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The Lower Jaws of Baenid Turtles

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ABSTRACT

The baenid lower jaw has a well-developed processus coronoideus, no ridges or pits on the triturating surface, a relatively small dorsal opening of the fossa meckelii, and, except in *Chisternon* and *Baena,* a large splenial bone. None of these features is unique to baenids nor is the combination unique. Distinctly expanded triturating surfaces are found in *Eubaena* and *Palatobaena.* *Chisternon* and *Baena* are the only baenids definitely known to lack splenials; the anteroventromedial wall of the fossa meckelii is open in these genera. An associated skull and jaws of *Plesiobaena putorius* show that previous identification of jaws with expanded triturating surfaces as pertaining to this species was in error, the two known species of this genus have narrow jaws.

INTRODUCTION

Previous work on baenids includes Gaffney (1972), a review of the systematics with literature references up to that date; Gaffney (1975a) discusses relationships of baenids to other turtles; Archibald and Hutchison (1979) describe new material of *Palatobaena*; and Gaffney (in press) deals with the cranial morphology of baenids. An introduction to turtle lower jaw morphology can be found in Gaffney (1979), and baenid lower jaws have been described and figured in Hay (1908) and Archibald and Hutchison (1979).

Figures 1 and 2 are the work of Ms. Lorraine Meeker, and I thank her and Mr. Chester Tarka for improving the quality of all the figures in this paper. I am grateful to Dr. David Archibald, Yale University, for allowing me to use new baenid material collected as part of his thesis work.

ABBREVIATIONS

INSTITUTIONAL

AMNH	American Museum of Natural History
NMC	National Museum of Canada
PU	Princeton University
ROM	Royal Ontario Museum
UCM	University of Colorado Museum
UCMP	University of California, Museum of Paleontology
UMMP	University of Michigan, Museum of Paleontology
USNM	National Museum of Natural History, Smithsonian Institution
UW	University of Wyoming

ANATOMICAL

ang	angular
art	articular
cor	coronoid
den	dentary
pra	prearticular
sp	splenial
sur	surangular

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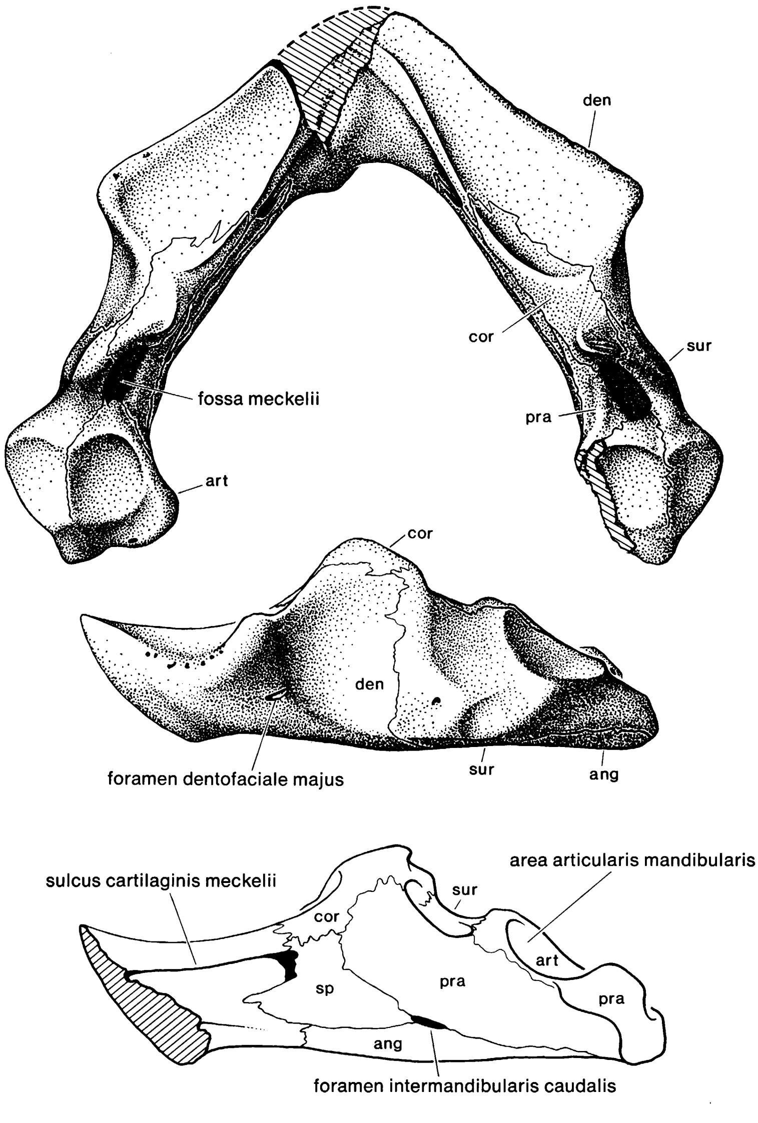

