to *Chisternon hebraicum* by Hay, 1908, pp. 87–89, figs. 76–81, pl. 21 figs. 3, 4, pl. 23 fig. 1), shell, skull, vertebrae, and limb elements. Locality: Grizzly Buttes West, Bridger Basin, Wyoming (label) (see Wheeler, 1961, pl. 2). Horizon: Bridger Formation, probably Bridger B, Eocene. Collector: L. S. Quackenbush, 1903.

AMNH 5962 (Hay, 1908, pp. 86, 87, figs. 73–75), shell, skull, vertebrae, limb elements. Locality: Grizzly Buttes West, Bridger Basin, Wyoming (label) (see Wheeler, 1961, pl. 2). Horizon: Bridger Formation, probably Bridger B, Eocene. Collector: L. S. Quackenbush, 1903.

AMNH 5964, shell. Locality: Grizzly Buttes West, Bridger Basin, Wyoming (label) (see Wheeler, 1961, pl. 2). Horizon: Bridger Formation, probably Bridger B, Eocene. Collector: Albert Thompson, July 11, 1903.

AMNH 5974, shell. Locality: "... mouth of Cottonwood Creek ..." (Hay, 1908, p. 86), Bridger Basin, Wyoming (see Wheeler, 1961, pl. 2, for map). Horizon: Bridger B, "B²" of Hay (1908, p. 86), "Low down in clay" (label), Eocene. Collector: L. S. Quackenbush, August 4, 1903.

CM 3441 (type of *Baena gigantea* Gilmore, 1915, figs. 5–7, pl. 20), shell. Locality: Wagon-hound Bend, on White River, Uinta County, Utah (Gilmore, 1915, p. 116). Horizon: Lower Uinta B, Uinta Formation, Upper Eocene (*ibid.*). Collector: Earl Douglass, 1915.

USNM 12839, skull and jaws. Locality: Uinta County, Wyo. (label). Horizon: Bridger, Eocene (label). Collector: Smithsonian Expedition, 1930.

YPM 3930, disarticulated skull. Locality:

Granger, Wyo. (label). Horizon: Bridger B (label). Collector: R. E. Son, 1873.

DISCUSSION: *Chisternon* Leidy, 1872, is based on *Baena undata* Leidy, 1871, and is represented by a type specimen consisting of a carapace and plastron lacking the anterior end. As in the case of *Baena arenosa*, the type specimen is not, strictly speaking, identifiable on the basis of my criteria as it lacks the anterior end. The original criterion by which Leidy separated this genus from *Baena* was the presence of mesoplastra. He named the form *Chisternon* in allusion to the cross-shaped "sternal" scutes which he thought resembled the Greek letter *chi*. In 1884, Cope (p. 148) suggested that *Baena* had mesoplastra also and put *Chisternon* into synonymy with *Baena*. This action can be seen in retrospect to have been quite correct as all baenids have mesoplastra. If Cope's suppression of *Chisternon* had been followed at that time, the present difficulty would be avoided. However, in 1906 (p. 156) Hay re-established the genus and referred new material to it. None of Hay's criteria (1906, p. 156; 1908, p. 84) can be determined in the type specimen of Leidy's *Chisternon*. The only feature that the type and Hay's specimens have in common is the relatively large size, not seen in most *Baena* shells. Hay does not mention this feature in his identification, and it is not really known why he chose to refer the new material to *Chisternon*. Hay (1908) also referred Cope's *Baena hebraica* to *Chisternon*, and this specimen does show the defining characters present in the referred specimens of *Chisternon*.

The problem, then, is that the current concept of *Chisternon undatum* is based on a suite of specimens to which the type may or may not belong. One alternative would be to treat *C. undatum* as a *nomen dubium* and establish a new generic name based on *Baena hebraica*. The name *Chisternon*, however, is established in the literature and its suppression would not be in the best interests of a stable nomenclature. Therefore, as in the case of *Baena arenosa*, it seems best to retain the name even though it is based on an indeterminate specimen, keeping in mind that the concept is based on the hypodigm and not the type specimen.

The genus *Chisternon* has been questionably recorded from the Paleocene by Hay (1909, pp. 194, 195). A Paleocene species, *Chisternon* (?) *interpositum* is based on shell fragments from the

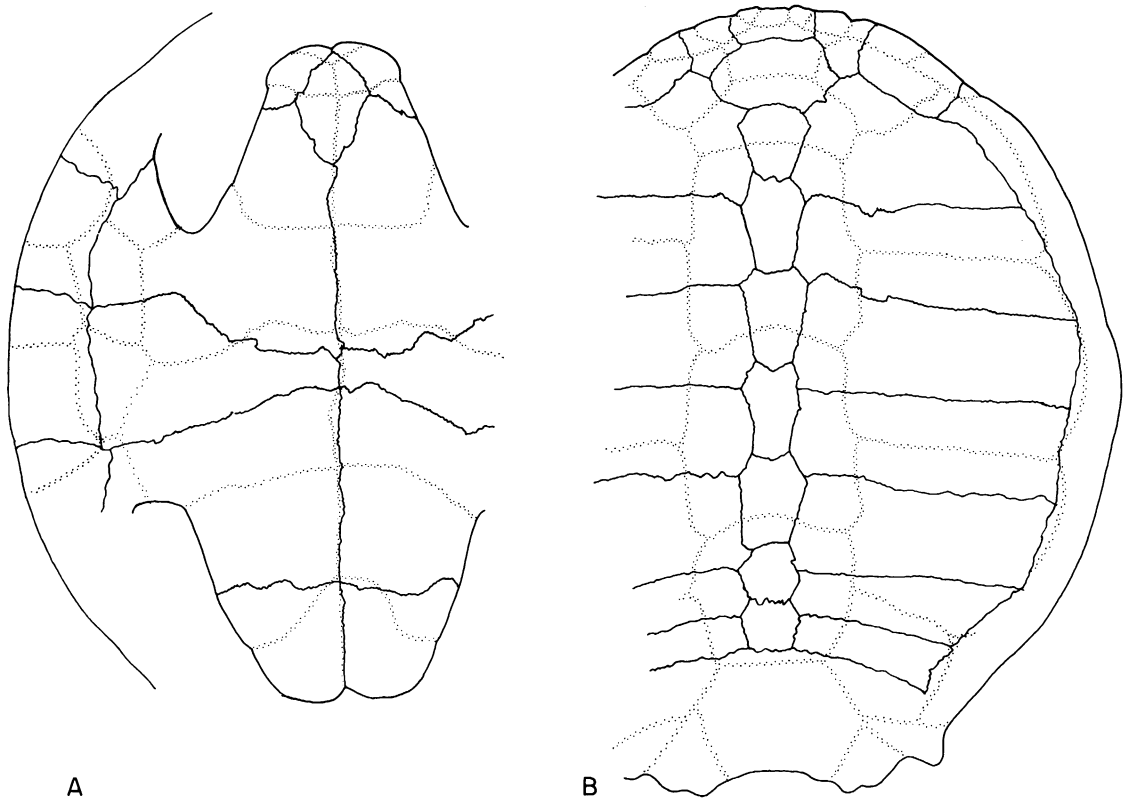


FIG. 36. *Chisternon undatum* (Leidy). Restored shell based on AMNH 5961 with additions from AMNH 5959 and 5974. Eocene Bridger Formation of Wyoming. AMNH 5961 approximate straight midline length 474 mm.

Livingston coal field of Montana. The data are as follows (*ibid.*):

TYPE SPECIMEN: USNM 6058, anterior portions of carapace and plastron. Locality: T. 5 S., R. 19 E., Carbon County, “. . . about 10 or 15 miles west of north of Red Lodge . . .,” on or near some of the sources of Red Lodge Creek, Livingston coal field, Montana (*ibid.*). Horizon: Fort Union Formation, Paleocene (*ibid.*). Collector: C. F. Kay, of the United States Geological Survey, 1908.

The specimen is referred to *Chisternon* on the basis of a preneural bone which is consistently known only from *Chisternon*. However, the sulci pattern in the anterior part of the shell lacks the hourglass configuration characteristic of *Chisternon*, and it would not be unusual for a preneural to appear as an anomaly. Therefore, the record should be ignored until further

material is forthcoming. The species is here considered a *nomen dubium* because of insufficient diagnostic characters.

The skull of AMNH 5961 has been the basis of a skull roof drawing by Hay (1908, fig. 78) which was repeated by Romer (1956, fig. 50B). This skull (fig. 56) unfortunately was broken probably during life by a sharp impact which caused cracks that Hay misinterpreted as sutures. The resulting problems of identification of baenid skull roof elements are dealt with in the anatomical section (Gaffney, in preparation; Gaffney, ms) but the figure is reproduced here to help substantiate my identification of the bones. At least two other specimens of *Chisternon* (USNM 12839 and YPM 3930) demonstrate the correct morphology and have been used in developing the restoration (fig. 34).

BAENID GENERA INDETERMINATE AS TO SUBFAMILY

A number of shells are known which have not been associated with skull material. Many of these are morphologically distinctive and warrant formal recognition. Because the systematics of baenids, as presented here, relies strongly on cranial features, these shell taxa cannot be formally incorporated into the phylogeny and classification presented here.

COMPSEMYS LEIDY, 1856

TYPE SPECIES: *Compsemys victa* Leidy, 1856, p. 312.

KNOWN DISTRIBUTION: Late Cretaceous to Paleocene of New Mexico, North Dakota, and Wyoming.

DIAGNOSIS: (For this and the following diagnoses of taxa based only on shell material, each character is numbered for ease of comparison): 1) shell shape oval, sides parallel; 2) ornamentation consisting of small, close-set enameled tubercles, not known in any other turtles; 3) nuchal scute small, wide, with very short anteroposterior length; 4) no anterior emargination of carapace; first peripherals meeting medially in front of nuchal, preventing it from being exposed on anterior edge of carapace; 5) preneural bone absent; 6) first vertebral larger than other vertebrae; rectangular, without supracostal scutes laterally; 7) supramarginal scutes absent; 8) last vertebral enclosed posteriorly by last pair of marginals meeting in midline, last marginals rectangular; 9) posterior edge of carapace not emarginated; 10) posterior edge of carapace not scalloped; 11) xiphiplastral notch present, shallow, varying from U-shaped to V-shaped; 12) paired intergulars placed at anterolateral corners of plastron separated by very wide, paired intergulars; humero-intergular sulcus and pectoro-humeral sulcus converge toward each other in midline.

DISCUSSION: See specific discussion.

Compsemys victa Leidy, 1856

Figure 37

Compsemys parva HAY, 1910, p. 308.

Compsemys vafer HAY, 1910, p. 311.

Compsemys puercensis GILMORE, 1919b, p. 19.

Compsemys torrejonensis GILMORE, 1919b, p. 21.

TYPE SPECIMEN: USNM 960 (Leidy, 1856,

p. 312; 1860, p. 152, pl. 6 figs. 5-7), a neural and two costal fragments.

LOCALITY: "... Long Lake, North Dakota" (Hay, 1908, p. 233).

HORIZON: "... of probable Laramie age ..." (*ibid.*). The horizon is probably late Cretaceous but any further precision is not possible.

DIAGNOSIS: Same as for genus.

HYPODGM: USNM 6548 (type of *C. parva* Hay, 1910, pp. 308-310, fig. 1, pl. 10 figs. 1-3), plastral fragments. Locality: "... Ojo Alamo, San Juan County, New Mexico" (*ibid.*). Horizon: "There is some doubt regarding the level at which the specimen was secured, but it is supposed that it came from the beds above the upper conglomerate; therefore above the dinosaur beds" (*ibid.*). Probably Paleocene, Nacimiento Formation. Collectors: J. H. Gardner and J. W. Gidley, 1909.

USNM 6551 (type of *C. vafer* Hay, 1910, pp. 311-313, figs. 2-5, pl. 10 figs. 4, 5) and USNM 6553 (*ibid.*, pl. 11 figs. 1, 2), fragments of shells. Locality: "... near Ojo Alamo, New Mexico ..." (*ibid.*). Horizon: "... about 50 feet above the upper conglomerate, and therefore above the dinosaur-bearing beds" (*ibid.*). Probably Paleocene, Nacimiento Formation. Collectors: J. H. Gardner and J. W. Gidley, 1909.

USNM 8528 (Gilmore, 1919b, fig. 1, pl. 1), an almost complete shell. Locality: "... 4 miles east of Kimbetoh, in sec. 35, T. 23 N., R. 9 W., " (*ibid.*). Horizon: "... 50 feet above the base of the Puerco ..." (*ibid.*). Nacimiento Formation, probably lower part, Paleocene. Collectors: J. B. Reeside and party, 1916.

USNM 8598 (*ibid.*, p. 16, pl. 19 fig. 3), plastron and carapace fragments. Locality: "... 8 miles N. 60° E. of Kimbetoh, in sec. 17, T. 23 N., R. 8 W., San Juan County, New Mexico ..." (*ibid.*). Horizon: "... 840 feet above the base of the Puerco, in the Torrejon formation" (*ibid.*). Upper part of the Nacimiento Formation, Paleocene. Collectors: as for USNM 8528.

USNM 8529 (*ibid.*, fig. 2, pl. 2), USNM 8530, 8600, partial shells. Locality: "San Juan Basin, New Mexico" (*ibid.*). Horizon: "Puerco formation" (*ibid.*). Collectors: same as for USNM 8528.

