

CRANIAL MORPHOLOGY OF THE  
EUROPEAN JURASSIC TURTLES  
*PORTLANDEMYS* AND *PLESIOCHELYS*

EUGENE S. GAFFNEY

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## ABSTRACT

A theory of relationships is presented in which the Jurassic turtle genera *Portlandemys* and *Plesiochelys* are hypothesized as members of the monophyletic group Chelonioidea based on the possession of the following shared derived characters: 1) dorsum sellae high and separated from sella turcica and foramen anterius canalis carotici interni by prominent bone surface that usually has a sagittal ridge, 2) posterior part of sella turcica not concealed by overhanging dorsum sellae. The relationships of these genera within the Chelonioidea are more difficult to test

owing to the fact that at present only the Recent forms are cranially as well known as *Portlandemys* and *Plesiochelys*. Nonetheless, I have suggested two contradictory hypotheses, one indicating *Plesiochelys* and *Portlandemys* as the sister group of the Dermochelyidae plus Cheloniidae, and the other indicating *Plesiochelys* as the sister group of the Toxochelyidae, Dermochelyidae, and Cheloniidae. The first hypothesis is consistent with derived characters of the palatine artery, whereas the second is consistent with postcranial derived characters.

## INTRODUCTION

This is the third paper in a series concerned with cranial morphology and relationships of European Jurassic turtles. The first paper (Gaffney, 1975a) was a treatment of the alpha taxonomy of *Portlandemys* and *Plesiochelys*; the second (Gaffney, 1975b) consisted of a detailed description of *Solnhofia*. The present paper describes the cranial morphology of *Plesiochelys* and *Portlandemys* and suggests some hypotheses about their phylogeny. The reader is referred to Gaffney (1975a) for an extensive diagnosis of the Plesiochelyidae, for a review of previous work on skulls of this family, for figures of skulls before and after preparation, and for reconstructions of the skulls in *Portlandemys* and *Plesiochelys*. These figures are particularly important to an understanding of the morphology described here.

My primary purpose here is the development

of a comparative morphology for the skull in plesiochelyids. For comparison the reader should have available other chelonoid descriptive papers. The most useful are: Siebenrock (1897), Kesteven (1910), Nick (1912), and Wegner (1959). *Portlandemys* is described in some detail in Parsons and Williams (1961) and an illustrated glossary of the terminology used here can be found in Gaffney (1972). I have developed (Gaffney, 1975c) a hypothesis of relationships about turtles but the present paper primarily deals with the hypothesis that plesiochelyids are not "Amphichelydia" but members of a monophyletic group Chelonioidea. Important features of the Chelonioidea are also discussed in Gaffney (1975c, pp. 417-420, 428, 429), as well as a discussion of my systematic methodology (*ibid.* p. 391).

## ABBREVIATIONS

### INSTITUTIONS

AMNH, the American Museum of Natural History  
BM (NH), British Museum (Natural History)  
MH, Natural History Museum, Basel  
OU, Oxford University Museum  
SM, Solothurn Museum

### ANATOMICAL

ang, angular  
art, articular  
bo, basioccipital

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

pf, prefrontal  
 pm, premaxilla  
 po, postorbital  
 pr, prootic  
 pra, prearticular  
 pt, pterygoid

qj, quadratojugal  
 qu, quadrate  
 so, supraoccipital  
 sq, squamosal  
 sur, surangular  
 vo, vomer

## DERMAL ROOFING ELEMENTS

*Nasal.* The nasals in *Plesiochelys* and *Portlandemys* agree closely. They are roughly rectangular with a slightly convex anterior margin, and can best be seen in MH 435, SM 136, and SM 134. The dorsal surface contacts are: maxilla laterally, prefrontal posteriorly, and the other nasal medially. SM 134 shows the ventral sutures exceptionally well and reveals that a narrow process of the frontal extends anteriorly beneath the prefrontal to reach the nasal. This condition can also be seen in *Portlandemys* BM(NH) R2914. Bräm's (1965) statement that the nasals are lacking in *Plesiochelys* is incorrect.

*Prefrontal.* The prefrontal is preserved (although not equally well) in all six specimens of *Plesiochelys* available to me. As in most turtles, the bone consists of a horizontal plate on the dorsal surface and a vertical plate extending ventrally as the anterior wall of the fossa orbitalis. The vertical plate in *Plesiochelys* and *Portlandemys*, as in the majority of turtles, has a lateral suture with the vertical process of the maxilla, forms the anterodorsal margin of the foramen orbito-nasale, contacts the palatine just medial to the foramen, and contacts the vomer ventromedially. The foramen orbito-nasale is slightly larger in *Plesiochelys* and *Portlandemys* than in *Chelydra* and living cheloniids and much larger than in *Toxochelys*.

The dorsal plate limits are completely unambiguous in only one specimen of *Plesiochelys*, MH 435. In this skull (illustrated in the principal restoration) the process is rectangular, with a transverse nasal suture anteriorly, a parallel transverse frontal suture posteriorly, and a sagittal prefrontal suture medially. On the ventral surface the contacts are different because the frontal sends a process anteriorly along the midline that separates the prefrontals and reaches, or nearly reaches, the nasals. In SM 134 the situation ap-

pears to be the same although the dorsal surface is a bit damaged. In OU J1582, however, the dorsal surface is nearly the same as the ventral contacts and each frontal sends a medial process anteriorly to separate the prefrontals and reach the nasals. This last specimen, however, is damaged in this area; the nasals and an undetermined amount of surface bone are gone, and there may have been a medial contact of the prefrontals. Among the other *Plesiochelys* specimens, SM 135 seems to agree with OU J1582 and in this skull the prefrontals do meet in a short sagittal suture

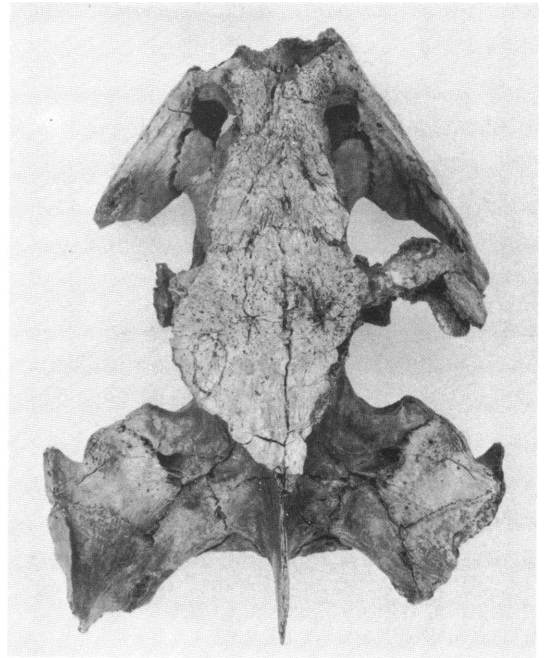


FIG. 1. *Plesiochelys planiceps*, OU J1582, type specimen of *Stegochelys planiceps* (Owen). Dorsal view of skull, see Gaffney (1975a, p. 18) for palate.



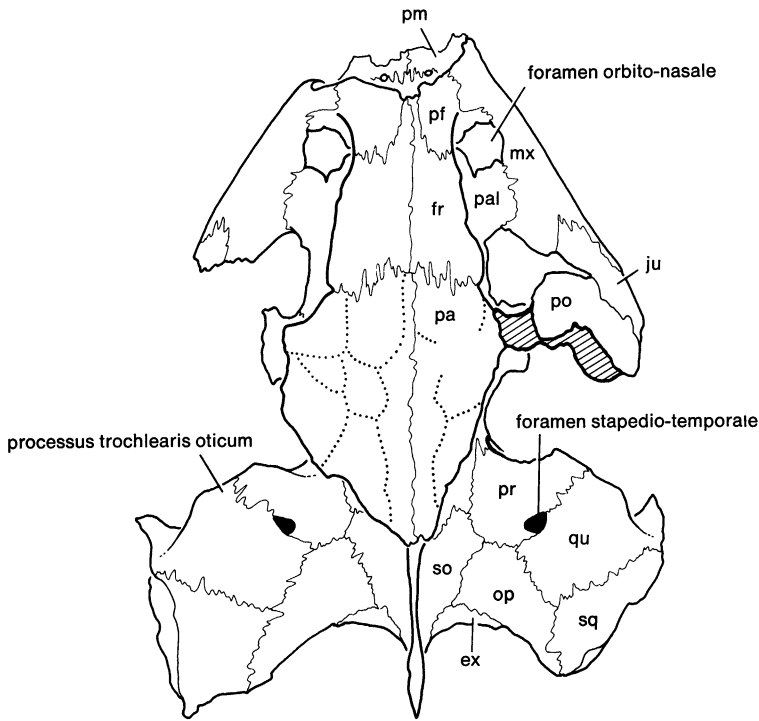


FIG. 2. Key for figure 1.

to separate the nasals from the frontals on the dorsal surface. SM 136 is obscured on the ventral surface and I cannot make out the dorsal sutures while SM 594 is badly damaged in this area and yields no sutural information.

Parsons and Williams (1961, p. 48) questionably identified the sutures of *Portlandemys* as approximating the condition described here for *Plesiochelys* MH 435, in which the dorsal plate is rectangular. My own examination of *Portlandemys* BM(NH) R2914 and the disarticulated frontal-prefrontal of BM(NH) R3163 (fig. 5) certainly substantiates the questionable nature of the sutures, although the disarticulated BM(NH) R3163 frontal and prefrontal do indicate that the dorsal surface suture trends anteromedially as in *Plesiochelys* OU J1582. These bones are eroded, however, and as in the case of OU J1582, a thin dorsal sheet of prefrontal could result in a rectangular surface pattern.

In summary, the ventral vertical plates of

*Plesiochelys* and *Portlandemys* differ from *Chelydra*, *Toxochelys*, living cheloniids, and most other cryptodires only in the relatively slight difference in size of the foramen orbito-nasale. The ventral surface of the dorsal horizontal plate is the same in *Portlandemys* and *Plesiochelys* but the dorsal surface suture pattern appears variable. A completely unambiguous suture pattern is visible in only one specimen of *Plesiochelys* (MH 435) and that shows a rectangular plate separating nasal and frontal, quite different from the ventral pattern in which the nasal and frontal meet or nearly meet sagittally. The other specimens of both *Plesiochelys* and *Portlandemys* cannot be determined without question and interpretations suggest that some specimens have an anteromedial process of the frontal that separates some or all of the sagittal prefrontal contacts and more closely resembles the ventral surface morphology. If the condition in MH 435 is accepted as the best known for comparative purposes,

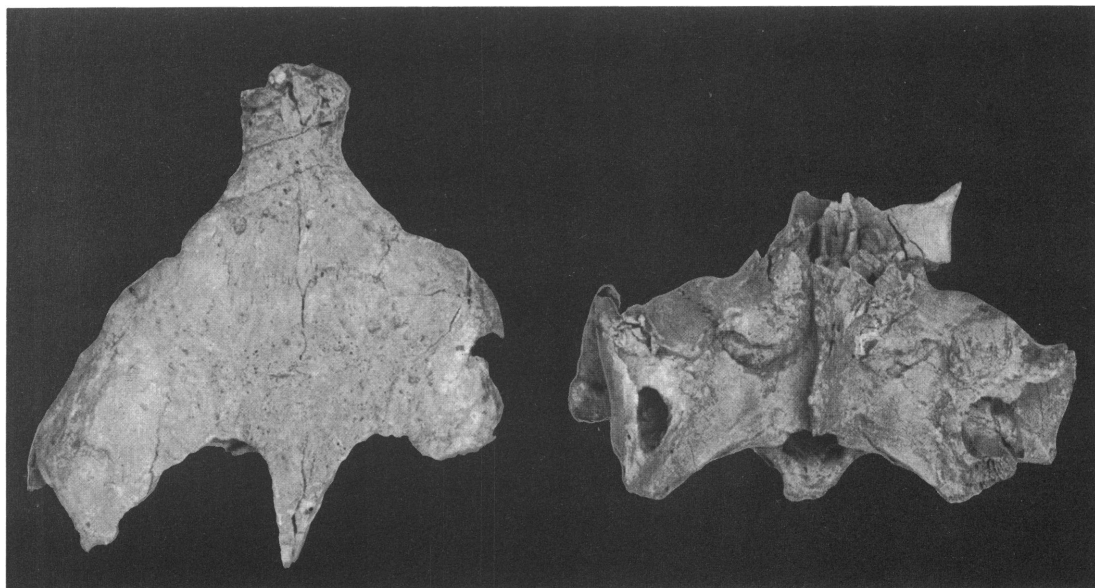


FIG. 3. *Plesiochelys etalloni*, SM 594. Dorsal view of skull roof (left), posterior part of basicranium (right). The specimen is the only *Plesiochelys* skull that appears to have most of the posterior temporal margin preserved (on the left side). See Gaffney (1975a, p. 12) for restoration.

then it can be seen that it is most similar to the situation in such forms as *Toxochelys* in which the prefrontals meet sagittally rather than the condition in such forms as baenids, *Desmatochelys* and *Rhinochelys*, where the prefrontals do not meet sagittally for most of their length.

**Frontal.** The frontal in *Plesiochelys* is a plate-like element having a roughly rectangular outline and meeting the prefrontal anteriorly, the orbital margin anterolaterally, the postorbital posterolaterally, the parietal posteriorly, and the other frontal medially. The frontal is preserved in all six *Plesiochelys* specimens and no differences are apparent. The bone is best seen in MH 435 and the disarticulated SM 134. The anterior limits of the bone on the dorsal surface are in doubt in most specimens and this is discussed under the prefrontal.

The ventral surface of the frontal bears a parasagittal ridge separating the medial sulcus olfactorius from the lateral fossa orbitalis. The sulcus olfactorius is widely open ventrally as in living cheloniids rather than partially enclosed ventrally as in *Chelydra*. The portion of the frontal form-

ing the sulcus extends anteriorly between the ventral processes of the prefrontals, forms the roof

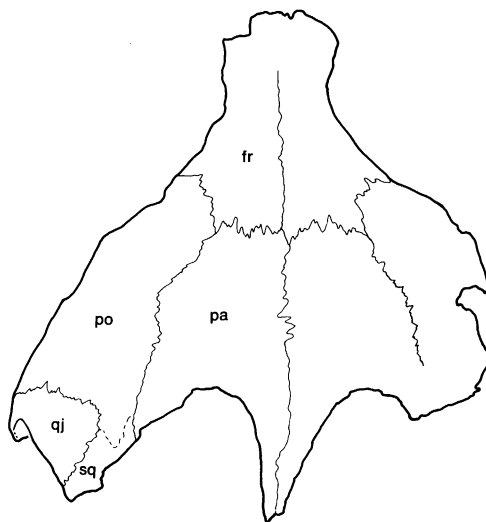


FIG. 4. Key to figure 3.



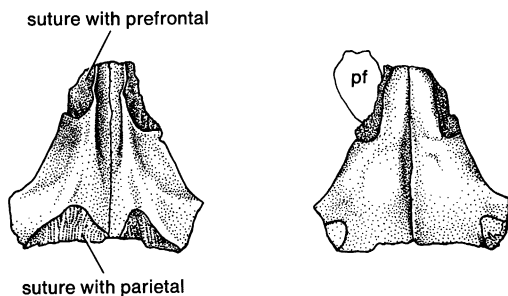


FIG. 5. *Portlandemys mcdowelli*, BM(NH) R3163. Ventral (left), dorsal (right) views of disarticulated frontal bones.