FIG. 1. *Palatobaena bairdi* (AMNH 8277), Hell Creek Formation, late Cretaceous, Bug Creek Anthills, McCone County, Montana. *Upper,* dorsal view; *middle,* lateral view of left ramus; *bottom,* medial view of right ramus. Note partially healed fracture near symphysis. Length of right ramus (measured parallel to axis of ramus), 56.7 mm.

DESCRIPTION

Baenid lower jaws (figs. 1 and 2) typically have a relatively large splenial (except in *Baena* and *Chisternon*), a well-developed processus coronoideus, an absence of ridges or pits on the triturating surface, and a relatively small dorsal opening of the fossa meckelii. None of these features is unique to baenids, nor is the combination unique being found in *Plesiochelys* (Gaffney, 1976). As far as I can determine, the only way to identify a baenid lower jaw is by using features diagnostic for a particular genus, and even this might be difficult for *Plesiobaena.*

DENTARY: The dentaries of baenids are comparable to the dentaries of other cryp-

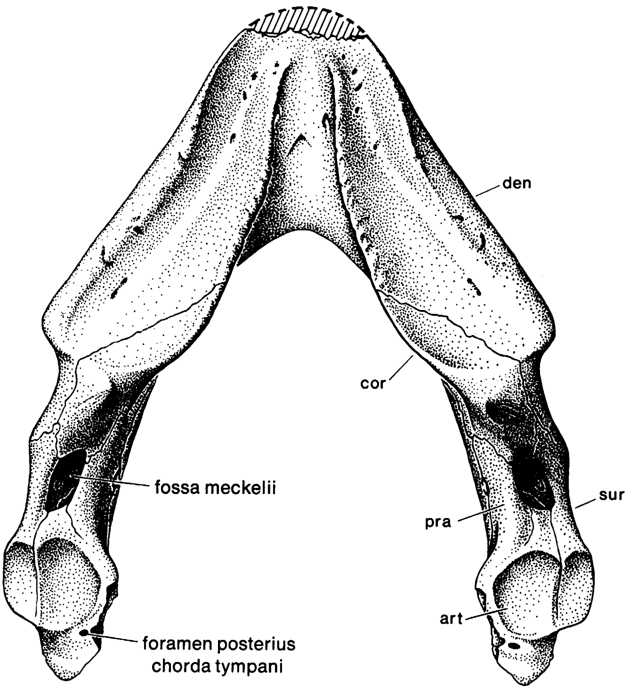

FIG. 2. *Eubaena cephalica* (AMNH 2604), Hell Creek Formation, late Cretaceous, 26 miles south of Lismas, Montana. Length of left ramus (measured parallel to axis of ramus), 64.7 mm.

todires. There is a broad medial symphysis with a variably developed dorsal projection or hook, best seen in *Baena* and *Plesiobaena.* No trace of a symphyseal suture has been observed.

The triturating surface of *Plesiobaena antiqua* (fig. 3) appears to represent the primitive condition compared with the lower jaws of other baenids. *Plesiobaena antiqua* has a narrow triturating surface with the labial and lingual ridges approximately parallel to one another as in *Baena* and *Chisternon.* The two ridges are slightly raised, forming a shallow trough between them. The labial ridge extends dorsally in the anterior section of the jaw to form a well-developed symphyseal "hook." The triturating surfaces, as in other baenid genera, closely approximate the maxillary triturating surfaces, indicating that in life the horny covering of the upper and lower jaws closely followed the bony morphology.