USNM 8544 (type of *C. puercensis* Gilmore,

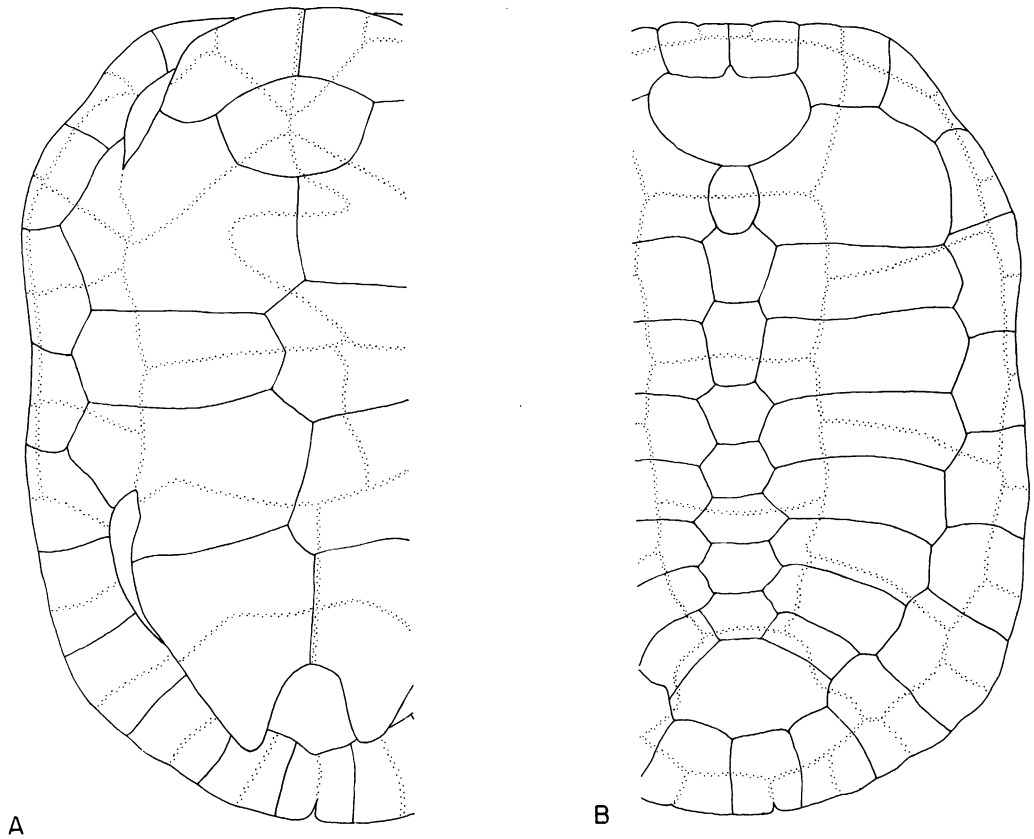


FIG. 37. *Compsemys victa* Leidy. Partially restored shell of USNM 8549 from the Paleocene Torrejon Formation of New Mexico. A. Ventral view. B. Dorsal view. Greatest straight line median length 280 mm. After Gilmore, 1919b.

1919b, p. 19, fig. 3, pl. 3), partial shell. Locality: "Four miles northwest of Kimbetoh, on the north line of sec. 27, T. 23 N., R. 9 W., San Juan County, New Mex." (*ibid.*). Horizon: "Puerco formation (50 feet above the base) . . ." (*ibid.*). Nacimiento Formation, Paleocene. Collector: J. B. Reeside, 1916.

USNM 8549 (type of *C. torrejonensis* Gilmore, 1919b, p. 21, fig. 5, pl. 4), USNM 8591. The former consists of an almost complete shell (the best described for this genus); the latter is a partial shell. Data: same as for USNM 8598.

DISCUSSION: Leidy (1856, p. 312) named this form on the basis of fragmentary material from the Upper Cretaceous of North Dakota. Since that time no better material has been found in the Cretaceous, but there are a number of other records of the genus based on fragments of bone with the characteristic ornamentation of the type (see Estes, 1964, p. 98). In 1877, Cope

described the species *Compsemys plicatulus* from the Upper Jurassic. Hay, in 1908, removed this species to the genus *Glyptops* Marsh and showed that *C. victa* Leidy, 1856, was not congeneric with *C. plicatulus* Cope, 1877. The Jurassic records of *Compsemys*, then, are correctly attributable to *Glyptops*. Hay (1908, p. 233) placed *Compsemys* in the "waste-basket" taxon Dermatemydidae because he did not have material showing the presence of mesoplastra. In 1910, however, he obtained better material from New Mexico (the horizon is in doubt, but it is probably Paleocene) that showed mesoplastra and Hay placed the genus in the Baenidae. Gilmore (1919b) described much better specimens from the same area, and he placed the genus in the Pleurosternidae, citing resemblances with *Glyptops* and *Neurankylus*. The possible relationships of *Compsemys* are discussed elsewhere.

Five species have been referred to this genus. Only the four Paleocene ones are based on relatively diagnostic material. The Cretaceous type specimen of *C. victa* only furnishes information about the sculpture and the fact that it is a turtle. The identification of the Paleocene types with the Cretaceous type is based solely on this sculpture pattern and the agreement in shape of the few elements that are present. It should be emphasized that this is a rather shaky association and it would not be unusual for two fairly unrelated turtles to evolve similar sculpture patterns. However, the sculpture of *Compsemys* is unique, as far as I know, and it is the same in the Cretaceous specimens and in the Paleocene specimens (compare Hay, 1908, pl. 34 figs. 2 and 3 with Gilmore, 1919b, pls. 1-3.)

The Cretaceous specimen, the type of *C. victa*, is so fragmentary that it cannot be adequately differentiated from the other described forms. I am provisionally synonymizing the Paleocene forms with *C. victa* Leidy because of the close agreement of sculpture pattern, but new material could very easily change this by demonstrating morphologic differences between them. The Paleocene species are a different matter. Here, the material is adequate, but I do not think that the differences represent different species. The differences defining the supposed species are within my subjectively determined limits of population variation.

NEURANKYLUS LAMBE, 1902

Charitemys HAY, 1908, p. 98.

TYPE SPECIES: *Neurankylus eximius* Lambe, 1902, p. 42.

KNOWN DISTRIBUTION: Campanian of Alberta and New Mexico; Maestrichtian of Montana.

DIAGNOSIS: 1) shell shape oval, sides parallel; 2) ornamentation mostly smooth, delicate striations marking growth lines in some specimens, large, raised ridges in others; 3) nuchal scute small, rectangular, bordered laterally by large first marginals; 4) no anterior emargination of carapace; peripherals not meeting in front of nuchal; 5) preneural bone absent; 6) first vertebral scute rectangular without supracostal scutes; 7) supramarginal scutes absent; 8) last vertebral scute not open posteriorly, last pair of marginals meeting medially behind vertebral, last marginals rectangular; 9) posterior edge of carapace not emarginated;

10) posterior edge of carapace sometimes with shallow scallops; 11) xiphiplastral notch absent; 12) paired intergulars meeting medially, gulars separated by intergulars.

DISCUSSION: See specific discussion.

Neurankylus eximius Lambe, 1902

Figures 38, 39

Charitemys captans HAY, 1908, p. 98.

Neurankylus baueri GILMORE, 1916c, p. 290.

Baena fluviatilis PARKS, 1933, p. 19.

TYPE SPECIMEN: NMC 1504, left costals 3, 5-9 (9 is anomalous); right costals 3, 4; 8th neural; and suprapygal.

DATA: Lambe (1902, p. 43) gave these data as: "Belly River series, Red Deer River, 1901." However, he indicated (p. 25) that the only area collected from in 1901 was: "... in an extensive area of 'badlands' on either side of Red Deer River between Berry creek and Dead Lodge cañon." Hay (1908, p. 94) gave the horizon as: "Judith River deposits, Belly River series, on Red Deer River." Presumably, Hay meant that the deposits were of Judith River age and not that the type came from the Judith River Formation. Currently the horizon would be considered to be Oldman Formation.

DIAGNOSIS: Same as for genus.

HYPODIGM: AMNH 6098 (type of *Charitemys captans* Hay, 1908, pp. 98-100, figs. 93-95), fragments of plastron and carapace. Locality: "... Montana" (Hay, 1908, p. 98). Horizon: "... Judith River deposits ..." (Hay, 1908, p. 98). Presumably Judith River Formation. Collectors: Sternberg and Isaac in 1876 for E. D. Cope (Hay, 1908, p. 98).

USNM 8344 (type of *Neurankylus baueri* Gilmore, 1916c, pp. 290-293, figs. 32, 33, pls. 74, 75), a complete shell. Locality: "About 30 miles south of Farmington and 4 miles east of reservation line, San Juan Basin, San Juan County, N. Mex. (Locality 80, section E, Pl LXIV)" (Gilmore, 1916c, p. 290). See also Bauer, 1916. Horizon: "Lower part of the Kirtland shale" (*ibid.*). The lower part of the Lower Shale Member of the Kirtland Formation of Baltz, Ash, and Anderson (1966). Collectors: C. Max Bauer and J. B. Reeside, Jr., 1915.

USNM 8531, shell (Gilmore, 1919b, pp. 11-12). Locality: "... 2 3/4 miles south of west of Kimbetoh, in sec. 3, T. 22 N., R. 10

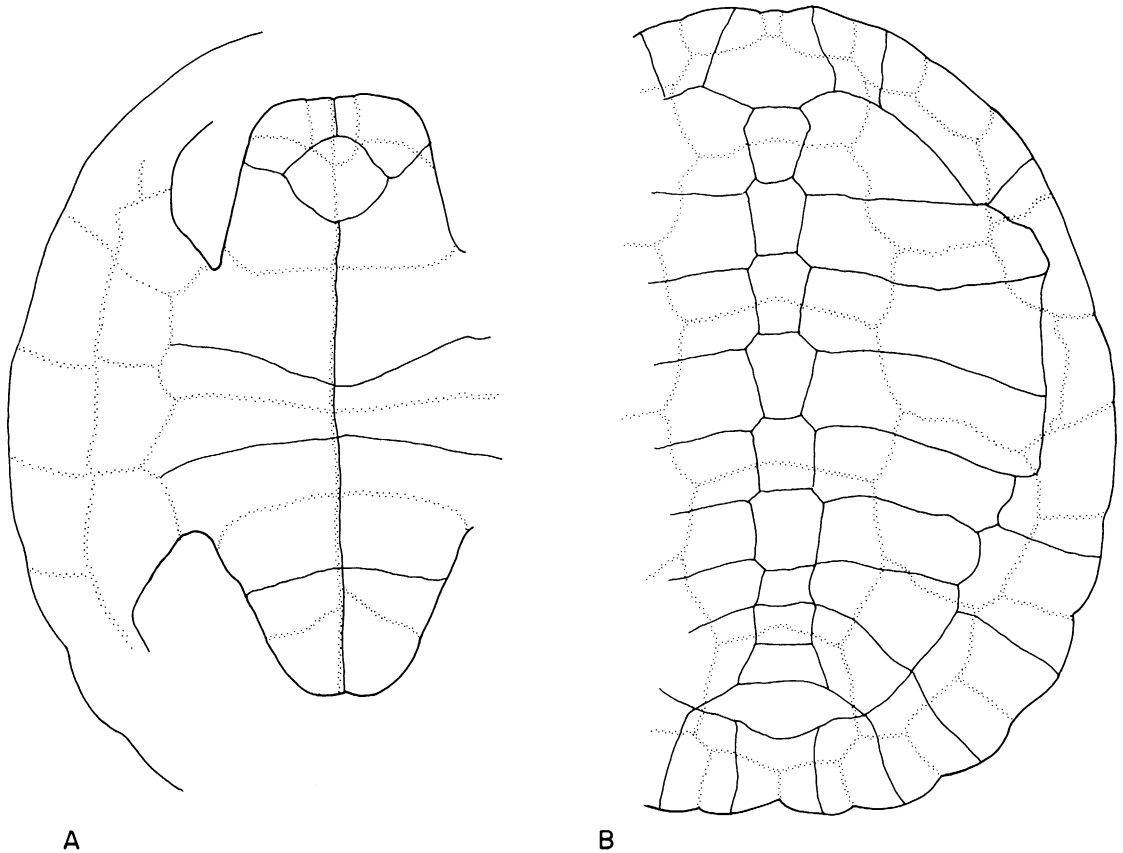


FIG. 38. *Neurankylus eximius* Lambe. Partially restored shell, USNM 8344, from the late Cretaceous Kirtland Formation of New Mexico. A. Ventral view. B. Dorsal view. Straight midline length 560 mm. After Gilmore, 1916c.

W., San Juan County, New Mexico" (*ibid.*). Horizon: "... 330 feet above base of the Kirtland formation" (*ibid.*). Collectors: J. B. Reeside, Jr., and F. R. Clark, 1916.

ROM 854 (type of *Baena fluviatilis* Parks, 1933, pp. 19–25, figs. 1, 2, pl. 7), partial shell, lacking much of left side and anterior edge. Locality: "... Sand Creek, Red Deer River, Alberta" (Parks, 1933, p. 25). Horizon: "... Belly River formation ..." (*ibid.*), Oldman Formation. Collector: University of Toronto expedition of 1919 (*ibid.*).

USNM 13228 (referred to *Neurankylus baueri* by Gilmore, 1935, p. 165), partial shell. Locality: T. 23 N., R. 10 W., San Juan County, New Mexico. Horizon: "... Kirtland formation" (*ibid.*). The locality information includes an area with outcrops of the Nacimiento Formation (Paleocene), the Ojo Alamo Sandstone

(Paleocene and/or late Cretaceous), and the Kirtland Formation (late Cretaceous) of Baltz, Ash, and Anderson (1966). The collector, G. F. Sternberg, presumably was able to identify the Kirtland here and this may be accepted as the correct assignment. Collector: G. F. Sternberg, 1929.