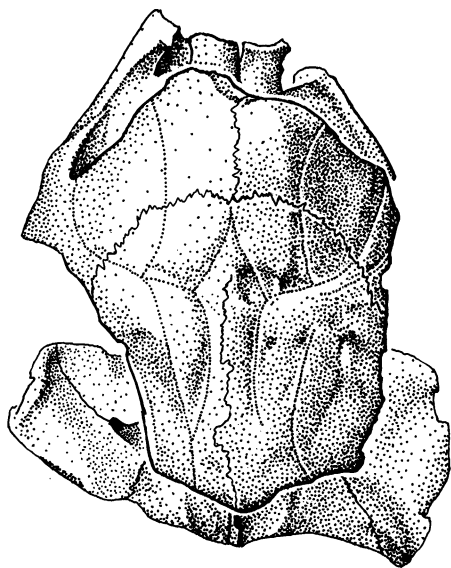


FIG. 6. *Portlandemys mcdowelli*, BM(NH) R3164. Dorsal view of skull.

of the fissura ethmoidalis, and meets or nearly meets the nasals.

The frontal of *Portlandemys* as described by Parsons and Williams (1961, p. 48) does not enter the orbital margin. However, reexamination of BM(NH) R3163 and BM(NH) R2914 seems to show that the frontal does form part of the orbital margin and that there is no prefrontal-postorbital contact. The frontal in *Portlandemys* then, seems to be the same as in *Plesiochelys*.

BM(NH) R3163 apparently has a nasal-frontal contact on the ventral surface as in *Plesiochelys*.

The frontal of both *Plesiochelys* and *Portlandemys* is nearly the same as in *Toxochelys*. The frontal-prefrontal suture on the dorsal surface is transverse in some specimens, at least, of *Plesiochelys*, but trends anteromedially in *Toxochelys* (but possibly also in some *Plesiochelys* and *Portlandemys*). There is no frontal-nasal contact in *Toxochelys*.

**Parietal.** The parietal of turtles consists of two plates at right angles to each other; a dorsal-horizontal plate and a parasagittal-ventral plate. The dorsal plate in *Plesiochelys* has a transverse suture anteriorly with the frontal and a long, slightly convex outward lateral suture with the postorbital. The dorsal plate of the parietal is complete in only one specimen, SM 594, and the restoration, although primarily on MH 435, reflects this information. The specimens of *Portlandemys* also lack most of the posterior parietal areas but the region that is preserved does not differ from *Plesiochelys*.

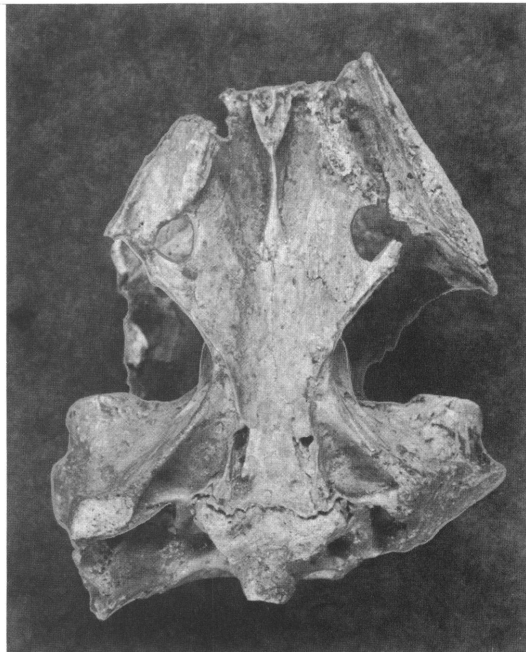


FIG. 7. *Portlandemys mcdowelli*, BM(NH) R3164. Ventral view of skull.

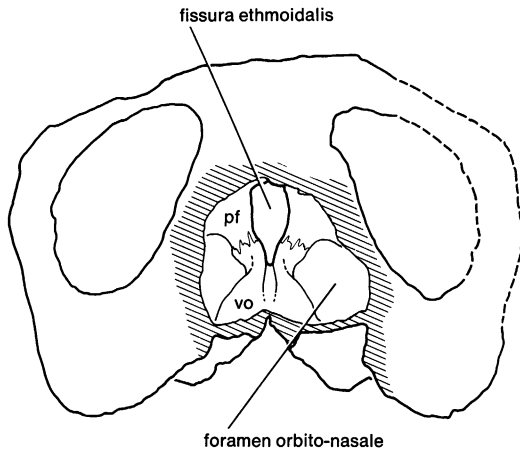


FIG. 8. *Plesiochelys planiceps*, OU J1582. Anterior view of skull, left side partly restored, hatching indicates eroded areas.

The temporal emargination in *Plesiochelys* exposes the foramen stapedio-temporale in dorsal view. The degree of emargination is about the same as that seen in *Toxochelys*, and less than in *Corsochelys* and *Chelydra*, but more than in *Rhinochelys* and living cheloniids. *Plesiochelys* differs from *Toxochelys* in lacking the posterolateral process of the parietal seen in that genus.

The ventral vertical plate of the parietal is the processus inferior parietalis and it articulates with the pterygoid, epipterygoid, prootic, and

supraoccipital. This area is especially well preserved in MH 435 and SM 134. The processus inferior parietalis meets the supraoccipital posteroventrally. The anterior margin of the processus inferior parietalis dorsally and the epipterygoid ventrally form the posterior limits of the foramen interorbitale. Most posteriorly the foramen nervi trigemini penetrates the side wall of the braincase and it is formed by the parietal anteriorly, dorsally and posteriorly, and by the pterygoid (and in most *Plesiochelys* by the epipterygoid) ventrally.

This formation of the foramen nervi trigemini mostly by the parietal is somewhat unusual. In most turtles the prootic forms a significant portion of the posterior margin of the foramen, but in *Portlandemys* and *Plesiochelys* a process of the parietal extends ventrally to meet the pterygoid along the posterior edge of the foramen nervi trigemini. This process, however, is only on the external surface of the skull; internally the prootic does form the margin of the foramen. In *Plesiochelys* and *Portlandemys* the parietal also reaches the quadrate thus separating the pterygoid and prootic (again on the outside of the braincase). Living cheloniids, *Toxochelys*, and *Chelydra* have the "normal" condition with the prootic exposed in the margin of the foramen nervi trigemini. A re-examination of *Corsochelys* (Zangerl, 1960) suggests that this form also has the condition seen in plesiochelyids. Although



FIG. 9. *Plesiochelys planiceps*, OU J1582. Lateral view of skull.



FIG. 10. *Portlandemys mcdowellii*, BM(NH) R2914. Lateral view of skull with lower jaws in place.

the ventral process of the processus inferior parietalis along the anterior edge of the prootic is absent, a distinct trough at this position in the prootic has the appearance of a sutural area and it seems likely that a parietal process was present originally but was disarticulated and broken off. Zangerl (1960, p. 286) stated that all skull bones of this specimen were disarticulated and collected separately. Other fossil chelonioids are not sufficiently well known in this area to determine if they have this condition or if it is unique to the Plesiochelyidae and *Corsochelys*.

Nick (1912) set up the morphologic sequence *Chelydra-Chelonia-Dermochelys* to show the progressive replacement of bone by cartilage in the processus inferior parietalis of adult chelonioids. Although the processus is thinner in cheloniids than in *Chelydra*, most testudinoids and trionychoids have a much broader processus than that in *Chelydra*. Testudinids, however, generally have a relatively thin processus, similar to cheloniids. In *Plesiochelys* and *Portlandemys* the processus is about intermediate between living cheloniids and *Chelydra*. Unfortunately the condition of the structure is not known in *Toxochelys*, but in *Corsochelys* the width of the processus is quite similar to modern cheloniids and slightly thinner than in *Plesiochelys*.

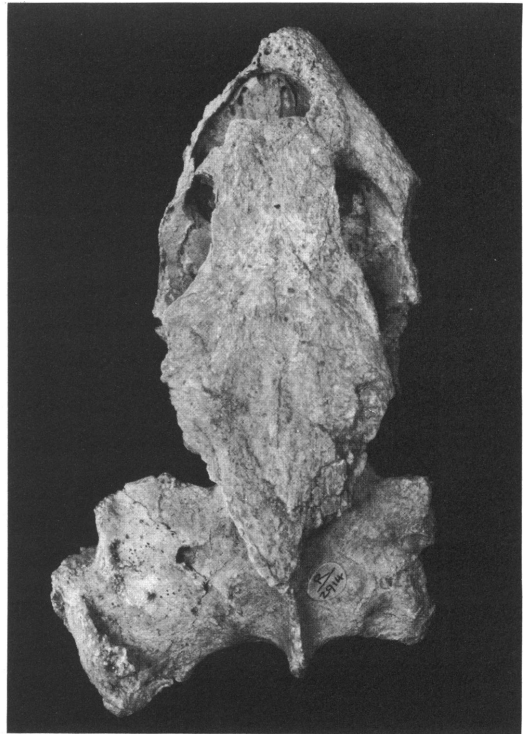


FIG. 11. *Portlandemys mcdowellii*, BM(NH) R2914. Dorsal view of skull.

*Postorbital.* The postorbital is not completely preserved in any one specimen of *Plesiochelys* but MH 435 lacks only the posterior portion, whereas SM 594 provides most of the posterior contacts. The bone has roughly the same relationships as in *Chelydra*. The orbit forms the anterolateral margin, there is a frontal contact anteromedially and a long medial contact with the parietal. Laterally the jugal anteriorly and the quadratojugal posteriorly border the postorbital, whereas posteriorly the bone seems to have a short contact with the squamosal. The postorbital appears to enter the temporal margin and separates the squamosal and parietal, although this area is damaged and ambiguous in SM 594, the one specimen preserving the posterior region. The postorbital of *Portlandemys* (Parsons and Williams, 1961, p. 50) is poorly preserved but agrees with *Plesiochelys* so far as is known.

The Recent cheloniids and *Dermochelys* have a squamosal-parietal contact that prevents exposure of the postorbital along the temporal margin. Although this is often presumed to be the primitive cryptodiran condition (Zangerl, 1948), some have argued that it is secondarily developed from a more emarginate ancestor (Zdansky, 1925). Toxochelyids have an exposed postorbital with a lateral parietal process reducing the amount of exposure, and the postorbital is exposed in the Cretaceous cheloniids *Corsochelys* (Zangerl, 1960) and *Desmatochelys* (Zangerl and Sloan, 1960). Both conditions occur in protostegids, *Rhinochelys* having an exposed postorbital (Collins, 1970), whereas *Protostega* has a limited squamosal-parietal contact (Zangerl, 1953). Other fossil cheloniids (Casier, 1968) also have a squamosal-parietal contact. At the present time I do not think that the systematic distribution of this feature allows a clear choice to be made as to the primitive condition for the Chelonioidae. It is interesting that in the Baenoidae, which is here considered as the sister group of all other cryptodires, the primitive condition is also in doubt although the most likely condition is very limited squamosal-parietal contact.

*Jugal.* The jugal is well preserved in OU J1582, MH 435, and SM 134. In these specimens the bone is a splintlike element with the following limits: the orbit anterodorsally, the maxilla

anteroventrally, the cheek emargination ventrally, the quadratojugal posteriorly and the postorbital dorsally. In general these contacts agree with the condition in most cryptodires. However, in nearly all turtles, the jugal has a medially directed process that lies above the maxilla and together with the maxilla forms the anterior wall of the fossa temporalis inferior and usually articulates with the pterygoid and often with the palatine. In *Plesiochelys* this process is absent and along with the absence of the posteromedial part of the maxilla results in an open foramen palatinum posterius. *Portlandemys* has a medial jugal process and an enclosed foramen palatinum posterius.

The absence of a medial jugal process is rare and I have found it to occur only in *Dermochelys* among the living turtles. Recent testudinids have a reduced zygomatic arch and the jugal-ptyergoid contact is lost but the jugal still sends a process medially that lies on top of the maxilla and forms the anterior wall of the fossa temporalis inferior. The condition of the process is not determinable in many fossil chelonioids but it seems to be absent in the Protosteginae. Specimens of *Protostega dixie* Zangerl, 1953 (FMNH P27315) and *Protostega gigas* Cope, 1871 (AMNH 1503, the type specimen) have what appear to be complete jugals preserved and these lack a medial process and agree with the jugal in *Dermochelys*. *Dermochelys* is also unusual in lacking any part of a recognizable foramen palatinum posterius. All Recent and most fossil cheloniids also lack this foramen but in these cases this seems to be associated with the development of a secondary palate involving considerable changes in the palatine bone. In *Eocheilone*, a presumed cheloniid (Casier, 1968), the secondary palate is not well developed and an open but recognizable foramen palatinum posterius is present. Furthermore, *Erquelinnesia* (a toxochelyid on the basis of shell structure) that has evolved a highly advanced secondary palate apparently independently of the Cheloniidae also lacks the foramen palatinum posterius. This suggests that the loss of the foramen in these forms is associated with the development of a secondary palate. Furthermore, all of these forms have a well-developed medial process of the jugal.

Therefore, only in *Plesiochelys*, Protosteginae,

and Dermochelyidae is the jugal process absent. Unfortunately, in *Rhinochelys*, which apparently has an open foramen palatinum posterius, the presence or absence of the jugal process is unknown, whereas in the other chelosphargine protostegid, *Chelosphargis*, neither structure is known. It would be interesting to determine whether the jugal process is lost in all protostegids.

*Quadratojugal*. The quadratojugal is not well preserved in any specimen but it can be seen best in MH 435. As preserved in this specimen it is roughly C-shaped, has an anterior contact with the jugal, an anterodorsal contact with the post-orbital, and a posterodorsal contact with the squamosal (seen best in SM 594), and a long posterior contact with the quadrate. This agrees well with the condition in *Chelydra* and most turtles. Chelonioids, however, tend to reduce the dorsal portion of the quadratojugal as the squamosal extends anteroventrally. There is no indication of this in *Plesiochelys*. The area is not preserved in *Portlandemys*.

As far as can be determined at present, the

quadratojugal is not exposed in the temporal emargination.

*Squamosal*. The squamosal may be seen in OU J1582, SM 594, and MH 435 although it is not well preserved in any of them. The bone is roughly cone-shaped, forming the antrum postoticum and opening anteroventrally into the cavum tympani of the quadrate. The form and contacts are much as in *Chelydra* and most other turtles: quadrate anteroventrally, quadratojugal anterolaterally, postorbital anterodorsally, and opisthotic posteromedially. The parasagittal crest on the dorsal surface of the squamosal is better developed than in *Chelydra* and is quite similar to the crest in *Toxochelys*.

The antrum postoticum of *Plesiochelys* is smaller than in *Chelydra* and other Testudinoidea but not so reduced as in the living cheloniids. The structure is not well preserved in *Toxochelys* but it seems to be larger in *Toxochelys* than in *Plesiochelys*.

Little of the squamosal is preserved in *Portlandemys* but what is preserved agrees with *Plesiochelys*.

## PALATAL ELEMENTS

*Premaxilla*. The premaxilla is present in SM 135, SM 136, MH 435, and OU J1582, but well preserved only in the last one. Parsons and Williams (1961, pp. 51-53) have described the premaxilla in *Portlandemys* and it is similar to that element in *Plesiochelys*. The two genera differ, however, in that the premaxilla of *Portlandemys* is relatively longer anteroposteriorly and there is a pronounced increase in the area between the lingual ridge and the foramen praepalatinum in comparison with *Plesiochelys*. The two forms also differ in that the angle between the labial ridges of each side is more acute in *Portlandemys* and the median channel between the lingual ridges is narrower in that genus.