A comparison of *Plesiobaena antiqua* with *Plesiochelys* (Gaffney, 1976) shows a close similarity between the two forms. The lingual ridge of *Plesiobaena,* however, trends laterally as it reaches the symphysis, narrowing the triturating surface, whereas in *Plesiochelys* the lingual ridge trends more medially, widening the triturating surface. The coronoid process of *Plesiochelys* is slightly higher and the entire jaw ramus is a bit more massive than in *Plesiobaena* but these are relatively minor features.

The discovery of an associated skull and jaws of *Plesiobaena putorius* (UW 3348, see notes on *Plesiobaena putorius* below) removes the earlier presumed disparity in lower jaw morphology between *Plesiobaena antiqua* and *Plesiobaena putorius.* The lower jaw of *Plesiobaena putorius* closely resembles that of *P. antiqua,* differing only in a slight medial expansion of the triturating surface.

Stygiochelys (fig. 3) is now known from associated skulls and jaws, one of which (UCMP 113316) is particularly well preserved with the jaws removed from the skull. These jaws are quite similar to *Plesiobaena antiqua,* and if the dorsal surface of the jaws in *Plesiobaena putorius* were available there might be some difficulty differentiating them.

Although symphyseal breakage and some bone loss prevent a completely confident restoration it appears that the rami met at a slightly more obtuse angle than in *Plesiobaena* but less obtuse than in *Palatobaena.* The labial ridge in *Stygiochelys* is the same as in *Plesiobaena antiqua* but the lingual ridge runs more medially; however, this difference is not great and may be obscured by age or individual variation. Both labial and lingual ridges of *Stygiochelys* are slightly more pronounced than in *Plesiobaena antiqua* but not to the extent seen in *Baena.*

Eubaena (fig. 2) has one of the more distinctive feeding surfaces, with an incipient secondary palate in the skull. The lower jaw reflects this condition and has characteristic lingual ridges that curve medially and dorsally to match the upper jaws. A shallow trough parallels the lower labial ridge. The lingual ridges do not meet in the symphysis, instead they become parallel and form a trough along the symphysis.

Lower jaws with associated skulls of *Palatobaena bairdi* were announced by Archibald and Hutchison (1979) substantiating the identification of Gaffney (1979, fig. 161; AMNH 8277) of an isolated but very well-preserved specimen. *Palatobaena* (figs. 1, 3) has a very distinctive lower jaw triturating surface morphology unique among baenids (assuming my re-identification of jaws previously ascribed to *Plesiobaena putorius* is correct). The triturating surface is triangular with labial and lingual ridges close together anteriorly and relatively far apart posteriorly. The triturating surface is relatively flat with low lingual and labial ridges but the surface does not lie horizontal, rather it is tilted to face anterolaterally. The rami are relatively thick and massive, particularly near the well-developed processus coronoideus.

The triturating surfaces of *Baena* and *Chisternon* (fig. 3) are most similar to those of *Plesiobaena.* The labial and lingual ridges are parallel to each other and expanded surfaces are not developed; a shallow trough is formed between the ridges. The trough is deeper in *Baena* than in *Chisternon,* whereas the latter has a shallow trough just anterior to the processus coronoideus. The jaw rami in *Baena* meet at a more obtuse angle than in *Plesiobaena* and *Chisternon.* Also, *Chisternon* has a symphyseal development of the labial ridge that approaches the symphyseal hook of *Plesiobaena.* Fully adult specimens of *Baena* have an upturned symphyseal "hook" that differs from *Chisternon* and *Plesiobaena* in the presence of a low midline ridge extending across the triturating surface.

Age variation in *Baena arenosa* apparently involves the mandible. The lower jaws of a presumed juvenile (AMNH 5977, see Gaffney, 1972, for a discussion of possible age variation in the skull) differs from the lower jaws of what is here concluded to be older individuals of the same species. These differences involve the triturating surface and, in general, suggest that juveniles of *Baena* have certain similarities to *Chisternon* and *Plesiobaena.* That is, the juvenile jaw resembles *Chisternon* in lacking the more massive proportions of adult *Baena* (AMNH 5971) and in having the jaw rami meet at a more acute angle as in *Chisternon.*

Most of the contacts of the dentary are the same in known baenid mandibles as well as in most cryptodires. Posterodorsomedially there is a deep suture with the coronoid. Posteroventromedially a long squamous suture with the angular extends about half the length of the dentary. Just below the sulcus cartilaginis meckelii and above the suture with the angular is a fairly restricted suture with the splenial in *Palatobaena* and *Plesiobaena.* In *Eubaena* and *Stygiochelys* a splenial seems to be present but none of the specimens show its contacts clearly. In *Baena* and *Chisternon* the angular extends dorsally to the ventral edge of the sulcus cartilaginis meckelii.