Wiman, 1933, "Exemplar No. 1" (referred to *N. baueri* by Wiman, p. 14, figs. 4–6, pl. 2 figs. 1–4, pl. 3 figs. 1–8b), an almost complete shell with limb girdles and vertebrae. Locality: "Head Meyers Cr., 6 miles west Kimbeto ..." San Juan County, New Mexico ... (Wiman, 1933, p. 15). Horizon: "Fruitland shales" (*ibid.*). The locality data indicate an area in which the boundary between the Fruitland and Kirtland formations may be found. Collector: C. H. Sternberg, 1921.

Wiman, 1933, "Exemplar No. 2" (referred

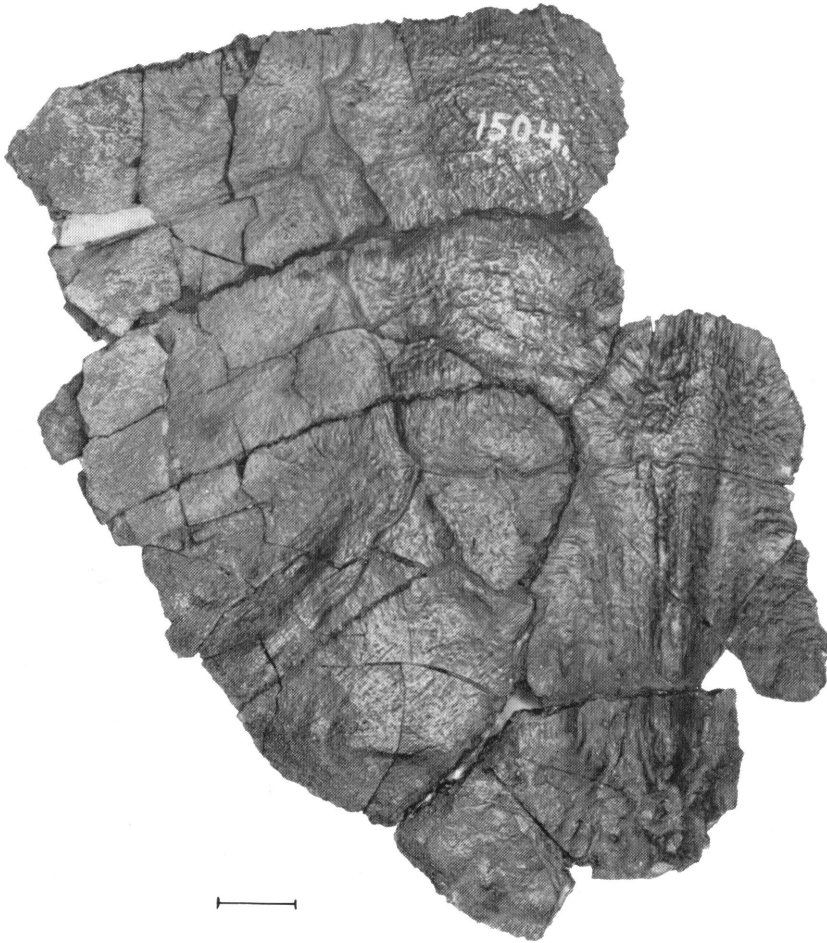


FIG. 39. *Neurankylus eximius* Lambe. Dorsal view of portion of type specimen, NMC 1504, from the late Cretaceous Oldman Formation of Alberta. Consists of left costals 6–9, the eighth neural, and a portion of the suprapygal. Scale equals 1 cm.

to *N. baueri* by Wiman, p. 19, pl. 2 fig. 2–2a), a partial shell. Locality: “‘Head west branch Meyers Cr., 6 miles West Kimbeto Trading Post.’ San Juan Co. New Mexico” (*ibid.*, p. 19). Horizon: “Kirtland Formation” (*ibid.*). See above. Either lowermost part of the Kirtland Formation or uppermost part of the Fruitland Formation. It is not known on what criterion Sternberg differentiated the units.

Wiman, 1933, “Exemplar No. 3” (referred to *N. baueri* by Wiman, 1933, p. 20, pl. 2 figs. 3, 3a), a partial shell. Locality: no original data. “San Juan Co. New Mexico” (*ibid.*). Horizon: no original data. “Ojo Alamo Schichten sens. lat.” (*ibid.*). There is no good reason to assign this specimen to the Ojo Alamo,

particularly not the Ojo Alamo of recent authors (Baltz, Ash, and Anderson, 1966). Its actual horizon is in doubt, although it may be the upper Kirtland.

Wiman, 1933, “Exemplar No. 4” (referred to *N. baueri* by Wiman, 1933, p. 21, pl. 2 fig. 4), a partial carapace. Locality: “1/2 mile oberhalb einer Stelle, die als ‘South Branch Meyers Cr., about 4 miles above Cattle ranch’ bezeichnet wurde” (*ibid.*). Horizon: “Kirtland shales” (*ibid.*). The horizon cannot be determined from the above locality information.

All the Wiman material was collected by the Sternbergs in 1921.

UNIV MINN VP2301, an almost complete shell, partially crushed. Locality: Sect. 33,

T. 25 N., R. 43 E., McCone Co., Montana, 1 mile southeast of Harbicht Hill (label). Horizon: Upper Hell Creek Formation, 96 feet below Z coal bed (label). Collector: R. E. Sloan, 1965.

ROM 864, an almost complete shell. Locality: Fruitland, New Mexico. Horizon: Fruitland Shale, Upper Cretaceous (label). No further data are available. Collector: purchased by the ROM from Ward's Natural Science Establishment.

DISCUSSION: Examination of the type specimen of *Charitemys captans* Hay (AMNH 6098) indicates that it cannot be separated from *Neurankylus*. The type of *Charitemys* includes some loose bridge peripherals that have the characteristic gutter or channel along their edge (see Gilmore, 1916c, fig. 32 for the peripherals of *Neurankylus*). Furthermore, a side by side comparison of Lambe's type of *N. eximius* and *Charitemys* shows that they both have the same type of ornamentation on the costal bones (fig. 39). As Hay stated (1908, p. 100), "The lower halves of the costals are marked [*sic*] by coarse ridges, which have been produced during the growth of the costal scutes." Lambe also noticed this sculpture on *Neurankylus* (1902, p. 43): "Comparatively large, concentrically curved groove-like markings also occur on two of the costals." This ornamentation is somewhat similar to that found on Tertiary and recent members of the Testudinidae (*sensu* Romer, 1956). Some of the questionably testudinid shell fragments reported by Estes (1964, p. 99) from the Lance Formation bear some resemblance to *Neurankylus* (fig. 39) and probably belong to this genus rather than to the Testudinidae.

The assignment of the type of *Baena fluviatilis* Parks (ROM 5724) to *Neurankylus* is somewhat less certain. The last peripherals meeting behind the fifth vertebral and the absence of a posterior emargination on the carapace indicate that the specimen does not belong in the form-genus "*Baena*." Gilmore (1935, p. 177) recognized this and referred the specimen to the genus *Thescelus* Hay. The specimen in question is crushed and lacks the anterior and much of the left side of the shell. The key character for identifying *Thescelus* is the anterior embayment of the carapace, an area not preserved in the type of "*B.*" *fluviatilis*. However, careful comparison of this specimen along with a number of specimens of *Neurankylus* and two specimens of

Thescelus (the types of *T. insiliens* Hay and *T. rapiens* Hay) suggests that "*B.*" *fluviatilis* belongs to *Neurankylus*. The anterior lobe of the plastron in "*B.*" *fluviatilis* is squared off anteriorly as in *Neurankylus* and does not taper strongly as in the better preserved specimens of *Thescelus*. The second and third vertebrae of "*B.*" *fluviatilis* are slightly restricted anteriorly which is the case in *Neurankylus*. Also, the posterior neurals show a slight keel, similar to *Neurankylus*. Therefore, it would be best to tentatively refer the specimen to *Neurankylus eximius*.

The separation of *Trinitichelys* from *Neurankylus* is based more on theoretical considerations than on distinctive morphology. The close similarity of the shells of *Glyptops* and *Trinitichelys* compared to the differences in the skulls of the two forms suggests that the possession of this shell pattern alone is not sufficient reason to place a specimen in one of these genera. It is likely that a form even further removed temporally from these genera will also have a different skull (see discussion under *Trinitichelys*). Provisionally, *Neurankylus* should be kept separate until cranial information is forthcoming. *Neurankylus* can be distinguished from *Trinitichelys* by the fact that *Neurankylus* lacks the "*Glyptops*"-type of ornamentation, but has (in most specimens) keeled neurals which are lacking in *Trinitichelys*.

The problem of species in *Neurankylus* is easier to solve than in *Baena arenosa* or in the forms assigned to the Cretaceous "*Baena*" as *Neurankylus* lacks the high degree of morphologic variation seen in these forms. The only obvious morphologic variation observed within *Neurankylus* is the absence of keeled neurals in a specimen from the Hell Creek Formation of Montana (UNIV MINN VP2301) and in a specimen from the Fruitland Formation of New Mexico. There are at least five other specimens from the Kirtland-Fruitland formations that have keeled neurals (only one of these is apparently from the Fruitland, see Wiman, 1933, "Exemplar No. 1," pl. 2 fig. 1, and this specimen is indicated as having keeled neurals). There are no other reported specimens of *Neurankylus* from the Hell Creek Formation. Therefore, it would be unwise at this time to use the presence or absence of keeled neurals as a species indicator without additional correlated characters. Also, it would be unwise to set up geographic or

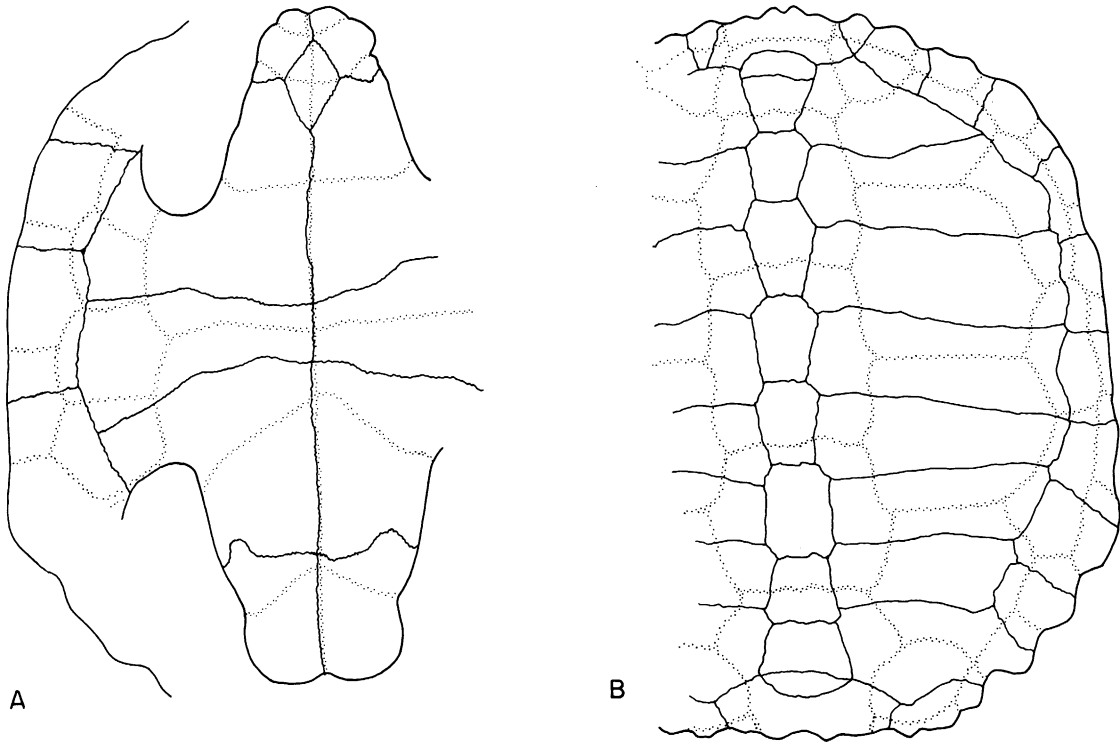


FIG. 40. *Boremys pulchra* (Lambe). Restoration of shell based on NMC 2281 and NMC 1130 from the late Cretaceous Oldman Formation of Alberta. A. Ventral view. B. Dorsal view. Maximum straight line length of NMC 2281 about 210 mm.

geologic species that have no morphologic criteria for identification.

Neurankylus wyomingensis (Gilmore, 1919a) is here considered a *nomen dubium* (see discussion under *Trinitichelys*).

BOREMYS LAMBE, 1906b

TYPE SPECIES: *Baena pulchra* Lambe, 1906a, p. 189.

KNOWN DISTRIBUTION: Campanian of Alberta and New Mexico.

DIAGNOSIS: 1) shell oval, sides roughly parallel; 2) ornamentation varied as in *Baena*; 3) nuchal scute much wider than long; 4) no anterior emargination; peripherals not meeting medially; 5) preneural bone present but much smaller than in *Chisternon*; 6) first vertebral scute roughly rectangular but anterior width invariably less than posterior width, paired lateral supracostal scute present; 7) supra-marginal scutes present, usually three pairs; 8) last vertebral scute opening widely on post-

erior edge of carapace, scute width narrowing posteriorly due to presence of paired lateral supracostal scutes; 9) posterior edge of carapace slightly emarginated; 10) posterior edge of carapace scalloped; 11) xiphiplastral notch absent; 12) paired intergulars meeting medially as do gulars.

DISCUSSION: Gilmore gave a summary of the species of *Boremys* as follows (1935, p. 170):

"*Boremys pulchra*: Small size, front of shell broadly rounded; costal scutes wider than long. Five vertebral scutes.

"*Boremys albertensis*: Small size, front of shell bluntly pointed; costal scutes longer than wide. Five vertebral scutes. Anterior lobe of plastron shorter than posterior lobe.

"*Boremys grandis*: Large size, front of shell broadly rounded; costal scutes longer than wide. Six vertebral scutes. Anterior lobe of plastron longer than posterior lobe."