The contacts and structure of the premaxilla in plesiochelyids is quite comparable with that in most cryptodires. It meets the other premaxilla medially, the maxilla posterolaterally, and the vomer posteromedially. Its dorsal surface forms the floor of the fossa nasalis and is convex upward along the midline. The foramen praepalati-

num penetrates each premaxilla along the posterior margin of that bone near the maxilla-vomer contact and the maxilla forms the posterior edge of the foramen. This agrees with the condition in *Chelydra*, *Toxochelys*, and many testudinoids. Cheloniids, however, apparently lack the foramen praepalatinum, even in forms such as *Eochelone* that lack a well-developed secondary palate (Casier, 1968). In *Dermochelys* there is a median opening partially separating the premaxillae; whether this represents a fused pair of foramina praepalatina or a *de novo* structure is not known, but as it received the symphyseal tusk of the lower jaw the latter is more likely.

The ventral surface of the premaxilla is involved in the formation of the triturating surface. As in most turtles there is a well-developed labial ridge quite similar to that in *Toxochelys* in that a *Chelydra*-like hook is absent and a slight dorsal curve is present. This region in *Portlandemys* is not preserved completely but what is present of the labial ridge agrees with *Plesiochelys*. The



lingual ridge is prominent on the premaxillae of *Plesiochelys* and *Portlandemys* and it appears to be higher and thicker in *Portlandemys* than in *Plesiochelys* (see maxilla for further discussion).

**Maxilla.** The maxilla is preserved in all *Plesiochelys* specimens except SM 594 although it is best seen in OU J1582, MH 435, and SM 134. The maxilla of *Portlandemys* is also known in detail (see Parsons and Williams, 1961, p. 54).

The maxilla may be divided into two plates: a dorsal-vertical one, and a ventral-horizontal one. In overall morphology the bone is comparable with the maxilla of *Chelydra*, *Toxochelys* and testudinoids having a primary palate. The dorsal plate forms the lateral wall of the fossa nasalis

and contains the foramen alveolare superius near the lateral edge of the foramen orbito-nasale.

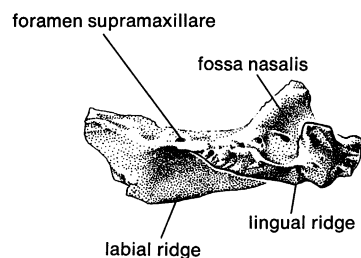


FIG. 12. *Portlandemys mcdowelli*, BM(NH) R3163. Medial view of left maxilla, anterior at right.

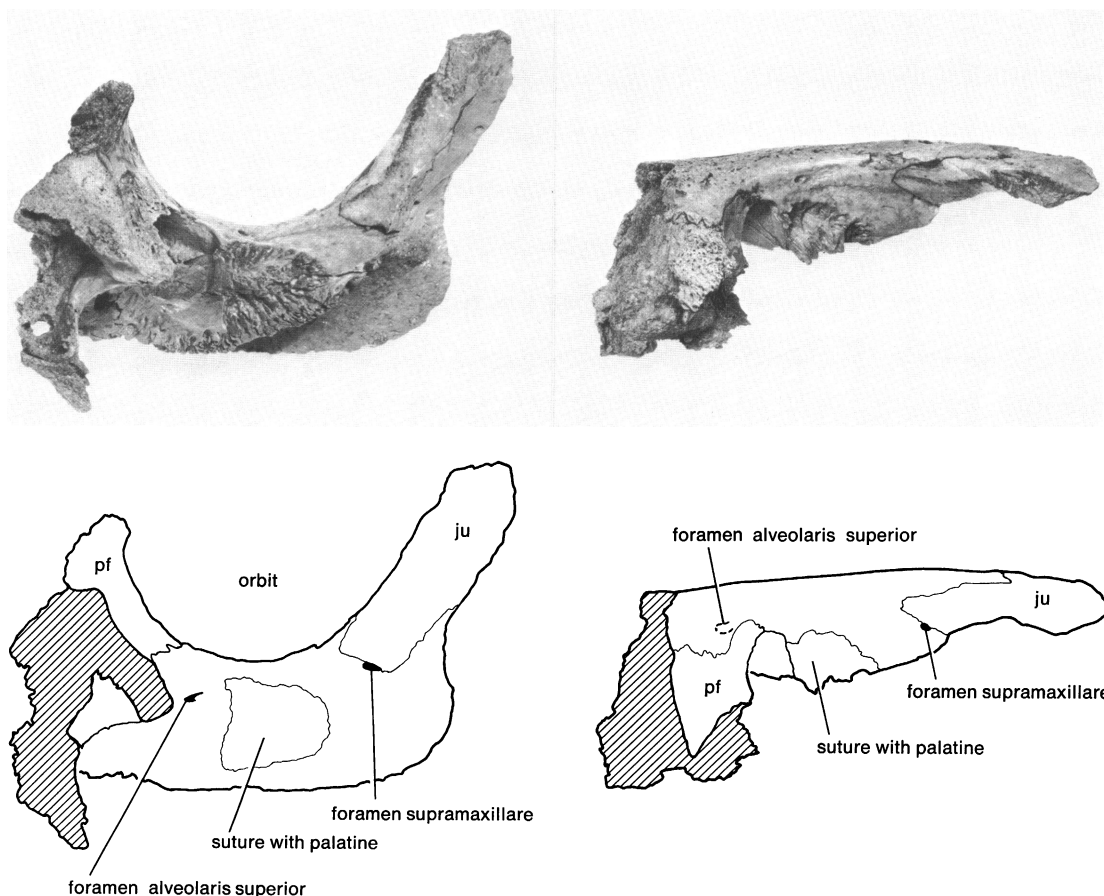


FIG. 13. *Plesiochelys planiceps* OU J1582. Medial (left), dorsal (right) views of right maxilla, jugal, and portion of prefrontal. Hatched areas are matrix. Foramen alveolaris superior is hidden in dorsal view but its position is indicated.

This plate meets the premaxilla anteroventromedially, the prefrontal dorsomedially, and the nasal dorsally. The horizontal plate forms much of the triturating surface, the floor of the fossa

orbitalis, and contacts the vomer anteromedially, the palatine medially, and the jugal posterodorsally.

The vascular canal system is the same in *Port-*

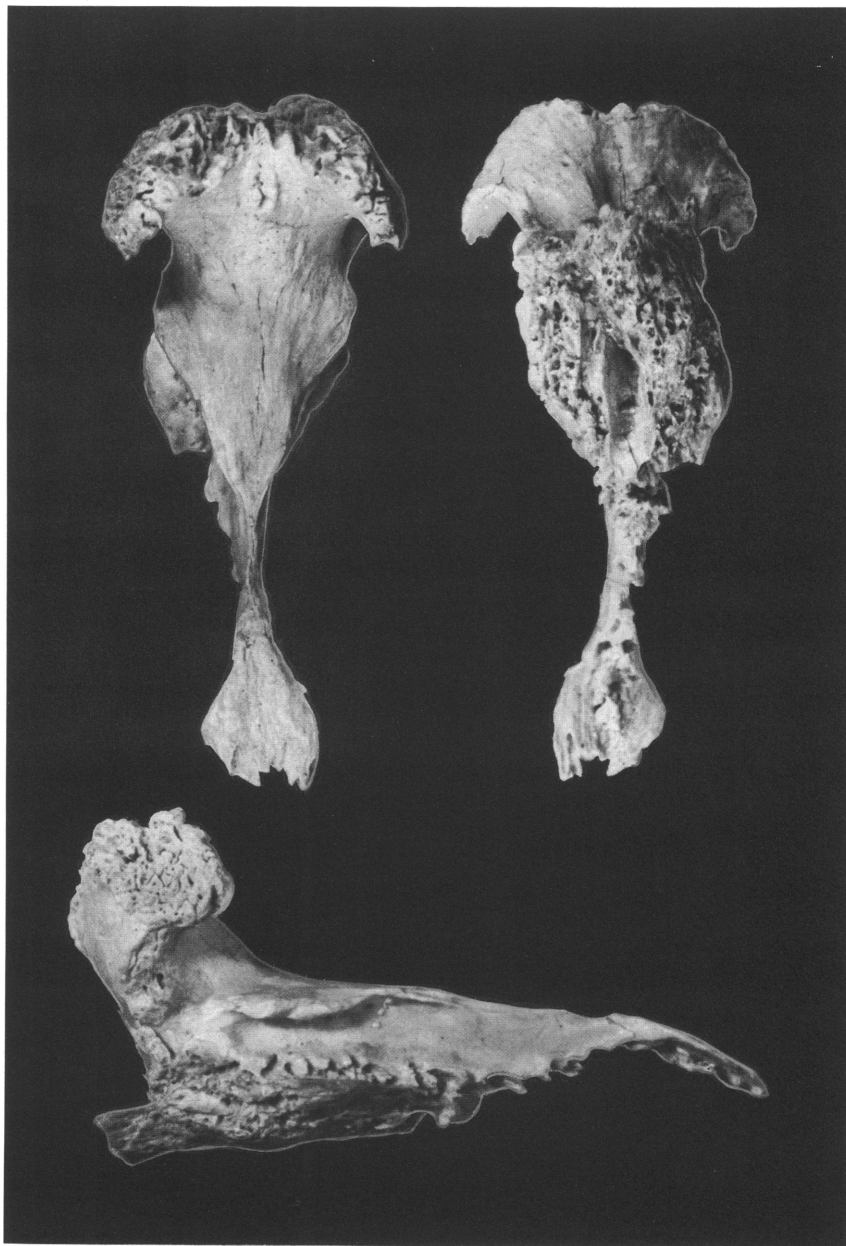


FIG. 14. *Plesiochelys etalloni*, SM 134. Disarticulated vomer, ventral (upper left), dorsal (upper right), and lateral (lower, anterior at left).

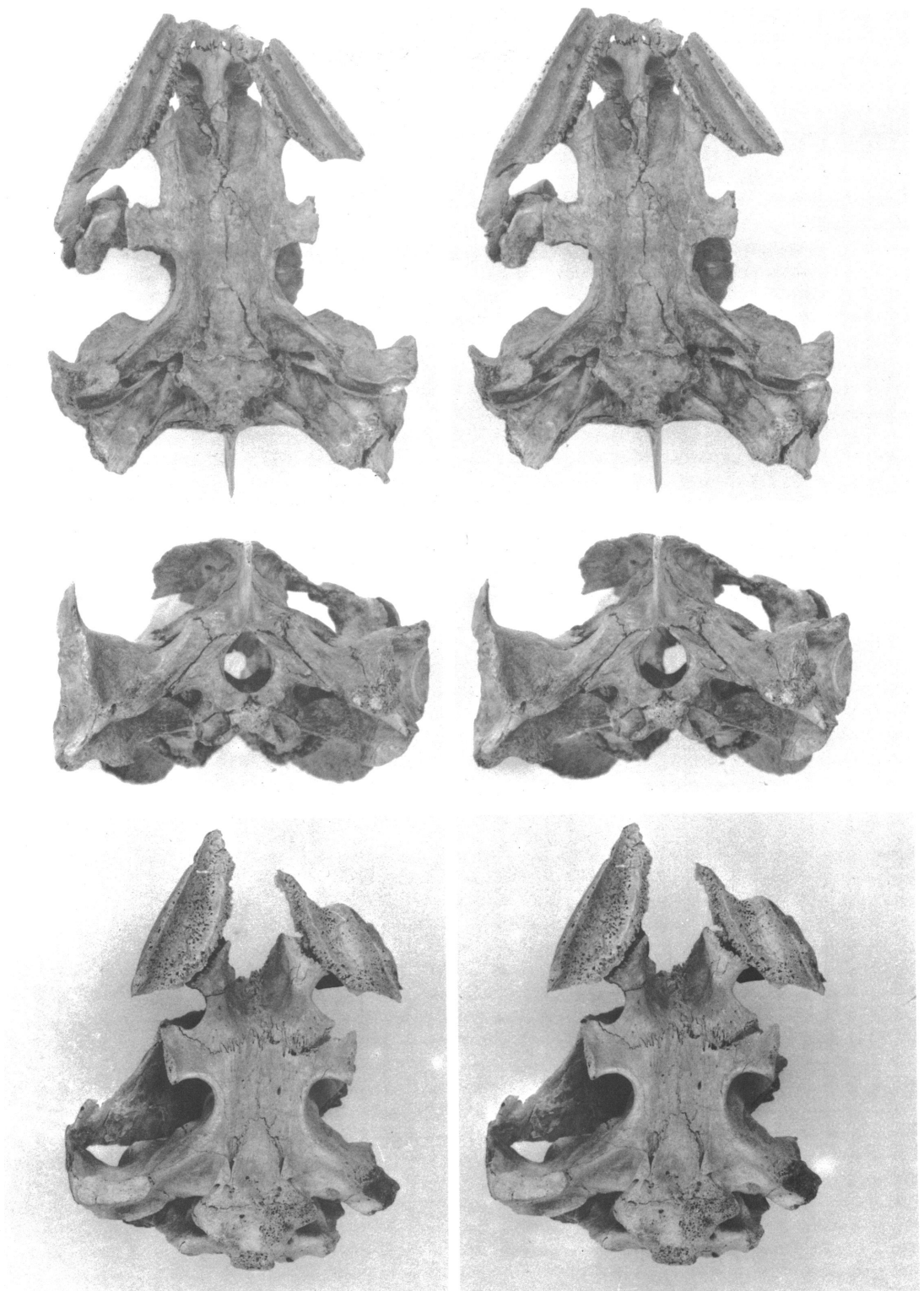


FIG. 15. Upper, *Plesiochelys planiceps*, OU J1582, palatal view, see Gaffney (1975a, p. 18) for partially restored palate; middle, *Plesiochelys planiceps*, OU J1582, occipital view, see figure 16; lower, *Plesiochelys etalloni*, SM 134, palatal view.

*landemys* and *Plesiochelys* and differs somewhat from *Chelydra*. In the plesiochelyids the foramen supramaxillare is relatively small and the foramen alveolare superius relatively large, whereas in *Chelydra* and most testudinids they are about the same in size. Recent chelonids lack the foramen supramaxillare but *Dermochelys* has a well-developed one and a smaller foramen alveolare superius. *Toxochelys* also has both foramina well developed as in *Chelydra* but the condition in other fossil chelonoids is not known. Plesiochelyids and *Toxochelys* have an unnamed foramen at the anteroventral corner of the orbit that apparently communicates with the canalis alveolaris superior. Unfortunately, only limited information is available on the internal canal morphology of the maxilla in plesiochelyids.

The maxilla forms the lateral wall of the foramen orbito-nasale as in most turtles (see prefrontal). *Toxochelys* is unusual in having a greatly reduced foramen orbito-nasale and the maxilla contributes very little if any of the foramen in this genus.

The posterior portion of the maxilla in *Portlandemys*, *Chelydra*, and most testudinids forms part of the foramen palatinum posterius and contacts the jugal posterodorsally and the pterygoid posteromedially. This is also the case in baenids and can be considered primitive for cryptodires and possibly for all turtles. However, *Plesiochelys* differs from this condition by having a foramen palatinum posterius that opens into the fenestra subtemporalis. In *Plesiochelys* this is the result of the absence of a medial jugal process (see jugal) and a reduction of the posterior portion of the maxilla with loss of the pterygoid contact. As mentioned elsewhere (see jugal) other forms (*Rhinochelys*, *Eochelone*) with an open foramen palatinum posterius are not well enough known in this area for detailed comparisons. As with the reduced jugal process, the reduced posterior part of the maxilla is a feature held in common with *Dermochelys*. In *Dermochelys*, however, the palatine has extended posteriorly to obliterate the remaining portion of the foramen palatinum posterius.