As in most other turtles, baenids (figs. 1, 4) have a foramen dentofaciale majus (see Gaffney, 1979, figs. 111, 112) on the lateral surface of the dentary near the margin of the rugose bone surface, marking the attachment of the horny rhamphotheca. On the medial surface, toward the posterior end of the sulcus cartilaginis meckelii is the foramen alveolare inferius. This foramen leads into the canalis alveolaris inferior. These nutritive foramina and canal can be seen in a number of broken baenid jaws but I have not been able to dis-

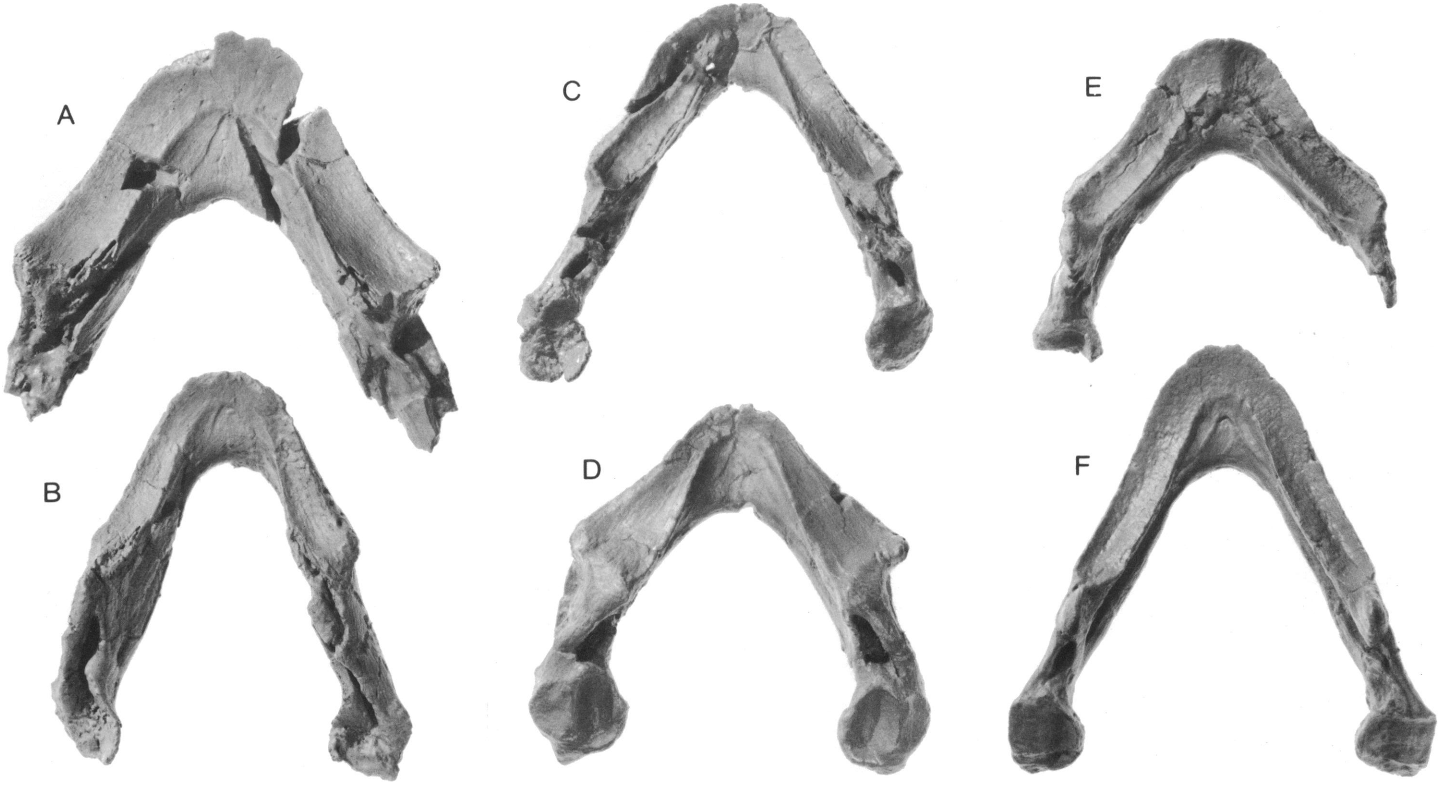

FIG. 3. Dorsal views of baenid lower jaws. A, *Plesiobaena antiqua* (NMC 8599), Oldman Formation; late Cretaceous, Alberta. Length of right ramus as preserved, 40.7 mm. B, *Plesiobaena antiqua* (ROM 674), Oldman Formation, late Cretaceous, Alberta. Length of right ramus, 39.9 mm. C, *Stygiochelys estesi* (UCMP 113316), Hell Creek Formation, late