The first two "species" are found in the Oldman Formation of Alberta, whereas the

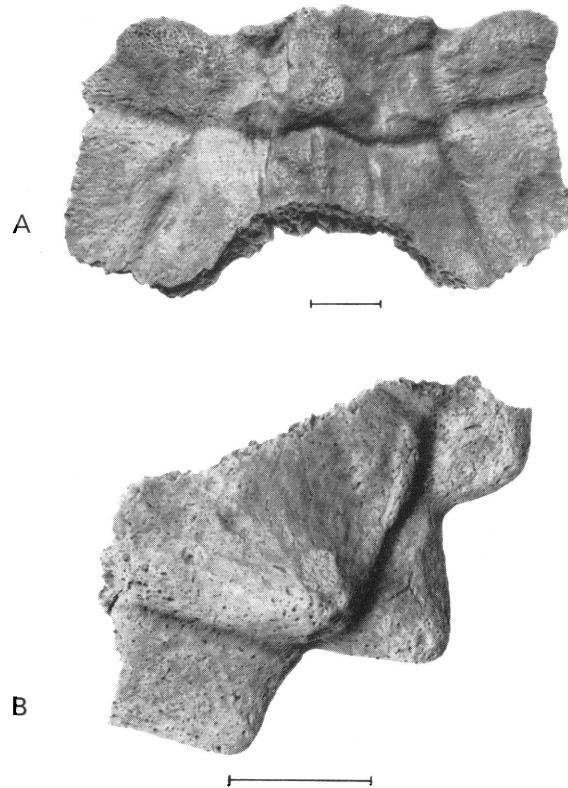


FIG. 41. *Boremys pulchra* (Lambe). Separate carapace elements of NMC 2183 from the late Cretaceous Oldman Formation of Alberta. A. Nuchal. B. Twelfth right peripheral. Scales equal 1 cm. each.

third is from the Kirtland Formation of New Mexico (Lower Shale Member). The Canadian "species" are not really distinguishable when population variability is taken into account, particularly as the available specimens include intermediates between *B. "pulchra"* and *B. "albertensis"* in the amount of rounding of the anterior shell margin.

Boremys grandis, however, may represent a valid species. The two specimens involved here are the type of *B. grandis* and a figured specimen of Wiman's (1933, pl. 1 fig. 6). Both of these shells have supramarginal scutes, as in the other specimens of *Boremys*, but they are distinctive in that the scute pattern is very irregular, particularly in Wiman's shell. As Zangerl and Johnson (1957, p. 341) have noted, "abnormalities" may become characteristic of certain species of turtles. This abnormal scute pattern

in the supramarginals might be used to define the species, but the evidence is rather limited.

Boremys pulchra (Lambe, 1906b)

Figures 40, 41

Baena pulchra LAMBE, 1906a, p. 189.

Boremys albertensis GILMORE, 1919a, p. 119.

Boremys grandis GILMORE, 1935, p. 170.

TYPE SPECIMEN: NMC 1130 (Lambe, 1902, pp. 43, 44, fig. 8, referred to *Baena hatcheri*; Lambe, 1906a, pp. 189–192, pl. 3 fig. 4, pl. 4 fig. 1; referred to *Baena pulchra*, new species; Lambe, 1906b, pp. 232–234, referred to *Boremys pulchra*, new genus), a complete plastron and partial carapace.

LOCALITY: "... Red Deer River, Alberta, near the mouth of Berry creek ..." (Lambe, 1906a, p. 189).

HORIZON: "... Belly River (Judith River) beds . . ." (*ibid.*). Oldman Formation.

COLLECTOR: L. M. Lambe, 1901.

DIAGNOSIS: Same as for genus.

HYPODIGM: USNM 8803 (Gilmore, 1919a, pp. 119–123, figs. 3, 4, pls. 33, 34, type of *Boremys albertensis*), a complete plastron and a partial carapace. Locality: "South Branch of Sand Creek, Province of Alberta, Canada" (*ibid.*). Horizon: "Belly River formation ('200 feet below the top'), Upper Cretaceous" (*ibid.*). Oldman Formation. Collector: Levi Sternberg, 1917.

USNM 12979 (Gilmore, 1935, pp. 170–173, figs. 9, 10, pl. 15, type of *B. grandis*), an almost complete shell. Locality: "SW 1/4, T. 24 N., R. 13 W., 3 miles northeast of Hunter's Store (Bisti P.O.), San Juan County, New Mexico." (*ibid.*). Horizon: "Kirtland formation, Upper Cretaceous" (*ibid.*). Lower Shale Member, Kirtland Formation. Collector: G. F. Sternberg, 1929.

Wiman, 1933, "Exemplar No. 9" of *Baena nodosa* (referred to *Boremys* by Gilmore, 1935, p. 173; figured by Wiman, pl. 1 fig. 6), a partial carapace. Locality: "'1/4 mile below' einer Stelle, die als 'South Side Alamo wash, 3 miles above Havlies Store' bezeichnet wird" (Wiman, 1933, p. 11). Horizon: "Fruitland Shales" (*ibid.*). Collector: C. H. Sternberg, 1921.

USNM 12978 (Gilmore, 1935, pp. 172, 173, figs. 9, 10, pl. 15), consists of a partial shell. Locality: "... Brimhalls Wash, San Juan County, N. Mex." (*ibid.*). Horizon: "... the Kirtland . . ." (*ibid.*). Lower Shale Member, Kirtland Formation. Collector: N. H. Boss, June 27, 1929.

NMC 1302, carapace. Locality: East side, Red Deer River (label). Horizon: Probably Oldman Formation. Collector: L. M. Lambe, August 21, 1901.

NMC 2281 (figured in Lambe, 1914, p. 14) an almost complete shell. Locality: Red Deer River, Alberta, near mouth of Berry Creek (*ibid.*, the reference says only that the specimen came from the "... type locality . . ." of the type specimen of *Boremys pulchra*). Horizon: Oldman Formation, Campanian, late Cretaceous. Collector: Charles H. Sternberg, 1913.

NMC 2183, assorted *Boremys pulchra* shell fragments, including a nuchal bone and the twelfth right peripheral bone (fig. 41). Locality: NMC locality number P 1401. A general locality

number for the C. H. Sternberg 1914 expedition which explored the following areas: sect. 6, 7 of T. 21, R. 10; and sect. 36 of T. 20, R. 11. This region is south of Red Deer River, southeast of Apple Jack ferry, and 10 miles southeast of Steeveville, Alberta, Canada. Horizon: Oldman Formation, Campanian, late Cretaceous. Collector: C. H. Sternberg, 1914.

NMC 1196, 1634, 1633 (*ibid.*, pp. 189, 190), plastron fragments. Data: same as for NMC 1130 (*ibid.*).

NMC 2235, partial shell. Data: Field no. 11–13, collected by Charles H. Sternberg, 1913.

Thescelus HAY, 1908

Baena LEIDY, 1870 (in part).

TYPE SPECIES: *Thescelus insiliens* Hay, 1908, p. 95.

KNOWN DISTRIBUTION: Late Cretaceous of New Mexico, Wyoming, and Saskatchewan.

DIAGNOSIS: 1) shell shape roughly round, sides not parallel; 2) ornamentation "an enamel-like surface, which is sculptured into raised dots and lines, the latter irregular in length and direction, with intervening pits and valleys" (Hay, 1908, p. 94); 3) nuchal scute very narrow anteroposteriorly but wide laterally, bordered by small first marginals curving around emargination; 4) anterior of carapace broadly emarginated, peripherals not meeting in front of nuchal scute; 5) preneural bone absent; 6) first vertebral rectangular, supracostal scutes present or absent; 7) supramarginal scutes absent; 8) last vertebral scute not open posteriorly, last pair of marginals meeting medially behind vertebral; last marginals rectangular; 9) posterior edge of carapace not emarginated; 10) posterior edge of carapace not scalloped; 11) xiphiplastral notch absent; 12) paired intergulars present or absent, when present meeting medially as do gulars in all cases.

DISCUSSION: See specific discussion.

Thescelus insiliens Hay, 1908

Figure 42

Thescelus rapiens HAY, 1908, p. 97.

Thescelus hemispherica GILMORE, 1935, p. 174.

Baena longicauda RUSSELL, 1934 (1935), p. 101.

TYPE SPECIMEN: AMNH 1108 (Hay, 1908, pls. 24, 25), an almost complete shell.

LOCALITY: "... Seven Mile Creek, about 5

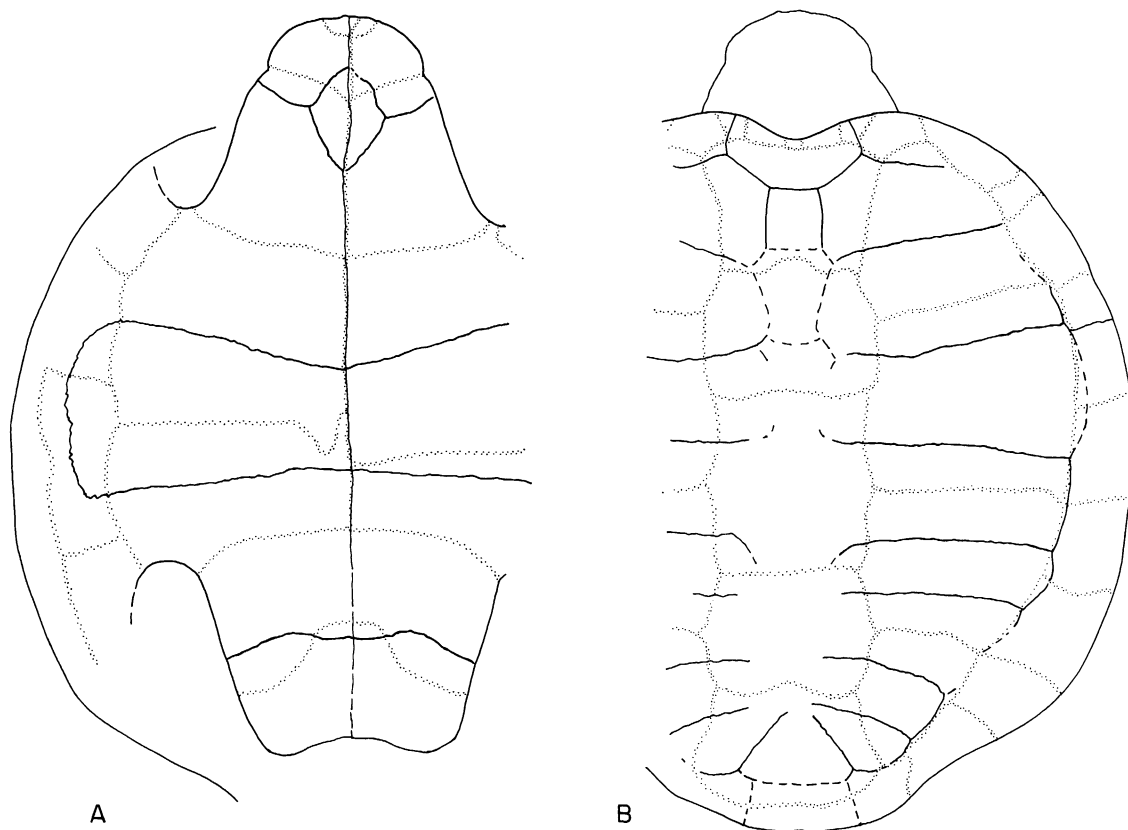


FIG. 42. *Thescelus insiliens* Hay. Restored shell based on AMNH 1108 from the late Cretaceous of Wyoming and AMNH 6606 from Kirtland Formation of New Mexico (with additions from other specimens). A. Ventral view. B. Dorsal view. Straight length of carapace on midline about 400 mm.

miles north of the Cheyenne River, and about 40 miles west of the town of Edgemont, South Dakota" (Hay, 1908, p. 95).

HORIZON: "... Laramie beds ..." (*ibid.*). Lance Formation on Wyoming Geologic Map (Love, Weitz, and Hose, 1955).

DIAGNOSIS: Same as for genus.

HYPODIGM: AMNH 6066 (type of *T. rapiens* Hay, 1908, p. 97, figs. 91, 92), partially damaged shell. Locality: "... Ojo Alamo, San Juan County, New Mexico ..." (*ibid.*). See below. Horizon: "... Laramie deposits ..." (*ibid.*). Gilmore (1916c, p. 295) stated in a footnote: "In a letter to me dated February 26, 1916, Mr. Brown says: '*Thescelus rapiens* came from the lower conglomerate just below the old Indian trading store in Ojo Alamo,' or from the Ojo Alamo sandstone. — C.W.G." In the current terminology (Baltz, Ash, and Anderson,

1966, p. D3) this would be the Naashoibito Member of the Kirtland Shale of Montana age (*ibid.*). Collector: Barnum Brown, 1904.

NMC 8678 (type of *Baena longicauda* Russell, 1934, pp. 101–104, pls. 1–3), a partial shell with limb material and caudal vertebrae. Locality: "S.E. 1/4, Sec. 23, Tp. 1, Rge. 5, W. 3rd. Merid., Morgan Creek (east branch Rocky Creek), Saskatchewan" (*ibid.*). Horizon: "Ravenscrag formation, 50 feet below coal seam; Lance equivalent" (*ibid.*). Collector: C. M. Sternberg, 1929.

Utah Field House of Natural History (Vernal, Utah) No. 230, shell. Locality: 4 miles south of Jensen, east of Green River, T. 6 S., R. 23 E., possible sections 8, 9, 14–18, Utah (data from Mrs. B. R. Untermann). Horizon: Mesa Verde Formation (*ibid.*). Collector: unknown.