The ventral surface of the horizontal maxillary plate bears most of the triturating or alveolar surface, which in life is covered by a horny rhamphotheca. *Plesiochelys* and *Portlandemys* have a similar triturating surface with both labial

and lingual ridges well developed and a deep trough between them. The ridges and trough are continuous with the same structures on the premaxillae. The labial ridge of *Plesiochelys* becomes lower anteriorly as it approaches the premaxillae and in lateral view it is broadly curved, concave downward. The labial ridge in *Portlandemys* is not well preserved but appears to be straight in side view. The lingual ridge of both genera is broader and blunter than the labial ridge. The lingual ridge parallels the labial ridge and in *Portlandemys* each pair forms a more acute angle than in *Plesiochelys*. The height of the lingual ridge is variable among the *Plesiochelys* specimens. It is higher and more acute in the largest skull (here considered to be a different species than the others), OU J1582, and lower and blunt in the smallest skull, MH 435. The other specimens are intermediate in these features and in skull size suggesting that this may be due to growth. A portion of the medial side of the lingual ridge forms part of the apertura narium interna but most of the maxilla contacts a thin, anterior process of the palatine.

The development of a high lingual ridge is rare in chelonoids and even the testudinoids, which have prominent lingual ridges, do not have them as greatly developed as in plesiochelyids. The closest similarity appears to be with *Rhinochelys*

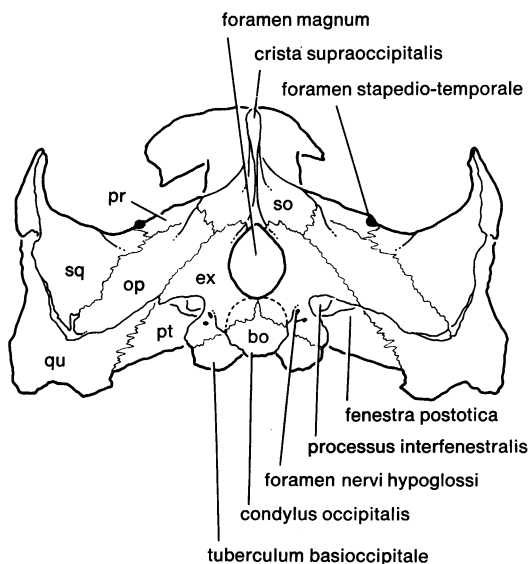


FIG. 16. Key to figure 15, middle.

(Collins, 1970), which does have a prominent lingual ridge. Furthermore, the lower jaw is similar and apparently fits into the maxilla the same way (*ibid.*, fig. 10). The posterior part of the

maxilla in *Rhinochelys*, however, is distinctly broader than in plesiochelyids and the lingual ridge is not so high or acute.

Bräm (1965) described *Plesiochelys* as having

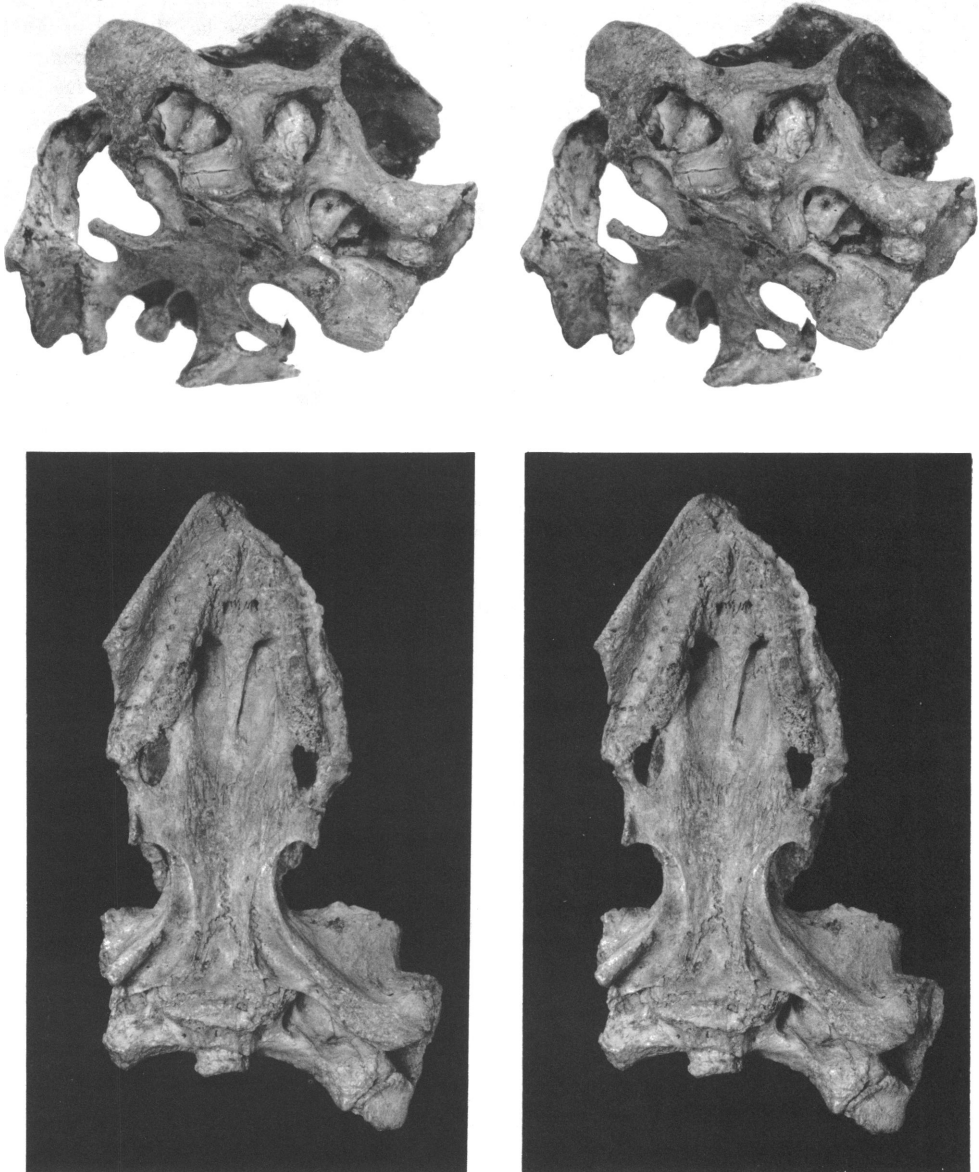


FIG. 17. Upper, *Portlandemys mcdowelli*, BM(NH) R3164, oblique occipital view, see figure 18; lower, *Portlandemys mcdowelli*, palatal view, see Gaffney (1975b, pp. 16, 17) for partial restoration and labeled diagram.



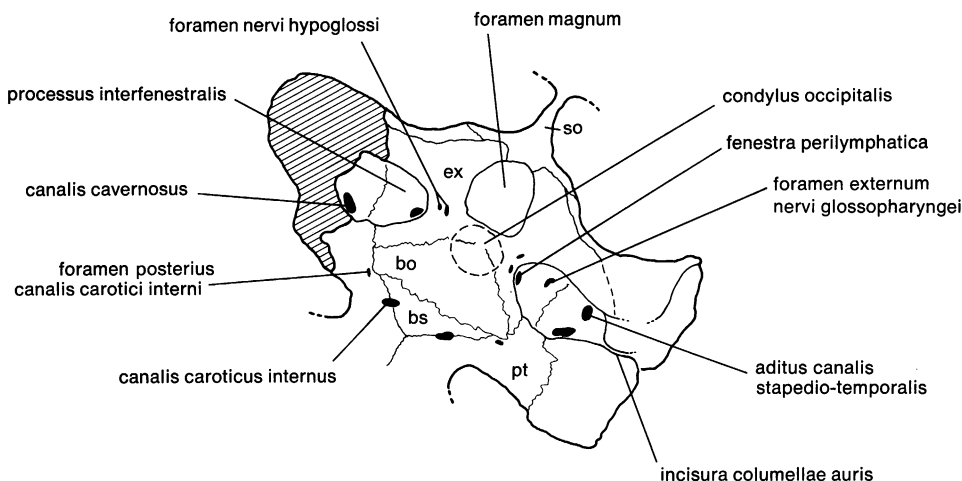


FIG. 18. Key to figure 17, upper. Hatched area is broken.

a secondary palate but this is not the case and, in fact, none of the specimens even approach it.

**Vomer.** The vomer is present in all the *Plesiochelys* specimens except SM 594. It is particularly well preserved in SM 134 where it has been disarticulated for easier study.

The vomer in *Portlandemys* and *Plesiochelys* is similar to that bone in *Chelydra*, most testudinoids, and most baenids. The contacts are as follows: premaxilla anteriorly, maxilla anterovenrolaterally, prefrontal anterodorsally (above the apertura narium interna), palatine laterally, and pterygoid posteriorly. The bone is roughly dumb-bell-shaped. The anterior enlargement forms part of the fossa nasalis which the sulcus vomeri extends along the dorsal surface. The middle of the vomer separates the paired apertura narium interna. Presumably this condition is primitive for turtles.

In most *Plesiochelys* specimens the vomer forms the posterior margin of the foramen praepalatium but in the right side of SM 135 the foramen is contained entirely in the premaxilla. In *Portlandemys* the vomer also forms the posterior margin of the foramen praepalatium.

The posterior portion of the vomer in *Plesiochelys* and *Portlandemys* reaches the pterygoids and separates the palatines on the ventral surface. But on the dorsal surface the palatines meet for

most of their length and the exposure of the vomer is limited to the area around the fissura ethmoidalis. In *Chelydra* the vomer separates the palatines on both the dorsal and ventral surfaces. The dorsal surface of this region is not known in most fossil chelonoids but the condition of the ventral surface is as follows: *Toxochelys*, vomer separates palatines; *Rhinochelys*, palatines meet for about half their length (Collins, 1970); *Archelon*, palatines apparently meet (Wieland, 1900); *Eochelone*, vomer separates palatines (Casier, 1968). Among Recent chelonoids, the chelonoids have a vomer greatly modified by the development of a secondary palate and *Dermochelys* has a vomer that separates the palatines (dorsally and ventrally) for most but not all of their length.

The posterolateral margin of the vomer in most testudinoids, *Chelydra*, baenids, and *Toxochelys* is expanded to form part of the palate roof, along with the palatines. In *Plesiochelys* and *Portlandemys*, however, this expansion is absent, and is presumably a derived character.

**Palatine.** The palatine is preserved in all *Plesiochelys* specimens except SM 594. The palatine in *Portlandemys* and *Plesiochelys* is nearly identical, the only difference appears to be that in *Portlandemys* the palatine is narrower due to the closer approximation of the triturating surfaces.

The description by Parsons and Williams (1961, pp. 56-57) will suffice for both genera:

"In palatal view the two palatines are separated by the vomer with which they are in contact throughout their entire length. Each forms a rather flat plate which is farthest dorsal at its anteromedial corner where it forms a short suture with the ventromedial portion of the prefrontal; from there it slopes posteroventrally. Posteriorly it possesses a rather irregular suture with the pterygoid. Laterally, it forms the medial margin of the foramen palatinum posterius and the posteromedial margin of the foramen orbitonasale. Between these foramina a massive process

extends ventrolaterally to meet the postero-medial edge of the maxilla where it forms a small posterior portion of the prominent lingual ridge. The medial half of the palatine forms the roof of the apertura narium interna. The vomer extends somewhat ventral to the medial portion of the palatine so that there is a distinct groove between the vomer and the lateral portion of the palatine.

"The dorsal surface of the palatine forms most of the floor of the orbit; its relations there are the same as on the ventral surface except that the two palatines meet in a sagittal suture dorsal to the vomer for the posterior two-thirds or three-quarters of their length."

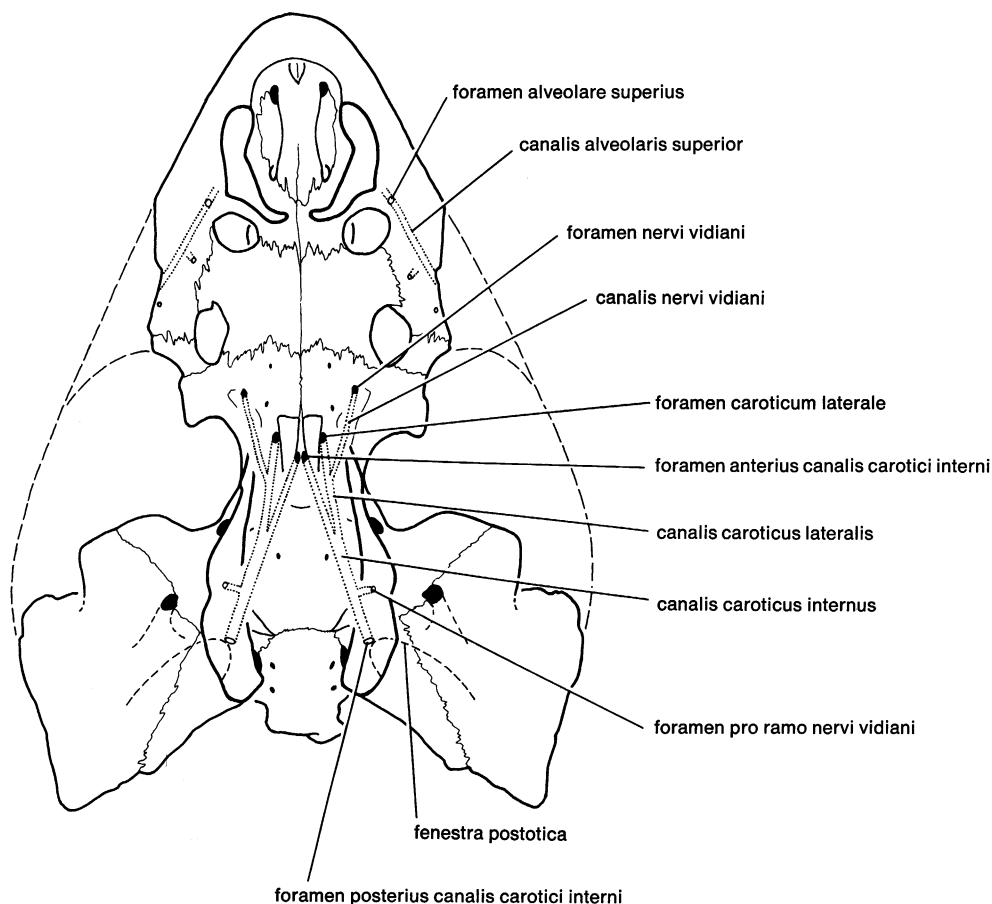


FIG. 19. *Portlandemys mcdowelli*, based primarily on BM(NH) R2914 and BM(NH) R3163. Dorsal view of horizontally sectioned skull (see fig. 21) with canals indicated by dotted lines. Canals determined by probing with bristle or examination of broken specimens and exact morphology somewhat stylized. Canal diameters slightly exaggerated for clarity but relative diameters accurate.

## BASICRANIAL AND BRAINCASE ELEMENTS

*Canalis caroticus internus and associated structures.* The arterial canal system of turtles is of considerable systematic interest and one of my primary goals in studying *Plesiochelys* was to determine its arterial pattern. The relative wealth and high quality of the specimens has allowed me to do this to the same extent that one could study a recent skull. Unfortunately many of the fossil groups are not known in equal detail so meaningful comparisons with other fossil forms are limited.