Cretaceous–Paleocene, Montana. Length of right ramus, 55.8 mm. D, *Palatobaena bairdi* (PU 17108), Polecat Bench Formation, Paleocene, Wyoming. Length of right ramus, 55.7 mm. E, *Baena arenosa* (AMNH 5971), Bridger Formation, Eocene, Wyoming. Length of left ramus, 55.5 mm. F, *Chisternon undatum* (USNM 12839), Bridger Formation, Eocene, Wyoming. Length of right ramus, 72.9 mm.

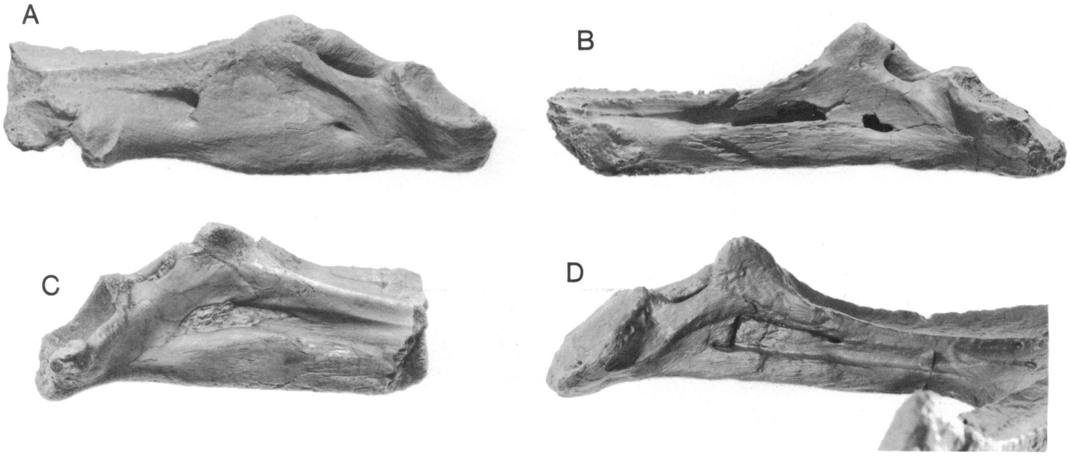

FIG. 4. Internal views of baenid lower jaws. A, *Plesiobaena antiqua* (UCMP 49759), Lance Formation, late Cretaceous, Wyoming. Length, 49.3 mm. B, *Eubaena cephalica* (AMNH 2606), Hell Creek Formation, late Cretaceous, Montana. Length, 57.3 mm. C, *Baena arenosa* (AMNH 2276), Bridger Formation, Eocene, Wyoming. Length, 43.5 mm. D, *Chisternon undatum* (USNM 12839), Bridger Formation, Eocene, Wyoming. Length of left ramus, 72.8 mm.

cern any systematic variation either within baenids or between baenids and eucryptodires.