USNM 12818 (type of *Thescelus hemispherica*

Gilmore, 1935, pp. 174–177, figs. 11, 12, pl. 16), an incomplete shell. Locality: “3 miles north-east of Hunter’s Store (Bisti P.O.), San Juan County, N. Mex.” (*ibid.*). Horizon: “Kirtland formation, Upper Cretaceous” (*ibid.*). This would be the Lower Shale Member of the Kirtland Formation of recent authors.

Wiman, 1933 (referred to *T. rapiens* by Wiman pp. 22–24, pl. 2 figs. 5, 5a), an incomplete shell. Locality: “South Side Alamo wash, 3 miles above Havlies Store; San Juan Co. New Mexico” (*ibid.*). Horizon: “Fruitland shales” (*ibid.*). Collector: C. H. Sternberg, 1921.

Wiman, 1933 (referred to *T. insiliens* by Wiman, pp. 24–25, pl. 2 figs. 7, 7a), partial shell. Locality: “Meyers Cr., etwa 3 miles oberhalb einer Stelle, die als ‘South Branch, Meyers Cr. about 4 miles above cattle ranch’ bezeichnet wurde. San Juan Co. New Mexico . . .” (*ibid.*). Horizon: “. . . Kirtland shales” (*ibid.*). Collector: C. H. Sternberg, 1921.

DISCUSSION: Although the Uppsala material of Wiman (1933) was not examined during the course of this work, published information provides no reliable basis for separating the New Mexico specimens specifically. Skull or vertebral material might show differences where the somewhat conservative shells do not.

The three species previously recognized are summarized as follows:

T. insiliens—posterior part of carapace constricted, no median depression along back, deep nuchal emargination.

T. rapiens—constriction of carapace not determinable, a median depression along back, nuchal not as deeply emarginated as above.

T. hemispherica—carapace without constriction, no median depression along back, nuchal not as deeply emarginated as in *T. insiliens*.

Of these characters, the median depression is probably an artifact of preservation as it is apparently not present in the other New Mexican specimens, the relative deepness of the emargination could easily be a population variable, and the carapace constriction could either be a variation or due to preservation. All the authors describing *Thescelus* reported a wide variety of sculpture patterns that do not seem correlated with other features or to distribution. Examination of the Uppsala specimens might help, but this is not likely.

The assignment of “*Baena*” *longicauda* Russell 1934, to *Thescelus* is due to further preparation of the specimen since its original description. The specimen has been reconstructed with a series of fragments that include parts of the nuchal, first right peripheral, and first neural. These pieces are fitted into a plaster restoration of the specimen and do not articulate with the figured portion of the shell. However, the pieces do certainly belong to *Thescelus* as they have the nuchal emargination and extremely thin nuchal scute. Russell (1934 [1935], p. 102) mentioned “a fragment from the right anterior margin of the carapace . . .” This probably refers to the pieces in question, which indicates that the pieces were originally associated with the specimen. The presence of marginal scutes closing off the last vertebral posteriorly would be sufficient to demonstrate the lack of affinity with the form-genus “*Baena*,” even if the recently added pieces were lacking.

The extremely long tail of this form combined with the emarginated nuchal region cause some wonder at what these adaptations might be for. The Recent genus *Platysternon* has a very long tail and has been observed using it as a balance when climbing.

CRETACEOUS SPECIES BASED ON SHELLS PREVIOUSLY REFERRED TO THE GENUS *BAENA*

Analysis of the available specimens of what is probably a single species of *Baena arenosa* (Bridger Formation, Wyoming), demonstrates that a considerable amount of variation is present in the shell morphology. A species that is sympatric with *Baena arenosa*, *Chisternon undatum*, has a quite distinct skull morphology but the shell morphology is very similar to *Baena*. If the

skulls of these two species were unknown, it would be very difficult to distinguish these taxa. A similar situation exists in the Cretaceous. A large number of shells are known which are as variable as are the Eocene shells of *Baena arenosa* and *Chisternon undatum*, but in this case there are very few (two specimens of *Plesiobaena antiqua*) associated skulls to aid in the deter-

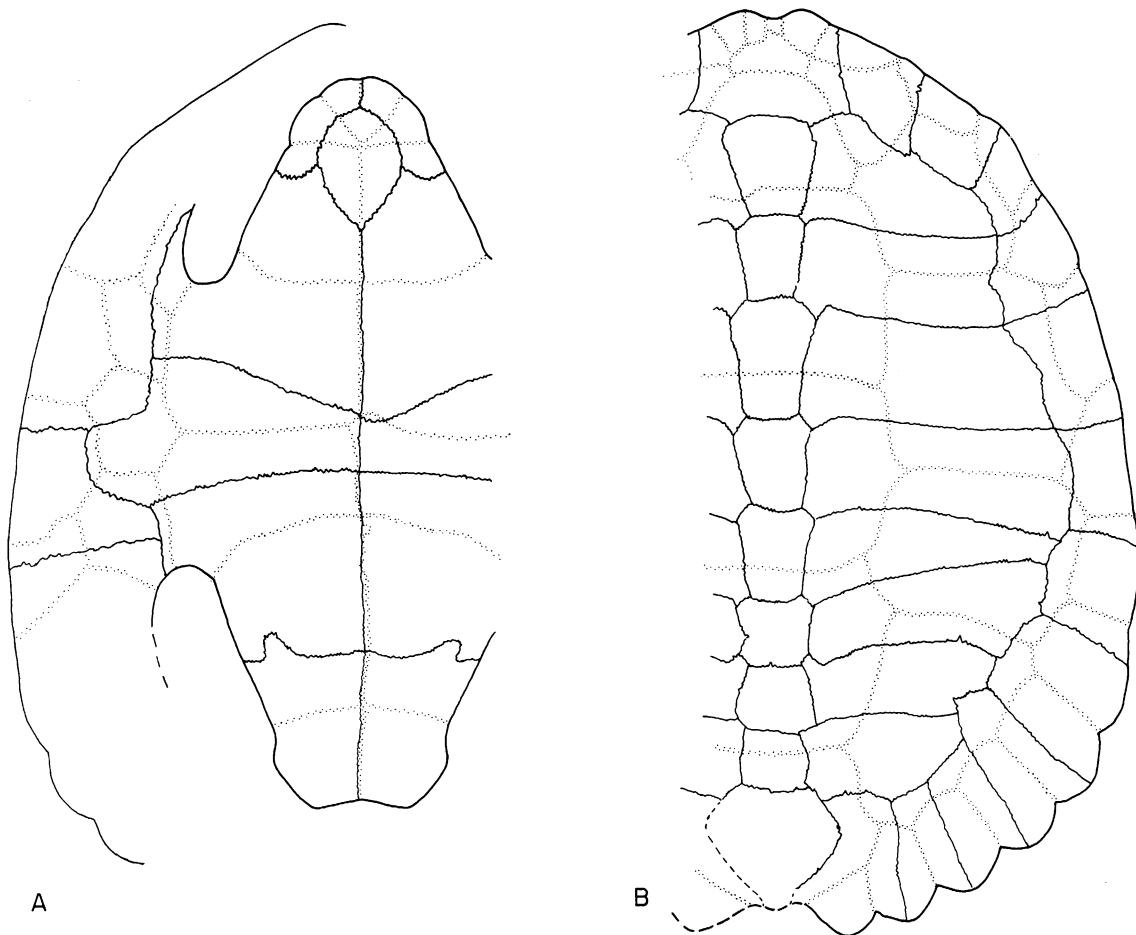


FIG. 43. Generically indeterminate shell, the type of "*Baena*" *hatcheri* Hay, CM 115, from the late Cretaceous Lance Formation of Wyoming, partially restored. Estimated total length of carapace 368 mm. After Hay, 1908, and specimen.

mination of taxa. The rather considerable geographic and geologic range of the Cretaceous shells suggests that more than one species is present, but there are no consistently correlated morphologic characters. However, instead of placing all of these forms into one species based on morphology, I am considering them indeterminate. The described nominal species are discussed and summarized below. It is likely that forms such as *Eubaena* and *Stygiochelys*, which are known only from skulls, will be eventually associated with one or more of the "shell taxa" listed below. It is hoped that this discussion will aid in such association.

Characters of form-genus "*Baena*" (fig. 43):

1) shell shape variable, usually oval or pointed anteriorly; 2) ornamentation highly varied, from smooth to nodular and ridged; rarely tuberculated or pitted; 3) nuchal scute small, highly variable, sometimes more than one; 4) nuchal not emarginated anteriorly; peripherals not meeting medially in front of nuchal; 5) preneural bone absent; 6) first vertebral scute possibly rectangular with no supracostal scutes present laterally; or subtriangular (four-sided but anterior dimension much less than posterior) with paired, lateral supracostal scutes; 7) supramarginal scutes absent; 8) last vertebral scute opening widely posteriorly on edge of carapace, last marginal scutes usually

triangular; 9) posterior edge of carapace emarginated; 10) posterior edge of carapace scalloped, varying from shallow scallops to very pronounced scallops; 11) xiphiplastral notch absent; 12) paired intergulars usually present, intergulars and gulars usually meeting in midline but possibly varying considerably.

"Baena" hatcheri Hay, 1901

Figure 43

TYPE SPECIMEN: CM 115 (Hay, 1901, pp. 325, 326, pl. 15; 1908, pp. 63, 64, figs. 40, 41, pls. 9, 10) an almost complete shell, crushed laterally.

LOCALITY: "... a sandstone bluff on the south side of Lance Creek, opposite the mouth of Dolgie Creek" (Hay, 1908, p. 63) Converse County, Wyoming, now Niobrara County. In the Lance Creek area (Clemens, 1963, map in pocket) there is no "Dolgie" Creek but there is a Dogie Creek. The mouth of Dogie Creek is well within the area of the Lance Formation.

HORIZON: "... *Ceratops* beds of the Laramie formation . . ." (Hay, 1908, p. 63). The Lance Formation of current usage (Clemens, 1963).

COLLECTOR: J. B. Hatcher, 1901.

DIAGNOSIS: None given by Hay who distinguished this species in his key (1908, p. 60) as follows: "Length of anterior lobe 0.92, its width 1.00, of width of bridge, width of hinder lobe 1.04 of width of bridge." It is distinguished by Hay from *B. marshi* by these criteria and it is distinguished from all other species of *Baena* by the horizon, "Laramie."

"Baena" marshi Hay, 1904

TYPE SPECIMEN: YPM 299 (Hay, 1904, pp. 261-263, fig. 1, pl. 11; 1908, pp. 62, 63, fig. 39, pl. 8 fig. 2), Hay mentioned but did not figure carapace elements, but the type currently consists only of the plastron.

LOCALITY: "... Converse County, Wyoming, between Buck and Lance creeks" (Hay, 1904, p. 261).

HORIZON: "... Laramie deposits . . ." (*ibid.*) Although the Fox Hills Sandstone and the Pierre Shale crop out in this area, it is most likely that the specimen came from the Lance Formation. The level was probably somewhat lower in the section than the locality for the type of "*B.*" *hatcheri*.

DIAGNOSIS: "This species differs from *B.*

hatcheri in the greater thickness of the bones of the carapace and in the shorter lobes of the plastron" (Hay, 1904, p. 263). "This species appears to differ from *Baena hatcheri* in the smaller plastron, the longer bridge, and in the greater thickness of the bones of the carapace, especially of the dorsal region" (Hay, 1908, p. 63).

"Baena" callosa Hay, 1905b

TYPE SPECIMEN: CM 330 (Hay, 1905b, p. 178, figs. 1, 2, pl. 9), a partial shell.

LOCALITY: "... Willow Creek, Montana" (*ibid.*).

HORIZON: "... Judith River beds . . ." (*ibid.*).

COLLECTOR: J. B. Hatcher, 1903.

DIAGNOSIS: "It is seen that *B. hatcheri* has, relatively to the width of the bridge, large anterior and posterior lobes; that *B. marshi* has both lobes small; and that *B. callosa* has the anterior lobe short and of moderate width, while the hinder lobe is broad at the base" (*ibid.*, p. 182).

"Baena" hayi Gilmore, 1916b

TYPE SPECIMEN: USNM 6728 (Gilmore, 1916a, pls. 32, 33), a carapace and plastron.

LOCALITY: "Lance Creek, Niobrara County (formerly a part of Converse County), Wyoming." (Gilmore, 1916b, p. 641).

HORIZON: "Lance formation, Upper Cretaceous or Lower Tertiary." The Lance Formation is currently assigned to the Upper Cretaceous although its age was disputed in Gilmore's day (see Clemens, 1963, pp. 9-16 for a discussion of this unit).

COLLECTOR: "... by the late J. B. Hatcher in the Lance formation of Wyoming, for the United States Geological Survey . . ." (Gilmore, 1916b, p. 641).

DIAGNOSIS: "*Baena hayi* is distinguished at once from all other species of the genus by the proportion of the carapace, it being the only one known in which the width exceeds the breadth. From *B. marshi* this species may be distinguished by having a sculptured carapace, and the wider marginal areas on the ventral surface. From *B. hatcheri* it differs in the contour of the shell, being short and truncated at both ends, whereas *B. hatcheri* is relatively long, with a somewhat pointed anterior end. The absence of supernumerary scutes lateral to the first vertebral

also serves further to distinguish it from the latter species" (Gilmore, 1916b, p. 643).

"Baena" nodosa Gilmore, 1916b

TYPE SPECIMEN: USNM 8345 (Gilmore, 1916c, figs. 34, 35, pl. 76), an almost complete shell.

LOCALITY: "Two miles northwest of Ojo Alamo store, San Juan County, N. Mexico. (See locality 60, section F. Pl. LXIV.)" (Gilmore, 1916c, p. 293).

HORIZON: "Kirtland shale" (*ibid.*). The upper part of the Naashoibito Member of the Kirtland Formation.

COLLECTOR: J. B. Reeside, Jr., and John Brittain, September 8, 1915.