The foramen posterius canalis carotici interni lies near the posterior edge of the pterygoid just anterior to the basisphenoid-ptyergoid suture. In all the specimens of *Portlandemys* and *Plesiochelys* the foramen is formed by bone that is to some extent broken and eroded. The best preserved examples, however, indicate a difference between the two genera. In *Portlandemys* the foramen posterius canalis carotici interni is formed entirely by the pterygoid (as reported by Parsons and Williams, 1961, p. 60, and substantiated by me) although the structure is near the

ptyergoid-basisphenoid suture. The foramen posterius canalis carotici interni of *Plesiochelys*, on the other hand, appears to be formed mostly by the pterygoid but the dorsomedial margin is formed by the basisphenoid. This is seen on the right hand side of SM 134, the best preserved example of the foramen.

The canalis caroticus internus extends antero-medially from the foramen posterius canalis carotici interni and is formed in both genera by the pterygoid laterally and ventrally and by the basisphenoid medially. The canalis is nearly straight rather than curved as in *Chrysemys* and has a relatively thin covering of bone ventrally. About halfway along its length the canalis caroticus lateralis branches off laterally from the canalis caroticus internus. This area can be seen in damaged specimens of *Portlandemys* (BM(NH) R3163) and *Plesiochelys* (SM 594, SM 135, SM 134). About midway between the opening into the canalis caroticus lateralis and the foramen posterius canalis carotici interni is a short, dorso-laterally directed canal formed in the pterygoid and containing the posterior branch of the facial (VII) nerve and termed the foramen pro ramo nervi vidiani. This structure allows communication between the canalis caroticus internus and the sulcus cavernosus and dorsally it is formed by the prootic and pterygoid.

The canalis caroticus internus is distinctly smaller in diameter than the foramen stapedio-temporalis, in most specimens the former is about one-third the diameter of the latter.

*Canalis caroticus lateralis and associated structures.* About midway along the canalis caroticus internus another canal is given off laterally; this is the canalis caroticus lateralis, which contains the palatine artery. In *Portlandemys* the canalis nervi vidiani can be probed and is seen to branch off the canalis caroticus lateralis, but in *Plesiochelys* the relations of the two canals cannot be determined. In both genera the canalis caroticus lateralis is formed by the pterygoid bone and is about the same diameter as the anterior part of the canalis caroticus internus.

The foramen caroticum laterale of *Plesiochelys* and *Portlandemys* lies in the sulcus cavernosus just lateral to the rostrum basisphenoidale. It

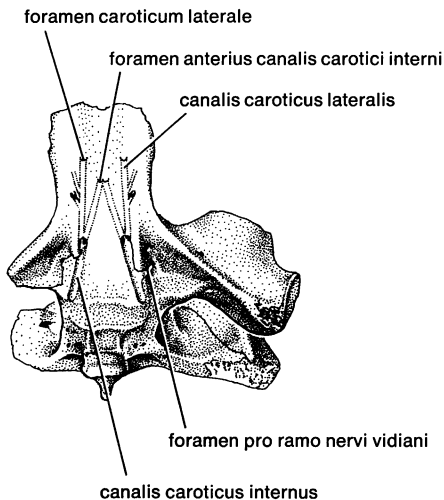


FIG. 20. *Portlandemys mcdowelli*, BM(NH) R3163. Ventral view of eroded braincase fragment showing internal canals. Dotted canals are within bone and were determined visually and with bristles. All canals seen here were contained in bone in life but some are now visible due to bone erosion.

is formed primarily by the pterygoid and is about the same diameter as the foramen anterius canalis carotici interni. The canalis nervi vidiani branches off the canalis caroticus lateralis in *Portlandemys* and goes anterolaterally to open at the anterior edge of the epipterygoid suture at the base of the crista pterygoidea. In most *Plesiochelys* specimens the foramen caroticum laterale and the foramen nervi vidiani open into a groove formed in the floor of the sulcus cavernosus between the crista pterygoidea and the rostrum basisphenoi-

dale. The foramen caroticum laterale usually marks the posterior limit of the groove, whereas the foramen nervi vidiani usually enters the groove more anteriorly. There is a marked constriction at the anterior end of the groove where the anterior tip of the rostrum basisphenoidale widens slightly to nearly meet the crista pterygoidea and/or epipterygoid, which runs medially at this point.

In view of the systematic interest of this region it would be best to describe the condition

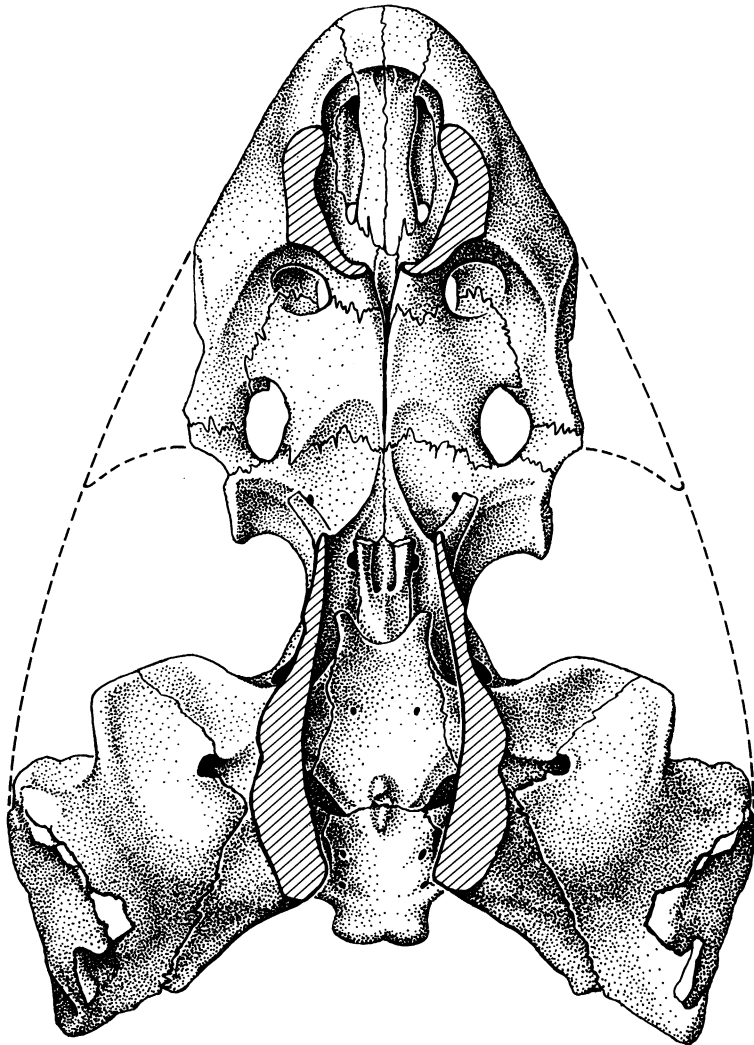


FIG. 21. *Portlandemys mcdowellii*. Dorsal view of horizontally sectioned skull, based on BM(NH) R2914 and R3164.

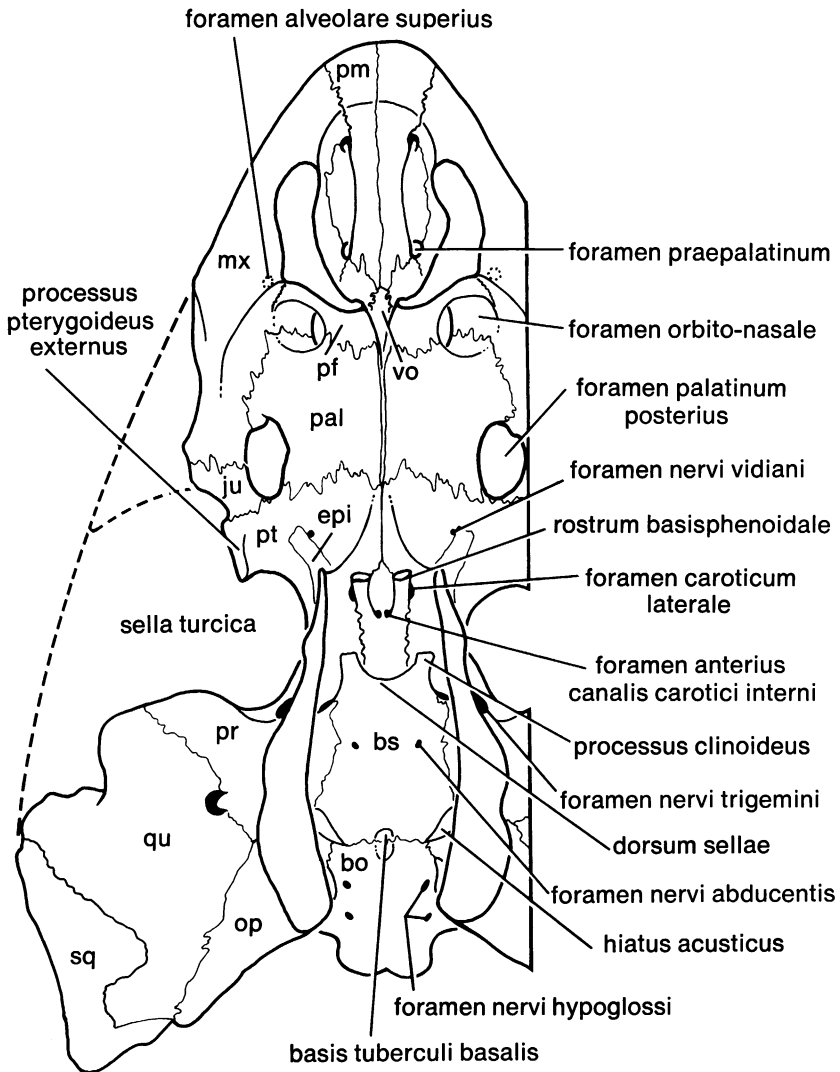


FIG. 22. Key to figure 21.

in each specimen of *Plesiochelys* because no two specimens agree in detail and each side of one individual may differ. The right side of SM 135 (the basis of the frontal section, fig. 23) is similar to most of the other *Plesiochelys* specimens in that the open groove is well developed and the foramen caroticum laterale is at the posterior end of the groove but the foramen nervi vidiani enters the groove just adjacent to the foramen caroticum laterale rather than more anteriorly. The contents of these foramina apparently

moved anteriorly with the palatine (vidian) nerve going ventrolaterally through the notch at the anterior end of the groove and the palatine artery going anteriorly into the snout but not going through the notch. The left side yields some support for this speculation. The foramen caroticum laterale is situated more anteriorly than on the right side and the foramen nervi vidiani is much farther anterior and nearly at the edge of the groove. On the right side, however, the groove is closed dorsally by a meeting of the pterygoid



portion underlying the rostrum basisphenoidale and the crista pterygoidea of the pterygoid. The notch present in most other *Plesiochelys* specimens is a foramen in this skull, SM 135, which contains the palatine (vidian) nerve. The anterior opening of the foramen is in the pterygoid just ventral to the epipterygoid suture and in a position that is quite similar to the foramen nervi vidiani in *Portlandemys*. In SM 594 and MH 435 the groove is narrower than in the other speci-

mens and the exact position of the foramen nervi vidiani is not readily seen. The anterior notch, however, is present and a foramen is not developed. In SM 134 the groove on both sides is much shorter than in the other specimens and both foramen caroticum laterale and foramen nervi vidiani are situated more anteriorly in comparison to the other skulls. A notch rather than a foramen is present. The rostrum basisphenoidale of SM 136 has short lateral spurs on the anterior

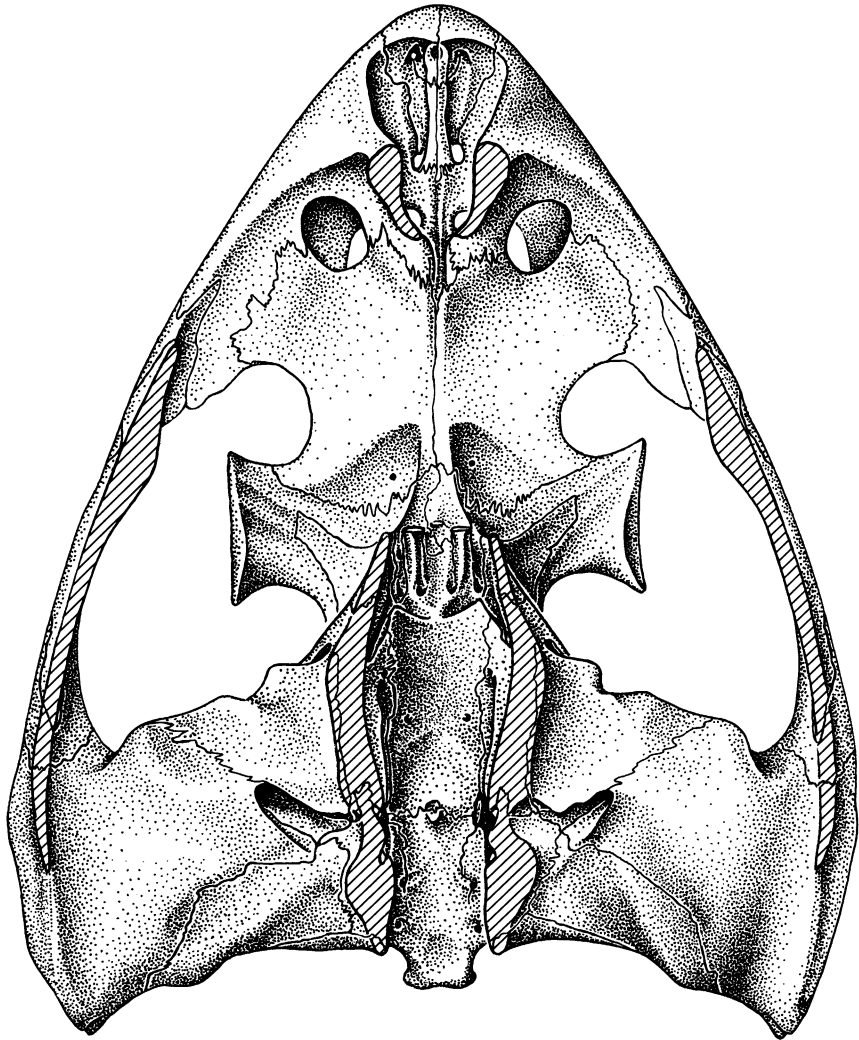


FIG. 23. *Plesiochelys etalloni*. Dorsal view of horizontally sectioned skull, based primarily on SM 135 (see Gaffney, 1975a, p. 11, for photographs).