ARTICULAR: The articular (fig. 1) occupies a position between the prearticular and surangular bones, with the angular attaching ventrally. The morphology of the bone in baenids is very similar to the articular of other cryptodires. It forms the medial two-thirds of the area articularis mandibularis with the surangular forming the lateral third. The dorsal surface of the articular is gently concave. The articular extends posteriorly to form a retroarticular process for the attachment of the M. depressor mandibulae. This process is largest in *Eubaena* and is small in *Chisternon, Baena,* and *Plesiobaena.* The dorsal surface of the retroarticular process in the last forms is oriented in a more vertical plane than in *Eubaena.*

The foramen posterius chorda tympani is usually in the posteromedial portion of the articular in the base of the retroarticular process, just behind the area articularis mandibularis. The canalis chorda tympani mandibularis seems to be formed between the articular and prearticular. The chorda tympani nerve enters the fossa meckelii through the foramen anterior chorda tympani which is also formed by the articular and prearticular.

SPLENIAL: Large and well-preserved splenials (figs. 1, 3) can be seen in *Plesiobaena* (ROM 674, UCMP 49759) and *Palatobaena* (AMNH 8277, PU 17108). The splenial in these baenids is quite similar to splenials described for *Solnhofia* (Parsons and Williams, 1961; Gaffney, 1975b) and *Plesiochelys* (Gaffney, 1976). It is a flat, roughly equidimensional bone forming the medial margin of the foramen intermandibularis medius and the anteromedial wall of the fossa meckelii. Fragments of a narrow splenial appear to be present in *Eubaena* (AMNH 2602). As I interpret the morphology in this specimen, the splenial in *Eubaena* would differ from that bone in *Palatobaena* and *Plesiobaena* in being lower, having a more extensive coronoid contact, and a less extensive prearticular contact. In the one useful jaw of *Stygiochelys* (UCMP 113316) the splenial was probably present, based on the other elements, but the area is so damaged that this is not directly determinable. *Baena* and *Chisternon* lack a splenial (fig. 4).

CORONOID: The coronoid of baenids (fig. 1) is very similar in shape and position to that bone in most eucryptodires. All baenids have a distinct processus coronoideus which is best developed in *Baena* (subject to individual variation, however), and least developed in *Plesiobaena.* As in other cryptodires, there is an anteromedial process of the coronoid that extends anteriorly along the medial surface of the jaw ramus and forms part of the lingual ridge of the triturating surface. In *Plesiobaena, Eubaena,* and *Palatobaena* the ventral margin of this anterior process contacts the splenial but in *Baena* and *Chisternon* it contacts the dentary (fig. 4).

ANGULAR: The angular of baenids (fig. 1) has the same basic relations as the angular of other cryptodires; it covers the posteroventral portion of the jaw curving anteromedially from the posterolateral jaw margin. In *Plesiobaena* (ROM 674, UCMP 49759), *Eubaena* (AMNH 2606) and *Palatobaena* (AMNH 8277, PU 17108) the anteromedial portion has a broad dorsal contact with the splenial. In *Stygiochelys* (UCMP 113316) the presence of a splenial is likely but not definite, however, the angular appears to be the same as in the preceding three genera in any case. In *Baena* (AMNH 2276, 3808, 5971) and *Chisternon* (USNM 12839, AMNH 5962) the splenial is absent and the angular forms the ventral edge of the fossa meckelii which is now open medially due to the absence of the splenial (fig. 4). The angular in these two forms extends farther dorsally on the medial surface and expands into the region occupied by the splenial in the other baenids.

The foramen intermandibularis caudalis is formed in the suture between the angular and prearticular in *Plesiobaena, Eubaena,* and *Palatobaena* (it is indeterminate in *Stygiochelys*) with the splenial entering or nearly entering the anterior margin of the foramen in some specimens. I have not been able to determine whether the splenial contribution to the foramen is of systematic significance, however, on the basis of the material at hand it appears to be an individual variation. In *Plesiobaena* the foramen is positioned more anteriorly than in *Eubaena* and *Palatobaena.*