DIAGNOSIS: "This species is distinguished from all others in the rough, node-like ornamentation of the carapace, in the triangular shape of the shell, and in having the greatest breadth posterior to the inguinal notches" (*ibid.*).

KNOWN DISTRIBUTION: San Juan Basin, New Mexico. Kirtland Formation, both upper and lower members, possibly Fruitland Formation. Although five specimens have been reported from the Fruitland, none of these has been substantiated by locality data.

Specimens identified by Wiman (1933) as *"Baena" nodosa*. These specimens were collected by C. H. Sternberg in 1921 in the San Juan Basin, New Mexico.

"Exemplar No. 1," an almost complete shell with pelvis (Wiman, 1933, p. 4, figs. 1-3, pl. 1 figs. 1, 1a). Locality: "Head S. Branch Meyers Cr., 3 miles west Kimbeto Trading Post" Horizon: "Unsicher, ob Fruitland oder Kirtland." Upper part of Kirtland Formation, undifferentiated, east of easternmost outcrop of Farmington Sandstone Member.

"Exemplar No. 2," an almost complete shell (pl. 1 figs. 2, 2a). Locality: "Below second conglomerate, 1 mile above Barrel Springs, 2 1/2 miles S. Trading Post . . . Barrel Springs Wash 3 miles NE old Trading Post." Horizon: "Kirtland shales." Could be anywhere in the Kirtland Formation, as currently conceived.

"Exemplar No. 3, 11, 12," partial shells (*ibid.*, pl. 1 figs. 3, 3a). Locality: "Von einem Lager am sudlichen Ast des Meyers Cr. etwa 4 miles oberhalb der Cattle Ranch aus gesammelt" (*ibid.*, p. 8). Horizon: "Kirtland shales," Probably correct.

"Exemplar No. 4," partial shell (*ibid.*, pl. 1 figs. 4, 4a). Locality: "'South Side Alamo wash, 3 miles above Havlies Store'" (*ibid.*, p. 10). Horizon: "Fruitland shales" (*ibid.*).

"Exemplar 6 and 8," partial shells. Locality: "'Barrel Spring, 2 1/2 miles S. Trading Post'" (*ibid.*, p. 11). Horizon: "Kirtland shales" (*ibid.*).

"Exemplar 10, 15, 16," partial shells (*ibid.*, pl. 1 figs. 7, 7a). Locality: "'1/4 mile below einer Stelle, die als 'South Side Alamo wash. 3 miles above Havlies Store' bezeichnet wird'" (*ibid.*). Horizon: "Fruitland shales" (*ibid.*).

"Exemplar 5, 7, 13, 14," partial shells (pl. 1 figs. 5, 10). No data.

The following specimens are reported in Gilmore, 1919b, p. 24, and were collected in 1916 by J. B. Reeside, Jr:

USNM 8603, shell. Locality: About 2 miles south of west of Kimbetoh, sect. 3, T. 22 N., R. 10 W., San Juan County, New Mexico. Horizon: 300 feet above the base of the Kirtland Formation.

USNM 8622, shell. Locality: About 5 miles south of Kimbetoh, sect. 26, T. 22 N., R. 10 W., San Juan County, New Mexico. Horizon: 50 feet above the base of the Fruitland Formation.

The following specimens are reported in Gilmore, 1935, p. 169:

USNM 12819, shell. Locality: ". . . 3 miles northeast of Hunter's Store, San Juan County, N. Mex. . . ." Horizon: Lower Shale Member, Kirtland Formation. Collector: G. F. Sternberg.

USNM 11327, an almost complete shell. Locality: "Coal Creek, 3 miles southeast of Tsaya, San Juan County, N. Mex." Horizon: ". . . Fruitland formation." Tsaya is no where within 3 miles of Coal Creek or of an exposure of the Fruitland, although it comes close in the northeast. Coal Creek does run through exposures of the Fruitland Formation and it is possible that the location of Tsaya has changed. The horizon should be accepted with reservations.

"Baena" ornata Gilmore, 1935

TYPE SPECIMEN: USNM 13229 (Gilmore, 1935, p. 165, figs. 7, 8, pl. 14), carapace and plastron.

LOCALITY: "3 miles northeast of Hunter's Store (Bisti P.O.), SW 1/4, T. 24 N., R. 13 W., San Juan County, N. Mex." (Gilmore, 1935, p. 165).

HORIZON: "Kirtland formation, Upper Cretaceous" (*ibid.*).

COLLECTOR: "... G. F. Sternberg, June 20, 1929" (*ibid.*).

DIAGNOSIS: "... the ornate sculpture of *Baena ornata* at once distinguishes this species from all described forms, with the possible exception of *B. nodosa*. From that species it may be distinguished by the more quadrangular form of the shell; greatest transverse diameter at mid-length; quadrangular shape of first vertebral and the absence of accessory scutes lateral to the first vertebral; and in having all the vertebrae wider than long" (*ibid.*, p. 168).

Other specimens identified as "*Baena*" *ornata* by Gilmore (1935, p. 168):

USNM 11083, shell. Locality: "'wash south of Ojo Alamo Wash,' 9 miles northeast of Tsaya, San Juan County, N. Mex." Horizon: "... Kirtland formation ..." Lower Shale Member, Kirtland Formation. Collector: C. H. Sternberg, 1923.

USNM 12821, shell. Locality: "... SW 1/4, T. 24 N., R. 13 W., 3 miles northeast of Hunter's Store, San Juan County, N. Mex. ..." Horizon. Lower Shale Member, Kirtland Formation. Collector: C. W. Gilmore, 1929.

PHYLOGENY OF THE BAENIDAE

DISTRIBUTION OF PRIMITIVE AND DERIVED CHARACTERS

THE MOST PRIMITIVE MEMBER of the Baenoidea is *Glyptops plicatulus*, represented by an almost complete skeleton and two skulls from the late Jurassic of North America. *Glyptops* possesses the following characters which are primitive for the Baenoidea and probably primitive for the Cryptodira:

- 1) Very narrow triturating surfaces on upper and lower jaws; no expansions along posterior half.
- 2) CAVUM TYMPANI widely open posteriorly.
- 3) Pterygoid not completely flooring CAVUM ACUSTICO-JUGULARE.
- 4) Basisphenoid extending length of pterygoids and completely separating them.
- 5) Prefrontal present on skull roof as small lappet extending above orbital margin.
- 6) Nasals, frontals, and parietals are only median skull elements, and lack lateral expansions.

The following features of *Glyptops* are primitive for the Baenoidea but probably advanced or derived with respect to the rest of the Cryptodira:

- 1) Elongate skull with short preorbital length and long postorbital length.
- 2) FORAMEN POSTERIOR CANALIS CAROTICI INTERNI situated midway along basisphenoid-ptyerygoid suture.

Trinitichelys hiatti, from the Albian of Texas has certain primitive baenoid characters that are held in common with *Glyptops*:

- 1) Skull length less than skull width.
- 2) Cranial emargination only slightly developed.
- 3) Median skull elements relatively unexpanded laterally.

The following features of *Trinitichelys* are derived or advanced with respect to *Glyptops*:

- 1) Prefrontal reduced on skull roof surface.
- 2) Triturating surface expanded posteriorly with anteromedial ridge on lingual edge.
- 3) CAVUM TYMPANI fully completed posteriorly as in later forms.
- 4) INCISURA COLUMELLAE AURIS almost enclosing stapes and eustachian tube.
- 5) Pterygoid completely flooring CAVUM ACUSTICO-JUGULARE.

- 6) Limits of basisphenoid not entirely determinable but apparently shorter than in *Glyptops*.
- 7) Postorbital length diminished.
- 8) Jugal entering orbital margin.

Hayemys latifrons, from the late Cretaceous of Wyoming, shares the following derived characters with *Trinitichelys*:

- 1) CAVUM TYMPANI fully completed posteriorly.
- 2) INCISURA COLUMELLAE AURIS almost enclosing stapes and eustachian tube.
- 3) Pterygoid completely flooring CAVUM ACUSTICO-JUGULARE.
- 4) Basisphenoid shorter than in *Glyptops*.
- 5) Postorbital length diminished.
- 6) Jugal entering orbital margin (condition of triturating surfaces indeterminate).

Hayemys has the following features that are derived or advanced in comparison with *Trinitichelys*:

- 1) Dorsal plate of prefrontal expanded on skull roof.
- 2) Frontals widely expanded laterally and posteriorly, more so than in any other baenoid.
- 3) Temporal emargination plus expanded postorbital separates squamosal from parietal.
- 4) Skull wedge-shaped in dorsal view, width equal or greater than length.
- 5) Temporal emargination reaching greatest extent in any baenoid, cheek emargination well developed.
- 6) Quadratojugal lacking anterior expansion seen in *Trinitichelys*.

Numbers 1 to 3 of these characters are unique for *Hayemys*, whereas the rest are held in common with the Eubaeninae.

The three genera *Eubaena*, *Plesiobaena*, and *Stygiochelys* are here considered to constitute a subfamily, the Eubaeninae. When compared with *Trinitichelys*, it can be seen that this group possesses the following derived characters:

- 1) Skull wedge-shaped in dorsal view, width equal or greater than length.
- 2) Temporal emargination reaching greatest

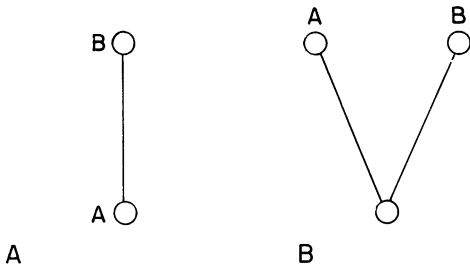


FIG. 44. A. Direct ancestor-descendant relationship between species A and B. B. Relationship by common ancestry. See text for discussion.

extent of any baenoid, cheek emargination well developed.

- 3) Extreme temporal emargination widely separating squamosal from parietal, whereas in *Trinitichelys* squamosal just touches parietal.
- 4) Quadratojugal lacking anterior expansion seen in *Trinitichelys*.

Within this group, *Eubaena* and *Stygiocelys* are united by the possession of uniquely specialized

tritulating surfaces. The surfaces are expanded medially, lacking the lingual ridge, and are broadly concave downward. *Plesiobaena*, on the other hand, retains the more primitive tritulating surface seen in *Trinitichelys*, where a moderate expansion is present posteriorly, and a medial lingual ridge is present anteriorly.

Baena and *Chisternon* have the wedge-shaped, short-snouted skull of the Eubaeninae and the basic morphology of the tritulating surface found in *Plesiobaena* and *Trinitichelys*. The Baeninae and Eubaeninae both possess a derived temporal roof condition in comparison with *Hayemys* and *Trinitichelys*, that is, the frontals are shortened relative to the parietals, and the parietals are expanded laterally. This evidence is the basis of the statement that the Eubaeninae and Baeninae have a common ancestor not shared with other baenids (*Palatobaena* is a probable exception).

When compared with the other Baenidae, *Baena* and *Chisternon* are seen to form a group sharing these specialized or derived characters:

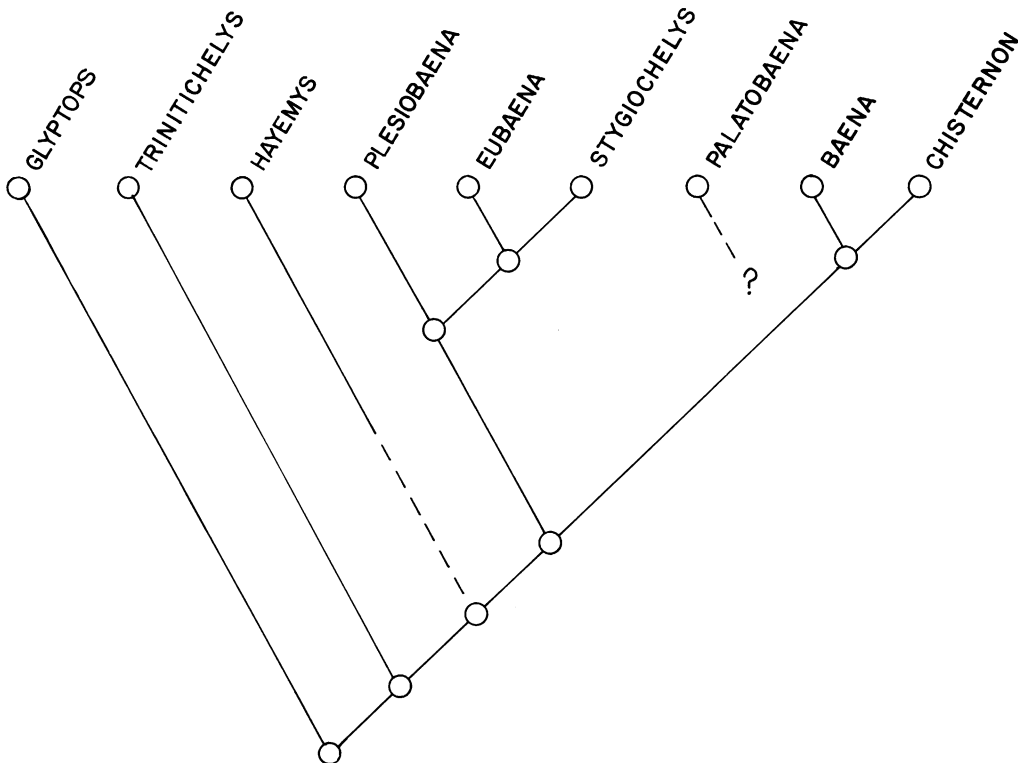


FIG. 45. Relationships of North American genera of baenoid turtles. Diagram indicates only relative position of common ancestors. Other temporal, morphological, and adaptational parameters not expressed.