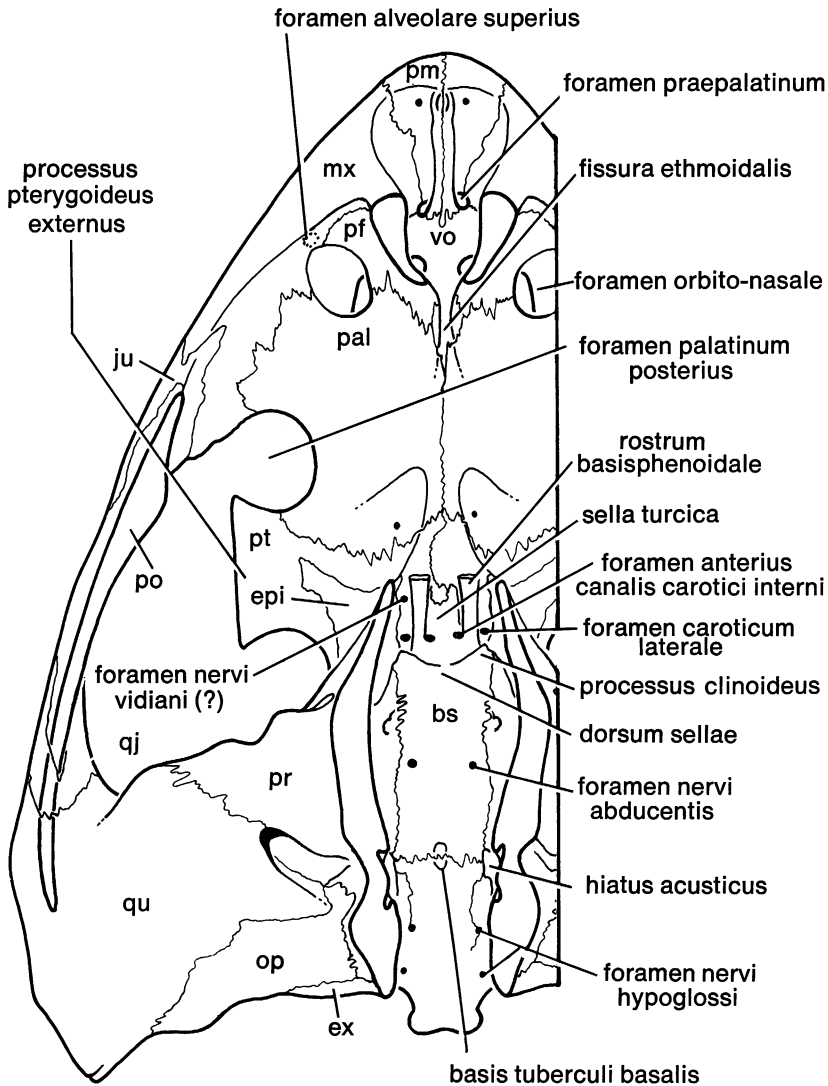


FIG. 24. Key to figure 23.

tip of each ossified trabecula that constrict the notch but otherwise the skull has the usual features seen in *Plesiochelys*: a well-developed groove, foramen caroticum laterale at the posterior margin, and the foramen nervi vidiani more anteriorly. In the Portland *Plesiochelys planiceps* skull, OU J1582, the groove appears to be completely absent, the foramen nervi vidiani lies near the pterygoid-epipterygoid suture as in *Portlandemys*, and the foramen caroticum laterale appar-

ently lies very near the anterior edge of the rostrum basisphenoidale.

An examination of this variation suggests to me the following hypothesis. The condition in *Portlandemys* and *Plesiochelys planiceps* may be primitive, that is, the foramen nervi vidiani lies outside the cavum epipterygoid near the pterygoid-epipterygoid suture, the foramen caroticum laterale opens near the anterior end of the rostrum basisphenoidale and no groove is present.

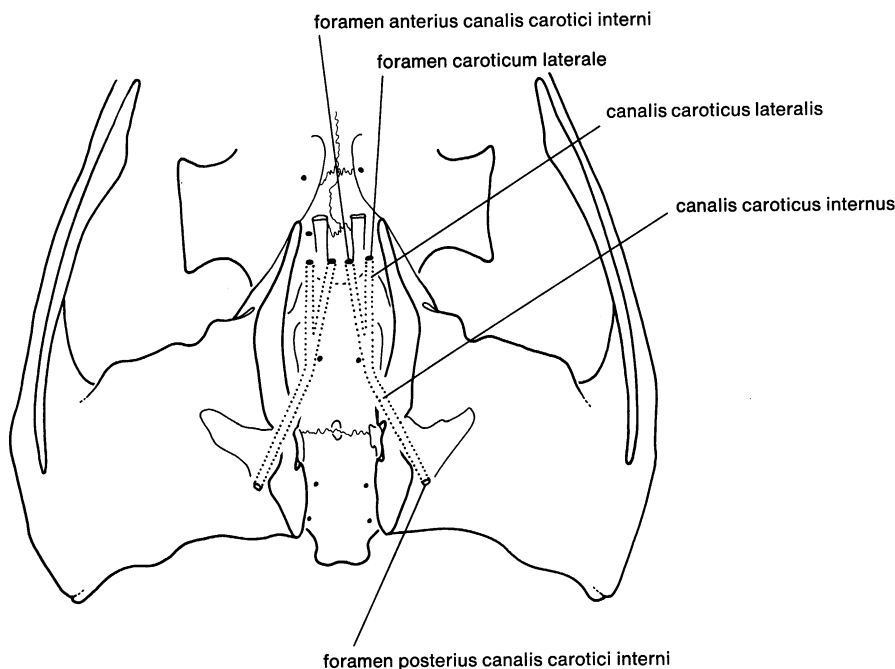


FIG. 25. *Plesiochelys etalloni*. Diagrammatic reconstruction of arterial canals in basicranium, based on bristle probing of all available specimens. Canal diameter based on foramen diameter.

More advanced conditions, seen in *Plesiochelys etalloni*, involve the loss of the dorsal roof of the canalis caroticus lateralis and the development of the groove in the floor of the sulcus cavernosus. The canalis nervi vidiani in this region is effectively obliterated and the nerve travels in the groove and exits from the cavum epiptericum via an open notch instead of a foramen.

One of the most characteristic specializations of the cheloniid skull is the absence of a closed canalis caroticus lateralis and the presence of an arterial system in which the internal carotid enters the sulcus cavernosus, gives off the palatine artery (which continues anteriorly in the sulcus), then turns medially to enter the foramen anterius canalis carotici interni. There has been no functional explanation offered in the literature for this condition but the cheloniids are unusual in having a palatine artery that is about the same size as the internal carotid (as the latter exits from the foramen anterius canalis carotici interni), and perhaps this is related to the "open" canalis caroticus lateralis.

McDowell (1961) and Albrecht (1967) have

suggested that an equal-sized palatine artery and internal carotid artery is the primitive condition for turtles. Perhaps, however, this is in fact a specialized condition developed only in cheloniids and *Dermochelys*. Support for this comes from examination of other turtle groups, particularly the "sister" groups of the Eucryptodira and Cryptodira (see Gaffney, 1975c). The Baenoidea is the sister taxon for the Eucryptodira and in the baenoids the palatine artery is reduced as in testudinoids. The sister group for the cryptodires is the Pleurodira and in pleurodires the palatine artery is reduced or absent. It would seem then that the reduced palatine artery is primitive for turtles in general and cryptodires in particular.

The relative size of the palatine artery in *Plesiochelys* can be estimated from the size of the foramen caroticum laterale and would appear to at least approach the size of the internal carotid. It is possible, then, that *Plesiochelys* has begun to modify the canalis caroticus lateralis and palatine artery in the cheloniid direction. In *Portlandemys* the foramen caroticum laterale is also about the same diameter as the foramen anterius

canalis carotici interni, but in *Toxochelys* the foramen caroticum laterale is reduced as in most other turtles. On this basis, the plesiochelyids could be considered more advanced with respect to cheloniids than *Toxochelys* (see discussion).

*Pterygoid.* Although the pterygoid is preserved in all six *Plesiochelys* specimens it is not equally well preserved or accessible for study. Sutures and overall preservation are best seen in SM 134, whereas internal details are visible in SM 135 and MH 435.

*Extracranial features.* The anterior edge of the pterygoid contacts the palatine, anteromedially there is a short contact with the vomer (only on the ventral surface) and anterolaterally the pterygoid forms the posterior margin of the foramen palatinum posterius. In *Portlandemys* the anterolateral edge contacts the jugal, whereas in *Plesiochelys* there is no contact and the foramen palatinum posterius is open (see jugal). A well-developed processus pterygoideus externus is formed on the anterolateral portion of the pterygoid just posterior to the foramen palatinum posterius.

The ventral surface of the pterygoid in *Plesiochelys* and *Portlandemys* is quite comparable with the morphology of this surface in *Chelydra* and other testudinoids. There is a concave embayment between the processus pterygoideus externus and the quadrate ramus of the pterygoid for the passage of the pterygoideus jaw musculature. Around the edge of this concavity portions of the pterygoideus may attach (see Schumacher, 1954, 1955a, 1955b, 1973). The attachment site is usually marked by a scar or depression and such a structure is prominent in *Portlandemys* and *Plesiochelys*. The form of the scar is the same in both genera. The attachment site seems to extend around the "waist" of the pterygoid to the processus pterygoideus externus but the anterior portion is very narrow and lies on the edge of the bone. The scar begins to expand medial to the processus and curves posteriorly to the area of the foramen posterius canalis carotici interni. Between the foramen and the quadrate ramus of the pterygoid there is a prominent depressed region within the pterygoideus attachment site. The trough area extends posterolaterally onto the quadrate where it merges with the attachment area of the depressor mandibulae.

The pterygoideus muscle attachment site in the two Jurassic genera has a form commonly

seen in turtles. Most Emydidae and Baenidae show a similar form with emydids in having the depression as well as the overall limits. *Chelydra* differs from the plesiochelyids in that the scar is more extensive anteriorly but less posteriorly and the attachment site margin roughly parallels the fenestra subtemporalis. In most specimens of *Toxochelys* and *Ctenochelys* the scar is similar to *Chelydra* but there is variation in relative width among specimens. In living cheloniids the pterygoideus attachment covers nearly all the ventral surface of the pterygoid and the surface is developed into a prominent trough (except in *Chelonia*).

Medially the pterygoid meets the other pterygoid for the anterior half of its length in a sagittal suture and meets the triangular basisphenoid for the posterior half of its length in a posterolateral suture. The posterior limits of the pterygoid are well preserved and clear only on the right side of SM 134. In this specimen there is a posteromedial contact with the basioccipital but not with the exoccipital, whereas in *Portlandemys* the pterygoid contacts the exoccipital as well as the basioccipital (Parsons and Williams, 1961, p. 65). Posterolaterally the pterygoid contacts the quadrate and between the quadrate and basioccipital it forms the ventral margin of the fenestra postotica.

The dorsal surface of the pterygoid is known only from articulated specimens of both *Plesiochelys* and *Portlandemys* and a detailed comparison cannot be made. The crista pterygoidea separates the intracranial from the extracranial areas and it appears to be quite comparable with most testudinoids and chelonoids. Due to the large size of the epipterygoid, particularly in *Plesiochelys*, the crista pterygoidea appears low on the external surface but it is actually about the same size and shape as in *Chelydra*. The crista forms the lower margin of the foramen nervi trigemini as in most turtles. This part of the pterygoid is isolated in lateral view from the more ventral pterygoid area by contact of the fully ossified epipterygoid and quadrate in *Plesiochelys* (SM 134), whereas in *Portlandemys* and other *Plesiochelys* (MH 435) the fossa cartilaginis epipterygoidei, formed in part by the pterygoid, lies between the quadrate and epipterygoid.

Anteromedially the pterygoid forms the posterior portion of a dorsolaterally facing concavity

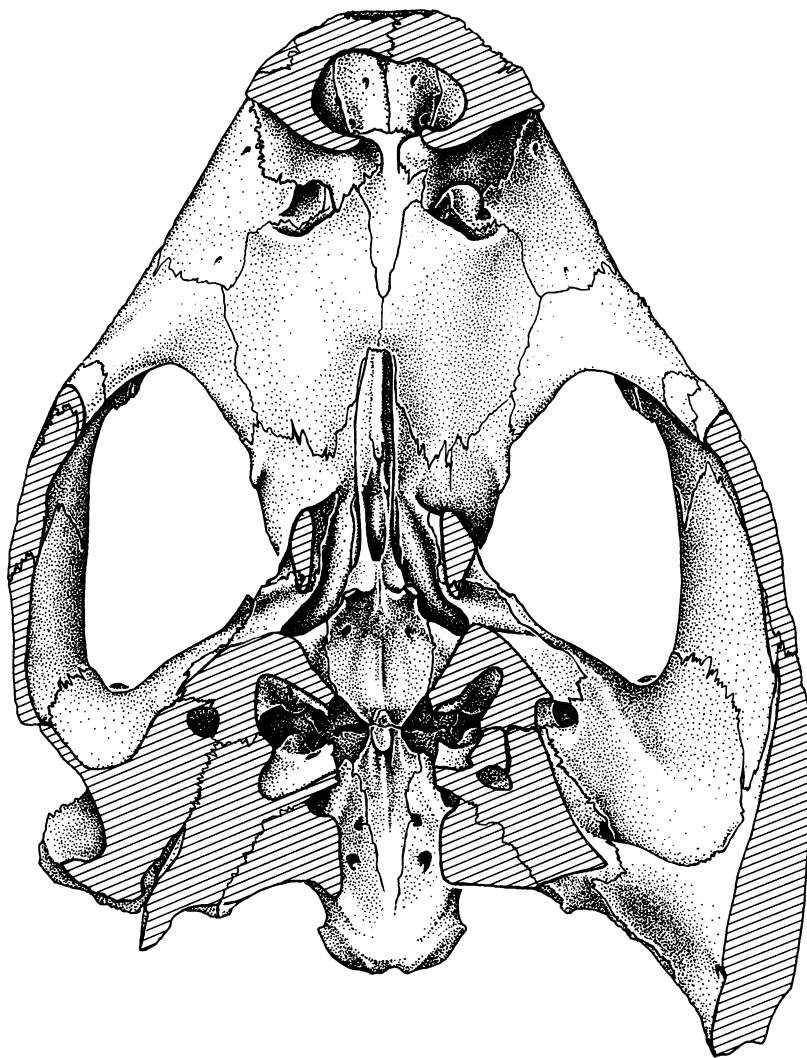


FIG. 26. *Chelonia mydas*. Dorsal view of horizontally sectioned skull, AMNH 111964.

that lies just anterior to the side wall of the braincase on the dorsal surface of the pterygoid. This depression occurs in both plesiochelyids and is apparently the attachment site of one of the eye muscles and although it occurs in some Recent turtles, it is usually not this prominent.

Medial to the crista pterygoidea the pterygoid forms the troughlike floor of the sulcus cavernosus and canalis cavernosus as in other turtles. The anterior end of the sulcus is involved with the foramen caroticum laterale and foramen nervi

vidiani which are described elsewhere (see canalis caroticus internus). The foramen pro ramo nervi vidiani penetrates the pterygoid and connects the sulcus cavernosus and canalis caroticus internus. Its relations are the same as in other eucryptodires.

*Epipterygoid.* The epipterygoid is present in all *Plesiochelys* specimens but best seen in SM 134 and MH 435. In *Portlandemys* the bone is readily observed in BM(NH) R3164 and BM(NH) R2914.



The epipterygoid is a platelike bone, roughly triangular in outline, that lies between the crista pterygoidea and the processus inferior parietalis in the side wall of the braincase. In *Plesiochelys* there is some variation in the degree to which the epipterygoid is ossified. In SM 134 the bone is completely ossified posteriorly, reaching the quadrate and obliterating the fossa cartilaginosa epipterygoidei. Anteriorly, a process extends

anterolaterally onto the dorsal surface of the pterygoid. In MH 435 the epipterygoid does not reach the quadrate, the fossa cartilaginosa epipterygoidei is well developed, and the anterior process barely extends onto the pterygoid. These differences appear to be due mostly to age because other features of MH 435 (small size, open sutures) suggest a young individual also.