PREARTICULAR: As in other cryptodires the prearticular of baenids (fig. 1) covers the posteromedial part of the jaw anterior to the articular, dorsal to the angular, and lateral to the fossa meckelii. The dorsal margin of the prearticular forms the medial edge of the dorsal opening of the fossa meckelii. Just anterior to this opening the prearticular lies lateral to the coronoid bone. In *Plesiobaena, Eubaena,* and *Palatobaena* the prearticular has a broad anterior contact with the splenial. In *Baena* and *Chisternon* the splenial is absent (fig. 4) but in contrast to most eucryptodires which lack a splenial (see Gaffney, 1979, fig. 112), the prearticular in *Baena* and *Chisternon* does not extend anteriorly to occupy the area of the absent splenial. Instead the anteroventral half of the fossa meckelii is open medially in these two baenids. The prearticular of these two genera forms the posterodorsal margin of this opening. The opening extends to and includes the foramen intermandibularis caudalis, which is therefore absent in *Baena* and *Chisternon* as a discrete foramen.

The prearticular of *Baena* and *Chisternon* has the same relation to the coronoid as the other baenids but the prearticular does have a well-developed anterior contact with the dentary above the fossa meckelii in *Baena* and *Chisternon,* which is absent in the other baenids presumably because they have a splenial which fits in this position.

SURANGULAR: In most eucryptodires the surangular is restricted to the posterodorsal margin of the lower jaw and most of the lateral surface is covered by the dentary. Baenids, however, still have the primitive condition of a large surangular covering relatively more of the lateral surface of the lower jaw (fig. 1). The dentary-surangular suture varies somewhat among the baenid genera from roughly vertical in *Palatobaena* to a Z-shape in *Chisternon, Eubaena, Baena* and most of the baenid genera. The surangular of baenids forms the lateral portion of the area articularis mandibularis, as in other cryptodires.

Archibald and Hutchison (1979, fig. 4) have argued that *Palatobaena bairdi* differs from *Plesiobaena putorius* in the presence in the former of a small fossa on the surangular just posterior to the large adductor fossa ventral to the processus coronoideus. Below, I argue that the lower jaw (PU 17108) was identified as *Plesiobaena putorius* based on my error in 1972 in fitting these jaws to a skull of *Plesiobaena putorius.* The discovery of an associated skull and jaws of *Plesiobaena*

TABLE 1
Comparisons of Baenid Lower Jaws

	Plesiobaena	*Eubaena*	*Stygiochelys*	*Palatobaena*	*Chisternon*	*Baena*
Triturating surface	Narrow, with parallel margins	Expanded, lingual ridge curves medially	Slightly expanded	Broadly expanded, triangular surface	Narrow, with parallel margins, trough anterior to coronoid process	Narrow, with parallel margins
Splenial	Large	Small	Probably present	Large	Absent	Absent
Fossa meckelii with anteroventral wall on medial side	Yes	Yes	Yes	Yes	No	No

putorius (UW 3348), however, shows that the jaws of *Plesiobaena putorius* are very similar to the jaws of *Plesiobaena antiqua.* I therefore identify PU 17108 as *Palatobaena bairdi* because of the very close similarity between PU 17108 and jaws such as AMNH 8277 and 2603. The absence of a small surangular fossa in PU 17108 I consider as taxonomically insignificant at present.

NOTES ON *PLESIOBAENA PUTORIUS*

In 1972 I named this Paleocene species on the basis of a nearly complete but crushed skull (PU 14984, the type specimen), and a series of partial skulls along with a lower jaw. The lower jaw (PU 17108) was identified on the basis of fitting it to the type skull and hypothesizing that the relatively close fit meant that they were the same taxon. Archibald and Hutchison (1979) accepted this identification but remarked on the very close similarity between this jaw (PU 17108) and lower jaws of *Palatobaena bairdi* that they could identify by association with skulls. They were able to distinguish the jaws of *Palatobaena* and PU 17108 primarily by the presence of a small fossa on the lateral surface of the jaw in *Palatobaena* (Archibald and Hutchison, 1979, fig. 4). They speculated that this fossa was related to the origin of a new muscle in *Palatobaena* that extended from this fossa to an attachment near the cheek emargination.