- 1) Temporal emargination nearly obliterated.
- 2) Squamosal secondarily in contact with anteriorly and laterally enlarged parietal.
- 3) Jugal widely entering orbital margin compared with the other Baenidae.
- 4) Quadratojugal not C-shaped, as in the other Baenidae, lacking dorsal extension present in the Eubaeninae.

Palatobaena from the late Cretaceous and Paleocene of Montana and Wyoming, is difficult to compare with the other baenids. The feeding mechanism in this form is highly modified with respect to other baenids and has involved extensive changes in the skull. Poor preservation of the cheek region in the known specimens precludes comparison of this region. *Palatobaena* has the following derived characters in common with other baenids:

- 1) Skull width equal or greater than length.
- 2) Temporal emargination present but probably not well developed as in the eubaenines.
- 3) Prefrontal lacking extensive dorsal exposure on skull roof.
- 4) Parietals expanded anteriorly and laterally (posteriormost limit not known, however) compared with *Hayemys*.
- 5) Nasals apparently fused to frontals and modified into anterior lip.

Characters 1, 3, and 4 are held in common with the Eubaeninae and the Baeninae, 2 is held in common with the Baeninae only and 5 is held in common only with the genus *Baena*. However, the characters in common with *Baena* and the Baeninae differ in detailed morphology and I doubt their homology. At any rate, the best estimate of relationship is with the Baeninae.

INTERPRETATION OF RELATIONSHIPS

Degree of relationship is here considered to mean the relative position of a common ancestor. The determination of common ancestry is best based on the sharing of derived characters, a technique recently expounded by Hennig (1966) and Brundin (1966, 1968). Figure 45 represents the relationships of the nine baenoid genera based on shared derived characters. This figure illustrates the relative position of common ancestors with respect to themselves and the nine genera under discussion. Neither time nor degree of morphological "distance" is taken into consideration in constructing the diagram.

On the basis of current evolutionary theory, two types of relationships can exist. Two species may be related either by common ancestry (fig. 44B) or they can be ancestor and descendant (fig. 44A). The first type (fig. 44B) is more easily tested by available criteria (i.e., morphology), whereas the second is operationally untestable. For the strictly logical procedure of erecting a set of relationships based on the most logically valid criteria, the hypothesis of common ancestry is more meaningful. For example, it can be argued that *Glyptops* and the Baenidae share a common ancestor not shared with any other known turtles. This statement can be objectively tested by comparison with all other turtles. On the other hand, the hypothesis that *Glyptops* is ancestral to the Baenidae

cannot be tested as objectively as the previous hypothesis. The former method of determining relationships is a somewhat more noncircular basis for further anatomic, ecologic, and stratigraphic studies.

The phylogeny in figure 46 is presented as an outgrowth of the above-determined set of relationships. It is hypothetical in that the ancestor-descendant relationship suggested for *Glyptops* and *Trinitichelys* is speculative and cannot be tested in a reasonable way. However, the addition of stratigraphic information to the previously determined set of relationships results in a more accurate history of the group. Although this hypothetical phylogeny is one of several equally valid ones based on the relationships expressed in figure 45, I believe that it is preferable for the following reasons:

- 1) I have been unable to recognize any unique derived characters in either *Glyptops plicatulus* or *Trinitichelys hiatti*.
- 2) There is no direct evidence of the existence of two separate lineages, one ancestral to *Glyptops* and one to *Trinitichelys*.
- 3) Stratigraphic data is consistent with this hypothesis, that is, *Trinitichelys* occurs later in time than *Glyptops*.

It should be emphasized again that the above statements do not constitute a telling argument for preferring one hypothesis above several that are equally valid. Any of these statements could be refuted by the discovery of new fossils.

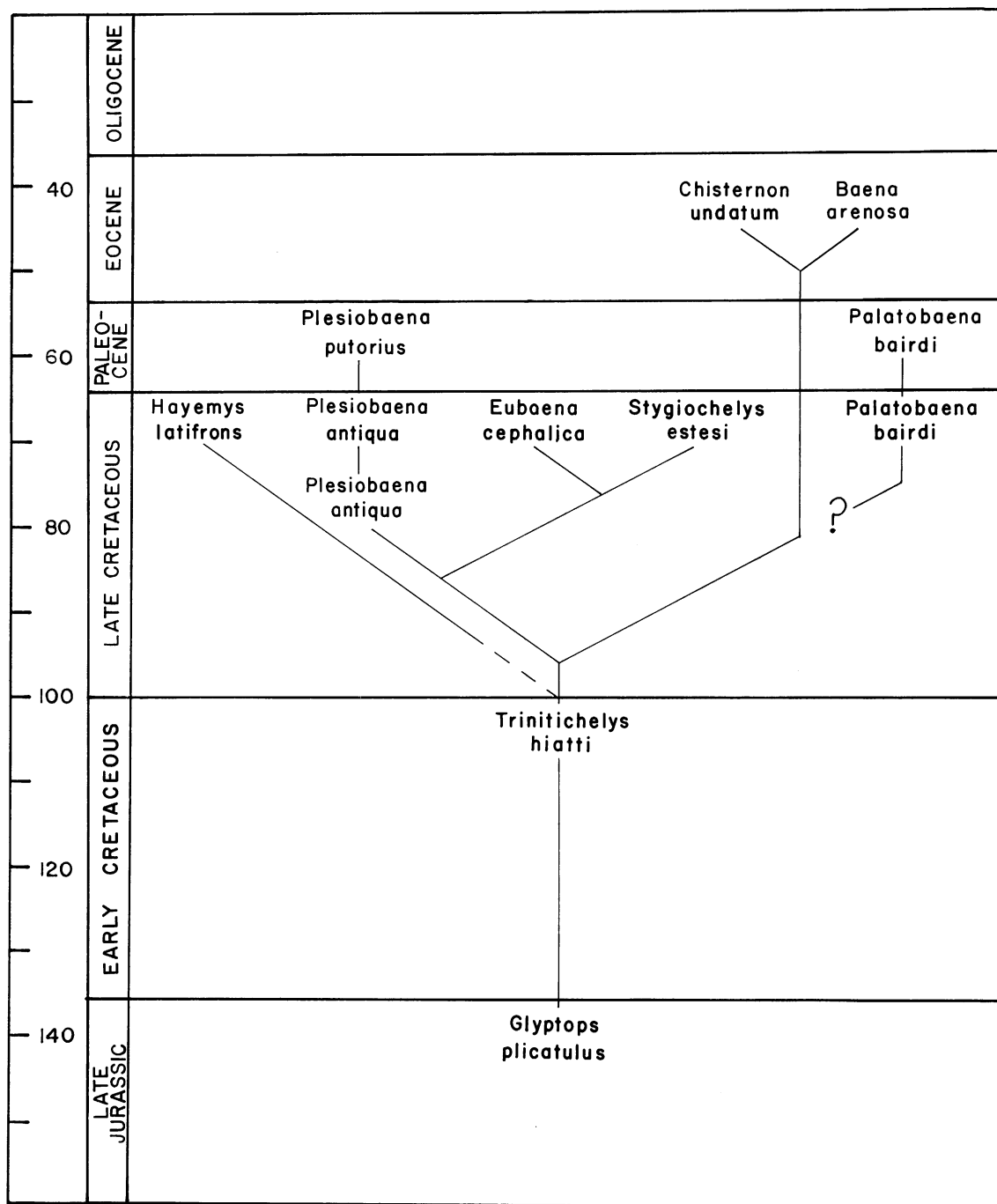


FIG. 46. Hypothetical phylogeny of North American baenoid turtles. Scale at left is in millions of years before the present.

CLASSIFICATION

The basis of a classification has been the subject of many papers and studies. I do not intend to examine them all, but I would like to present a strictly phylogenetic classification, such as that favored by Hennig (1966), as well as the one which I favor here, based on "practical" but semi-arbitrary criteria.

A strictly phylogenetic classification would completely reflect the relationships expressed in figure 45 and would be as follows:

- Superfamily Baenoidea
 - Family Glyptopsidae
 - Glyptops plicatulus*
 - Family Baenidae
 - Subfamily Trinitichelyinae
 - Trinitichelys hiatti*
 - Subfamily Baeninae
 - Infrafamily Hayemodd¹
 - Hayemys latifrons*
 - Infrafamily Baenodd

- Tribe Eubaenini
 - Subtribe Plesiobaenina
 - Plesiobaena antiqua*
 - Plesiobaena putorius*
 - Subtribe Eubaenina
 - Eubaena cephalica*
 - Stygiochelys estesi*
- Tribe Baenini
 - Baena arenosa*
 - Chisternon undatum*
- Incertae sedis*: *Palatobaena bairdi*

There have been a number of criticisms of this method of classification (Bock, 1968; Mayr, 1969; Darlington, 1970), and I do not intend to review them here. At the present time I prefer to use a classification of the sort advocated by Mayr (1969). As other individuals may not wish to use my "semi-arbitrary" or adaptational classification, they may find my strictly phylogenetic one more valuable.

SPECULATIONS ON THE RELATIONSHIPS OF GENERA KNOWN ONLY FROM SHELLS

The baenoid phylogeny and classification are based, for the most part, on skull morphology simply because more information is available from the skull than from the shell. Genera based only on shell material cannot be included in this classification with any degree of precision. Most of the difficulty arises because there are not enough associated shells for the skulls that are known. Still, some speculations can be made about the possible relationships of these genera.

The genera based on shells are as follows: *Neurankylus*, *Compsemys*, *Thescelus*, and *Boremys*. Of these forms, only *Compsemys* persisted into the Tertiary. One of the changes that does seem to take place in the baenid shell is the development of the "Baena" shell pattern in which the posterior edge of the shell is emarginated and the last vertebral scute is not enclosed posteriorly by the meeting of the last pair of marginal scutes. This condition is present in *Boremys* but not in the other three shell genera. In fact, *Boremys* differs from the "Baena" shell

pattern only in the possession of supramarginal scutes. The other three shells fit the pattern of *Glyptops* and *Trinitichelys*. *Trinitichelys* and *Neurankylus* are extremely similar in shell pattern and are separated primarily because of ignorance at the present time (see discussions under these genera in the systematics section). *Thescelus* differs from *Neurankylus* by the emarginated nuchal area. *Compsemys* differs from *Neurankylus* more than the other forms do, and it is placed in the Baenidae on the basis of medially meeting mesoplastra—a rather weak character on which to found relationships.

Neurankylus, then, might be expected to have a skull similar to *Trinitichelys*. However, of the Cretaceous forms the skull that is closest to *Trinitichelys* is that of *Plesiobaena*, which is known to have a shell of the "Baena" pattern. *Hayemys* has certain features that are more similar to *Glyptops* than to the Baenidae and if *Hayemys* did evolve separately from the *Trinitichelys* line, then it might have a shell that was very similar to *Glyptops*. *Neurankylus*, under this suggestion, might be the shell of *Hayemys*. Unfortunately, there are no other indications of this. The only

¹ Infra-families lack standardized endings and I have arbitrarily used the ending *odd*.

known skull of *Hayemys* is from an area that is not known to have produced any shells of *Neurankylus*. Furthermore, the Hell Creek Formation (Bug Creek Anthills locality) has yielded no cranial material that could be identified as belonging to *Hayemys*, although the same formation has yielded *Neurankylus* shell material.

Thescelus and *Palatobaena* may be the same. The modifications of *Thescelus*, although they are not known in living turtles, are consistent with a bottom living habitat as suggested by Hay (1908, p. 95). The emarginated nuchal of *Thescelus* and the dorsally directed orbits of

Palatobaena may be part of the same adaptation to a bottom environment. *Palatobaena* is found in the Hell Creek and *Thescelus* is from the Lance, but *Palatobaena* also extends into the Paleocene, whereas no shells of *Thescelus* have been reported.

Boremys, because of its close resemblance to the "*Baena*" shell pattern, is presumably closely related to *Plesiobaena*. Still, this is not very good evidence, as *Baena* and *Plesiobaena* have very similar shells but quite different skulls.

These statements are speculations. *Neurankylus*, *Boremys*, and *Thescelus* are probably Baenidae, but any more precise relations with other forms are speculative.

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FIG. 47. *Trinitichelys hiatti*, new genus and new species. Ventral stereophotograph of type specimen, MCZ 4070, from the early Cretaceous Trinity Formation of Texas. See also figure 2A. Fragments of hyoid apparatus in posterior area. Condyle-premaxilla length 55 mm.

FIG. 48. *Hayemys latifrons* (Hay), new genus. Ventral stereophotograph of type specimen, AMNH 6139, from the late Cretaceous Hell Creek Formation of Wyoming. See also figure 7. Approximate condyle-premaxilla length 73 mm.

FIG. 49. *Plesiobaena antiqua* (Lambe), new genus. Ventral stereophotograph of UMMP 20490 from the late Cretaceous Hell Creek Formation of Montana. Portion of left jaw ramus and hyoid apparatus present. See also figure 9. Condyle-premaxilla length 48 mm.