The epipterygoid in both genera is relatively

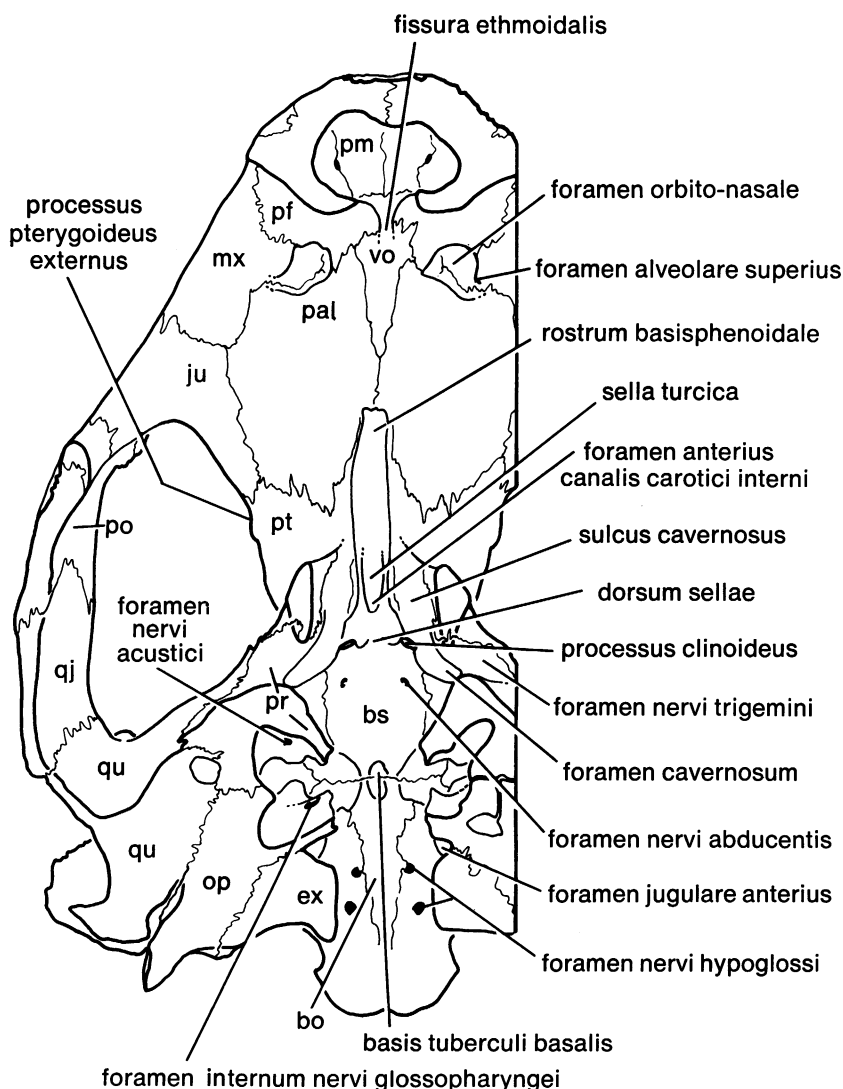


FIG. 27. Key to figure 26.

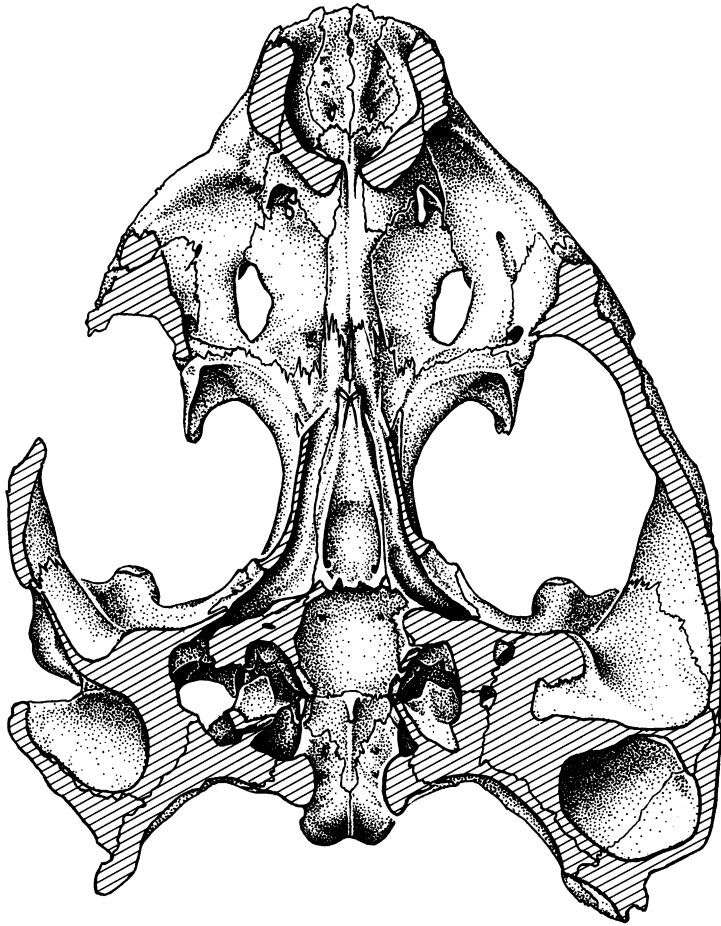


FIG. 28. *Chelydra serpentina*. Dorsal view of horizontally sectioned skull, AMNH 67015.

large but comparable in size with some testudinoids. In one specimen of *Plesiochelys*, SM 134, the bone enters the margin of the foramen nervi trigemini but does not in *Portlandemys* or the other *Plesiochelys* skulls. In both forms the epipterygoid is broadly exposed in the margin of the foramen interorbitale. The epipterygoid is exposed on the internal surface of the braincase wall and in *Plesiochelys* there is a low projection on the epipterygoid near the parietal-pterygoid suture that tends to separate the space above the sulcus cavernosus into dorsal and ventral portions.

*Basisphenoid.* The basisphenoid is preserved in

all six *Plesiochelys* skulls but a disarticulated element is not available. One specimen, SM 135, has had the skull roof removed so that the basiocranium is completely visible.

The ventral features of the basisphenoid are the same in *Portlandemys* and *Plesiochelys*. As in most turtles the bone is triangular, has antero-lateral contacts with the pterygoids, and a transverse contact with the basioccipital. There is no indication in either genus of the curved depression found in living cheloniids and in *Toxochelys*.

The basisphenoid of baenids and most other cryptodires does not extend laterally for the

whole width of the basioccipital but this is the condition in *Plesiochelys* and *Portlandemys*, and is therefore presumed to be derived with respect to other cryptodires. In *Toxochelys* and *Ctenochelys* the basisphenoid and basioccipital are the same width but both bones are relatively narrower than in plesiochelyids.

The foramen posterius canalis carotici interni lies very near the posterior edge of the pterygoid-basisphenoid suture and in *Plesiochelys* the basisphenoid contributes to a small portion of the foramen but in *Portlandemys* the foramen posterius canalis carotici interni is formed en-

tirely by the pterygoid (see canalis caroticus internus).

The dorsal surface of the basisphenoid is divided into an anterior and a posterior region separated by the dorsum sellae. In most turtles the anterior region (consisting of the sella turcica and rostrum basisphenoidale) is equal to or longer than the posterior region, but in *Portlandemys*, *Plesiochelys*, and baenids the anterior region is distinctly shorter than the posterior one. In *Toxochelys* the two portions are about the same size. Lack of ossification of the anterior portion of the trabeculae in the rostrum basi-

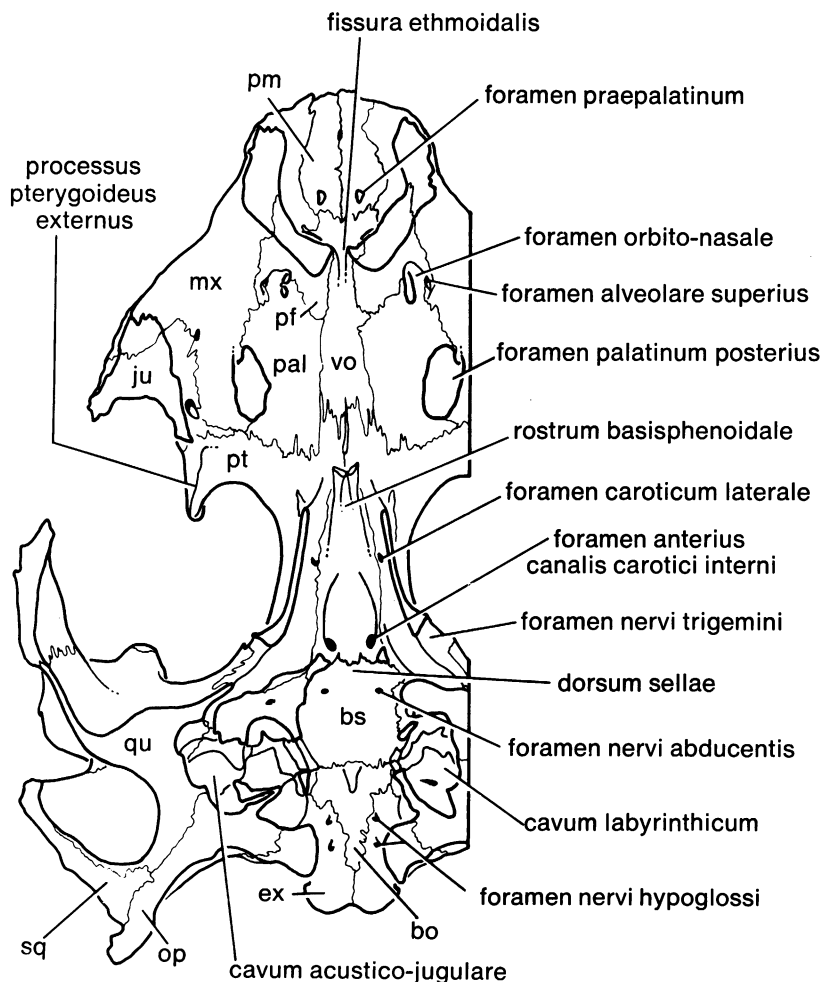


FIG. 29. Key to figure 28.

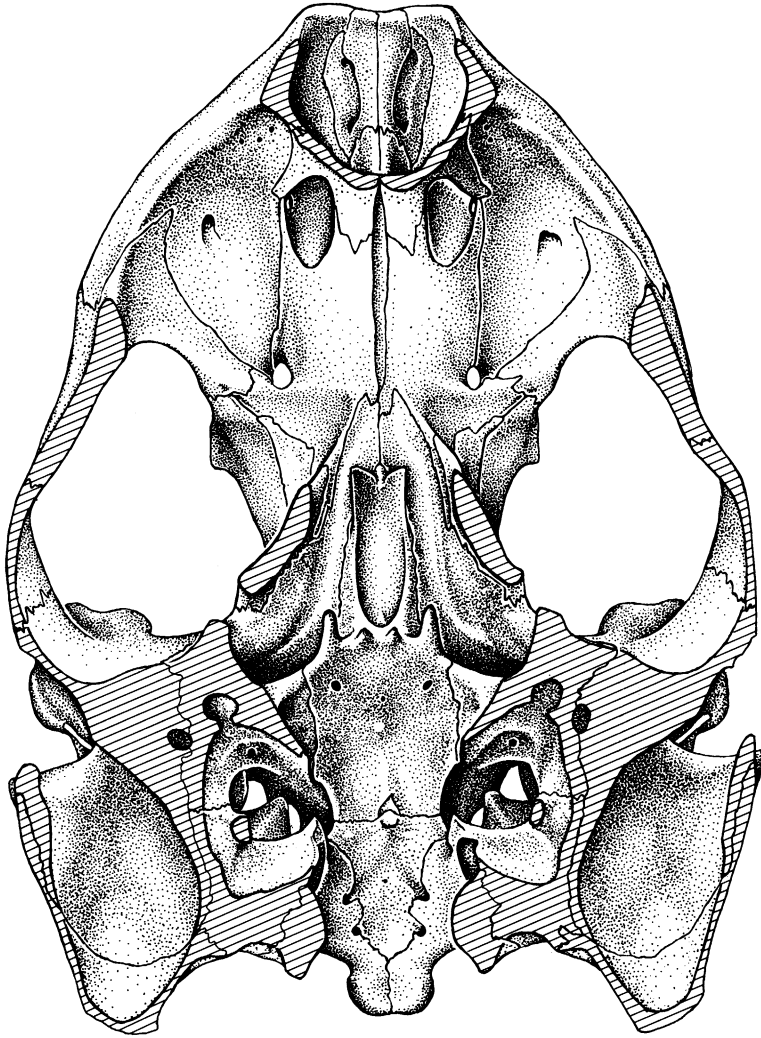


FIG. 30. *Chrysemys concinna*. Dorsal view of horizontally sectioned skull, AMNH 111960.

sphenoidale causes this condition to a certain extent but the posterior portion does seem relatively long in comparison with most turtles, especially *Chelydra* and cheloniids.

The abducens (VI) nerve in *Plesiochelys* enters the basisphenoid about midway along the length of the posterior basisphenoid length. This position of the paired foramen nervi abducentis is more posterior than in most turtles but it is similar to the position in *Portlandemys*, *Glyptops*, and baenids, and it may be primitive

for cryptodires. The anterior foramen nervi abducentis in both *Portlandemys* and *Plesiochelys* is ventral and posterior to the base of the processus clinoides, very near the pterygoid-basisphenoid suture in *Plesiochelys*, and almost in the floor of the sulcus cavernosus. In most turtles, including baenids and pleurodires, the canalis nervi abducentis penetrates the processus clinoides anterior and dorsal to its position in the Jurassic genera resulting in the posterior foramen nervi abducentis being anterior to its

position in the Jurassic forms and the anterior foramen nervi abducentis being anterodorsal to its position in these genera. Presumably this condition of the canalis nervi abducentis is a derived character shared by *Plesiochelys* and *Portlandemys*.

The processus clinoides in *Portlandemys* is

best preserved in BM(NH) R3164 where it "extends a short distance dorsolaterally as well as anteriorly, and ends bluntly" (Parsons and Williams, 1961, p. 64), as in most turtles. In *Plesiochelys*, however, the processus clinoides curves dorsolaterally and is broadly sutured to a process from the prootic. The processus clinoides is an

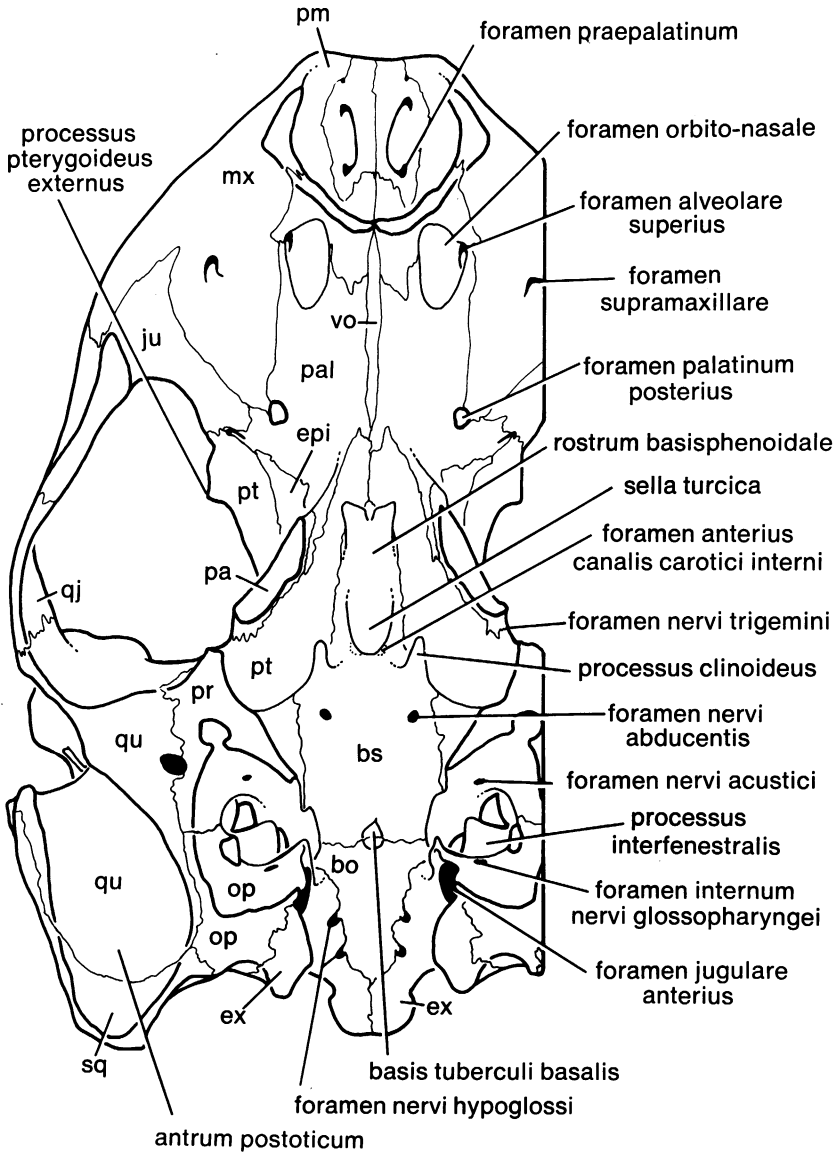


FIG. 31. Key to figure 30.