Unfortunately, the discovery of an associated skull and lower jaws of *Plesiobaena putorius* (UW 3348, Tiffanian, Wyoming) shows that the lower jaws I originally identified as *Plesiobaena putorius* (PU 17108) do not belong to this species. The new specimen is readily identified as *Plesiobaena putorius* because it has the characteristic semicircular expansion of the skull roof overlying the crista supraoccipitalis. The degree of temporal emargination is less than that seen in PU 20600 and PU 14984 (Gaffney, 1972, figs. 14, 17). The lower jaws have not been removed from the skull due to the extremely hard matrix and tight fit but enough of the jaws can be seen to show that they are very similar to the jaws of *Plesiobaena antiqua* rather than of *Palatobaena.* The *Plesiobaena putorius* lower jaws (UW 3348) differ from *Plesiobaena antiqua* in having a slightly larger triturating surface due to medial expansion but otherwise they are the same. In particular the jaws of the two species of *Plesiobaena* have the following features in common in contrast to PU 17108.

1. Jaws less massive.
2. Narrower triturating surface.
3. Rami meet at more acute angle.
4. Lower coronoid process.
5. Symphyseal area projects anteriorly to a greater degree.

I conclude from this that PU 17108 belongs to *Palatobaena,* probably *P. bairdi,* in spite of the absence of a small lateral fossa.

A comparison of the skulls involved suggests that UW 3348 is better preserved and less distorted than the type skull which is somewhat crushed. The referred skull, PU 20600, is better preserved than the type but lacks the right half of the triturating surfaces. Due to these circumstances the original restoration (Gaffney, 1972, fig. 15) probably has an unnaturally widened palate. Similarly, the close fitting of the lower jaws, PU 17108, with the type skull, PU 14984, is probably due to the crushing and lateral distortion of the type skull. The new specimen of *Plesiobaena putorius* (UW 3348) has no difference in width or other proportions from *Plesiobaena antiqua*. As far as I can determine with the material at hand, *P. putorius* differs from *P. antiqua* in only two features: the semicircular projection overlying the crista supraoccipitalis and the medial expansion of the triturating surface. As more specimens accumulate the consistency of the features remains to be seen.

APPENDIX I

LOWER JAWS USED IN THIS STUDY

Literature citations refer to sources of locality and geologic data. Asterisk (*) indicates skull associated with lower jaws.

Plesiobaena antiqua

NMC 8599 (Gaffney, 1972).

ROM 674, near Steveville, Red Deer River Alberta, Oldman Formation (see also Gaffney, 1972, for figures).

UCMP 113318*, V73023, McCone Co., Montana, (?) Paleocene.

UCMP 49759* (Gaffney, 1972).

UMMP 20490* (Gaffney, 1972).

Plesiobaena putorius

UW 3348*, Tiffanian, Wyoming.

Eubaena cephalica

AMNH 2604 (Gaffney, 1972).

AMNH 2605 (Gaffney, 1972).

AMNH 2606 (Gaffney, 1972).

UCMP 107617*, V73023, McCone Co., Montana, (?) Paleocene.

UCMP 114706, V73023, McCone Co., Montana, (?) Paleocene.

UCMP 114710, V73023, McCone Co., Montana, (?) Paleocene.

Stygiochelys estesi

UCMP 113316*, V73023, McCone Co., Montana, (?)Paleocene.

UCMP 113317*, V73023, McCone Co., Montana, (?)Paleocene.

Palatobaena bairdi

AMNH 2603 (Archibald and Hutchison, 1979).

AMNH 8277 (Archibald and Hutchison, 1979).

PU 17108 (Gaffney, 1972; Archibald and Hutchison, 1979; identified in both as *Plesiobaena putorius*).

UCMP 114539* (Archibald and Hutchison, 1979).

UCMP 114680 (Archibald and Hutchison, 1979).

UCMP 117154, V72208, Garfield County, Montana, Hell Creek Formation.

UCM 37738 (Archibald and Hutchison, 1979).

Chisternon undatum

AMNH 5904 (Gaffney, 1972).

AMNH 5962* (Gaffney, 1972).

USNM 12839* (Gaffney, 1972).

Baena arenosa

AMNH 2276*, Cottonwood Creek, Wyoming, Bridger Formation.

AMNH 3808*, Grizzly Buttes East, Wyoming, Bridger Formation (B).

AMNH 5907*, Wyoming, Bridger Formation (B).

AMNH 5971* (Gaffney, 1972).

AMNH 5977 (Gaffney, 1972).

AMNH 5984 (Gaffney, 1972).

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