Fig.47

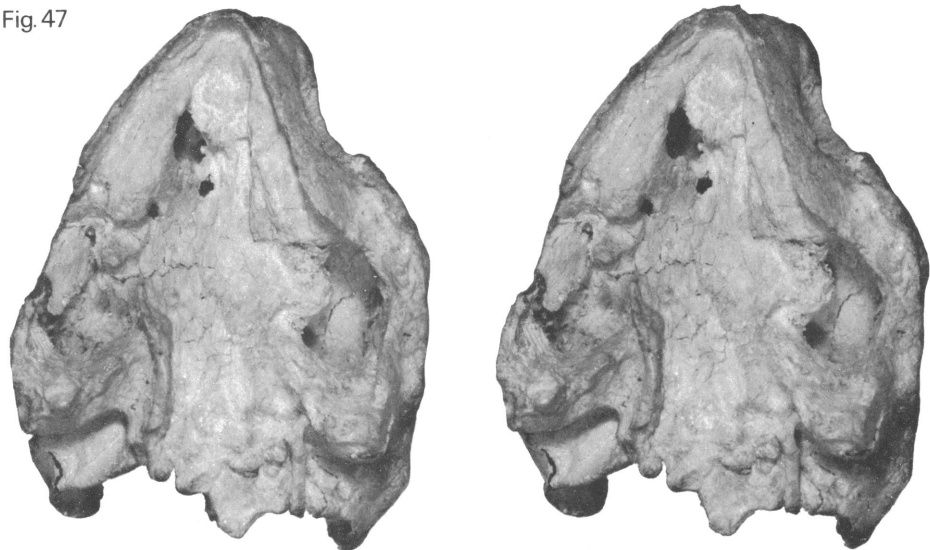


Fig.48

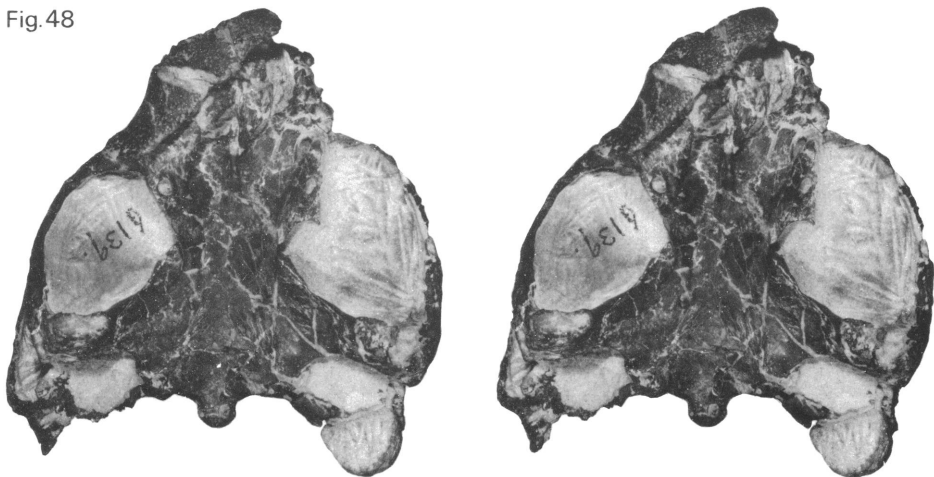


Fig.49



FIG. 50. *Plesiobaena putorius*, new genus and new species. Ventral stereophotograph of PU 20600 from the Paleocene Fort Union Formation of Wyoming. See figure 15 for restoration and figure 17 for scale.

FIG. 51. *Palatobaena bairdi*, new genus and new species. Ventral stereophotograph of type specimen, PU 16839, from Paleocene Fort Union Formation of Wyoming. See figure 24 for dorsal view and figure 23 for restoration. Estimated condyle-premaxilla length 54 mm.

FIG. 52. *Baena arenosa* Leidy. Ventral stereophotograph of CM 2956 from the Eocene Uinta Formation of Utah. See also figures 27, 53, 54. Condyle-premaxilla length 73 mm.

Fig. 50



Fig. 51



Fig. 52

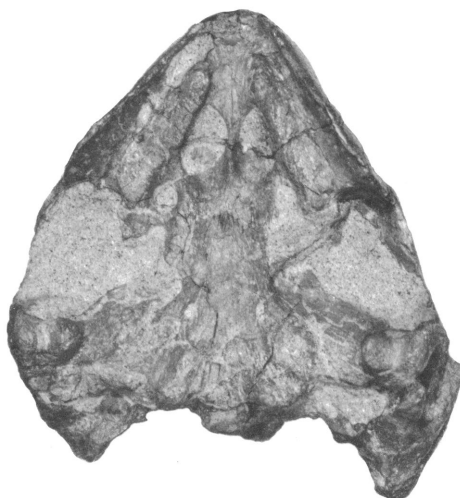
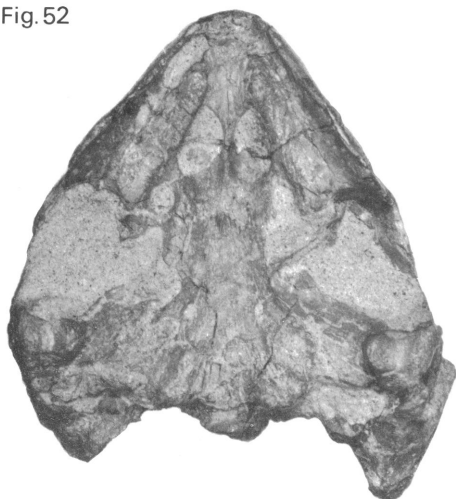


FIG. 53. *Baena arenosa* Leidy. Ventral stereophotograph of AMNH 5971 from the Eocene Bridger Formation of Wyoming. See figures 27, 28, 52, and 54. Estimated condyle-premaxilla length 64 mm.

FIG. 54. *Baena arenosa* Leidy. Ventral stereophotograph of USNM 17998 from the Eocene Bridger Formation of Wyoming. See also figures 27, 52, 53. Estimated condyle-premaxilla length 65 mm.

FIG. 55. *Chisternon undatum* (Leidy). Ventral stereophotograph of AMNH 5961 from the Eocene Bridger Formation of Wyoming. See also figure 35. Condyle-premaxilla length about 68 mm.

Fig. 53

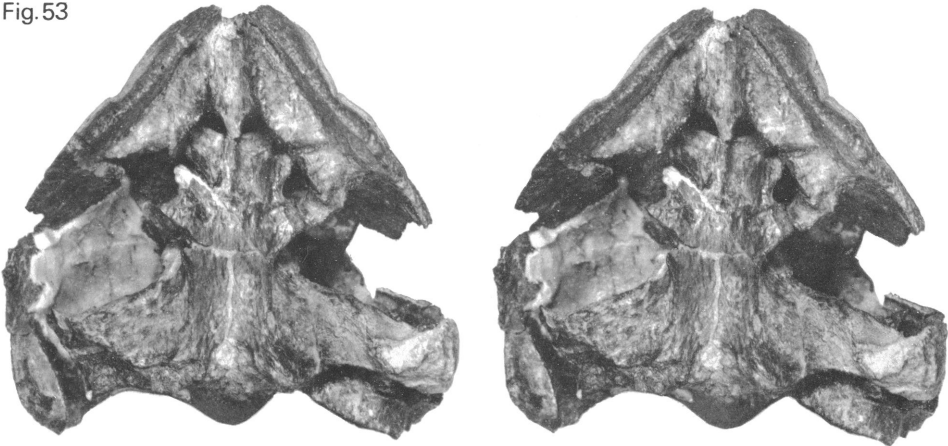


Fig. 54

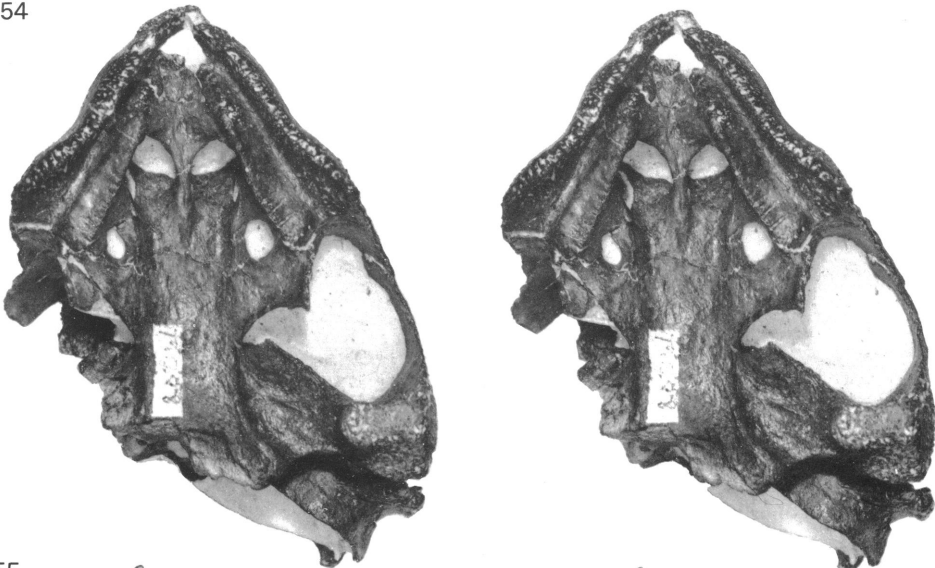


Fig. 55

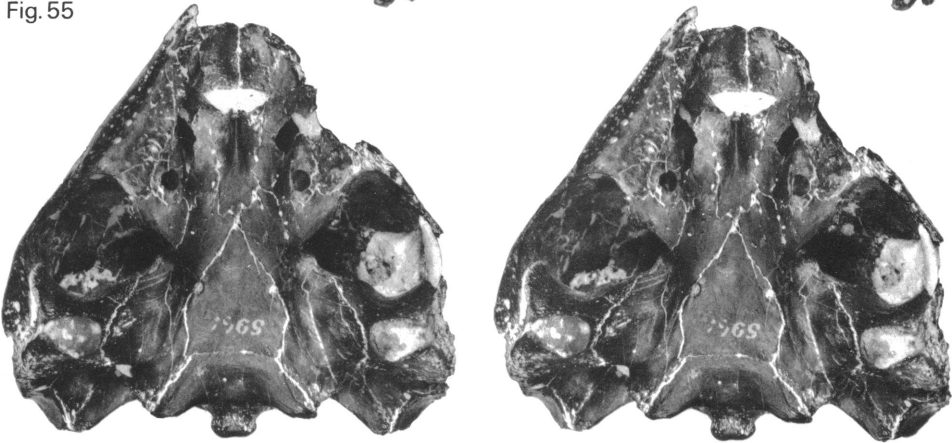


FIG. 56. *Chisternon undatum* (Leidy). Dorsal stereophotograph of AMNH 5961 from the Eocene Bridger Formation of Wyoming. Indentation on right parietal, partially healed in life, possibly caused by a predator. Resulting fractures have been the basis of frequent but erroneous identification of skull elements (see text).

FIG. 57. *Eubaena cephalica* (Hay). Ventral stereophotograph of type specimen, YPM 1785, from the late Cretaceous Lance Formation of Wyoming. See also figure 19. Condyle-premaxilla length 66 mm.

FIG. 58. *Stygiochelys estesi* Gaffney and Hiatt. Ventral stereophotograph of type specimen, AMNH 2601, from the late Cretaceous Hell Creek Formation of Montana. See also figure 21. Condyle-premaxilla length about 63 mm.

Fig. 56

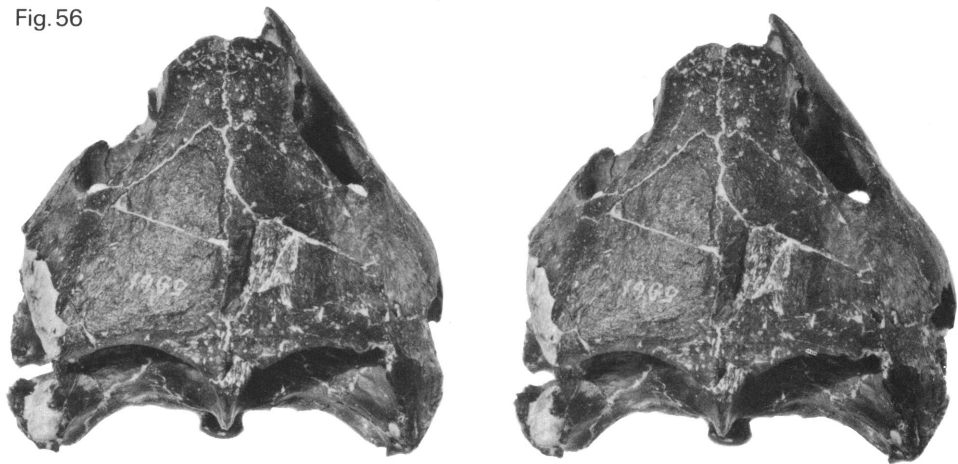


Fig. 57

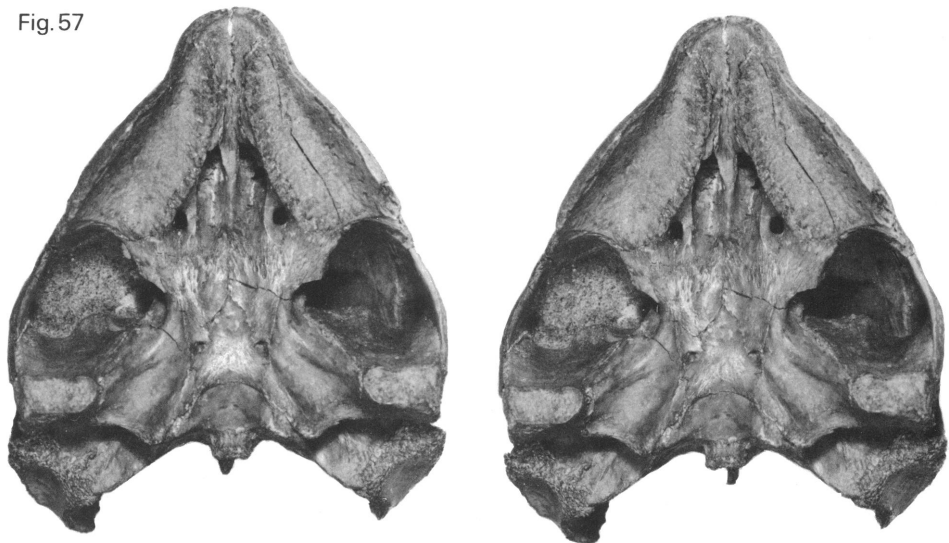


Fig. 58