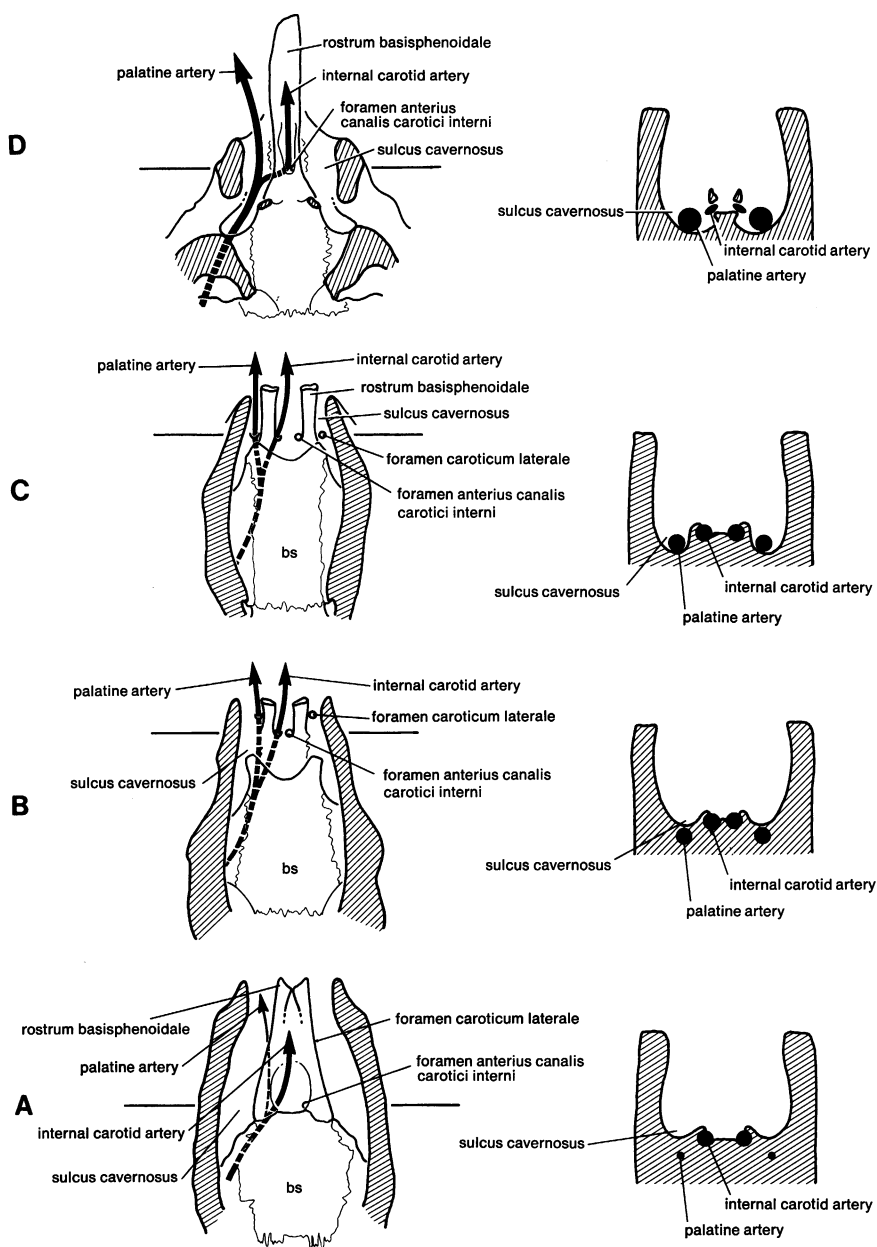


FIG. 32. Comparison of basicranial structures used in developing a hypothesis of relationships of chelonoid turtles. A, *Chelydra serpentina*; B, *Portlandemys mcdowellii*; C, *Plesiochelys etalloni* (SM 135); D, *Chelonia mydas*. Left-hand figures are dorsal views of basisphenoids and associated structures; right-hand figures are transverse sections taken at positions indicated on dorsal views by a pair of heavy lines. All figures are diagrammatic, actual diameter of restored arteries is exaggerated but relative diameters are accurate.

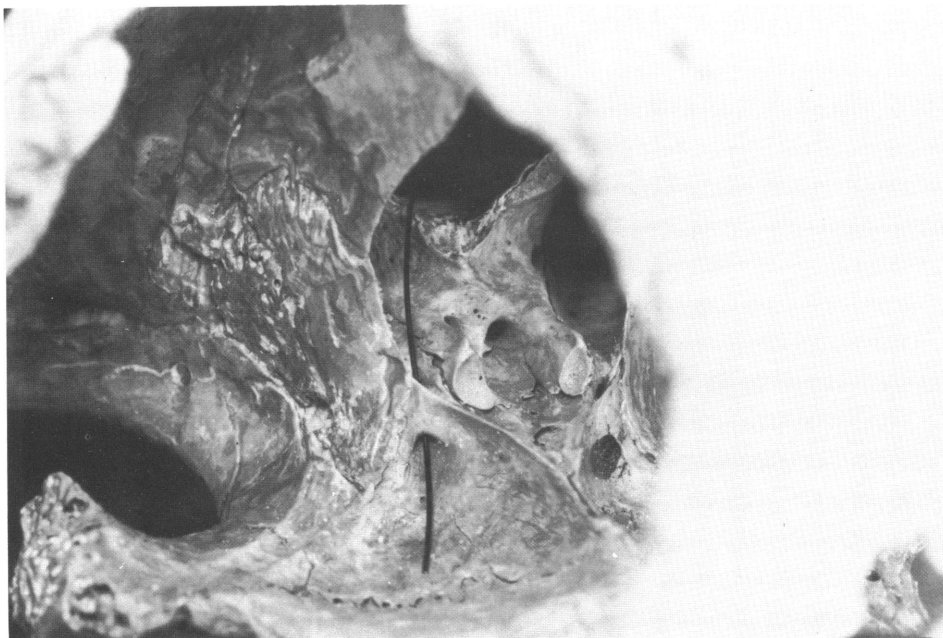


FIG. 33. *Plesiochelys planiceps*, OU J1582. View of basisphenoid and surrounding area through right orbit. Bristle (arrow in key) is in foramen nervi vidiani. See figures 34-36.

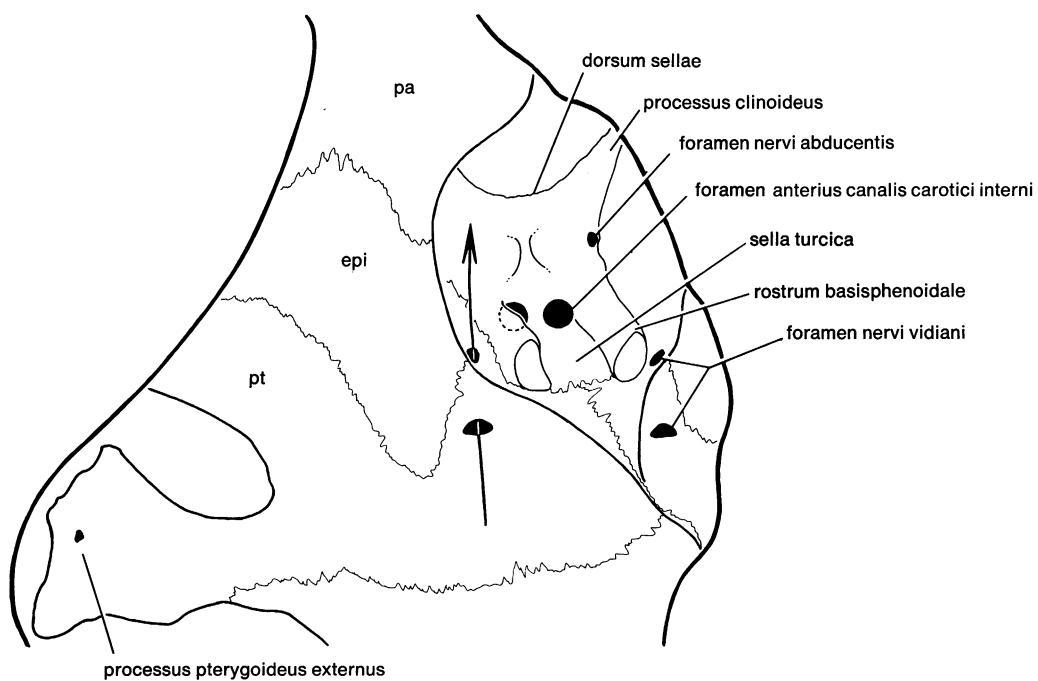


FIG. 34. Key to figure 33.



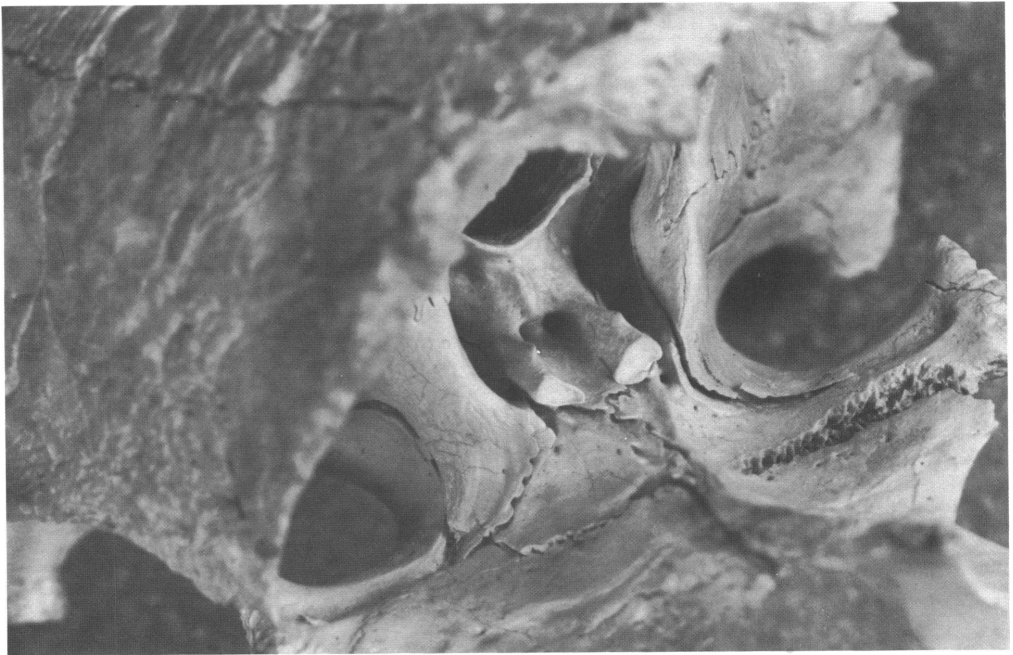


FIG. 35. *Plesiochelys etalloni*, SM 134. View of basisphenoid from same angle as in figure 33 (figure 34 can be used to identify structures seen here as well).

ossification of the embryonic pila prootica (see Kunkel, 1912) and in all turtles except *Plesiochelys* only the ventral portion ossifies. In *Plesiochelys*, however, it would seem that the whole pila prootica has ossified. I have no idea of the functional significance of this and as it apparently occurs only in *Plesiochelys* it has limited systematic significance.

The degree to which the pila prootica is ossified varies among the *Plesiochelys* specimens, but due to the fragile nature of the structure its reduction is in part due to postmortem damage, especially in OU J1582 and SM 594. MH 435 is interesting in that the processus clinoides is extended toward but does not reach a short process from the prootic. The unfinished, depressed ends of these processes suggest that the cartilage connected them. In SM 134 and SM 135 the pila prootica is a complete band connecting the prootic and the processus clinoides but there is a depressed, unfinished anterior margin to the structure that suggests further unossified cartilage in life.

The anterior portion of the basisphenoid consists of the sella turcica and the ossified trabeculae of the rostrum basisphenoidale. This region of the basicranium is of some phylogenetic interest in chelonoids and is one of the few basicranial regions that has figured in phylogenetic ideas about turtles. This is primarily due to the fact that the living chelonoids have a highly modified basisphenoid. Embryologic work has also supported the idea that this area is distinctive in chelonoids. First I summarize the chelonoid condition and then I compare this with other turtles, particularly *Portlandemys* and *Plesiochelys*.

The living Cheloniidae are characterized by having a rostrum basisphenoidale that is a rod-like, median bar, elevated off the underlying bone (pterygoids). The sella turcica is essentially obliterated owing to the rodlike nature of the rostrum and the medial position of the paired foramen anterior canalis carotici interni. In other turtles the trabeculae that ossify to form the rostrum are distinct paired elements that lie

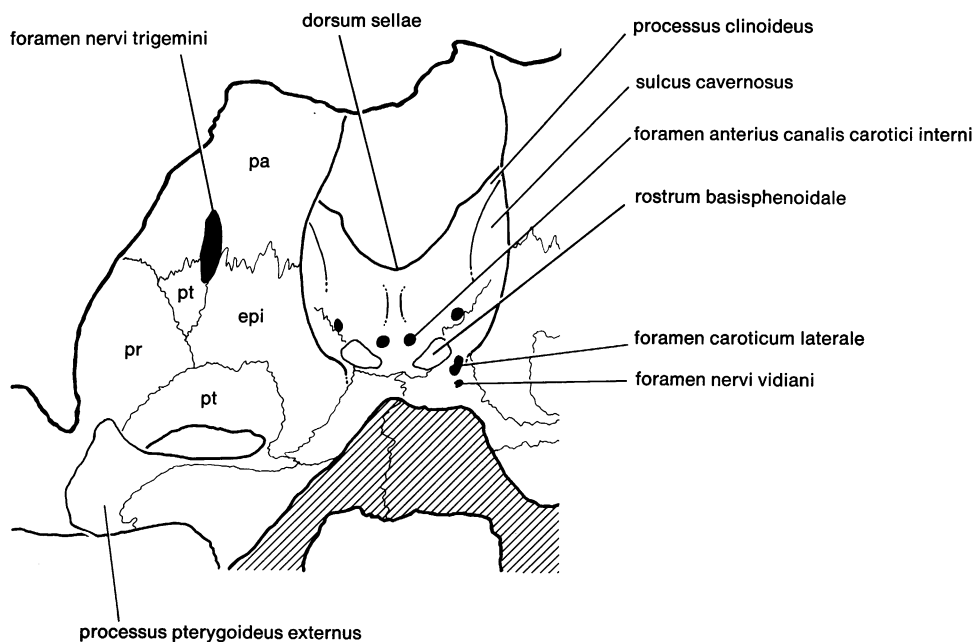
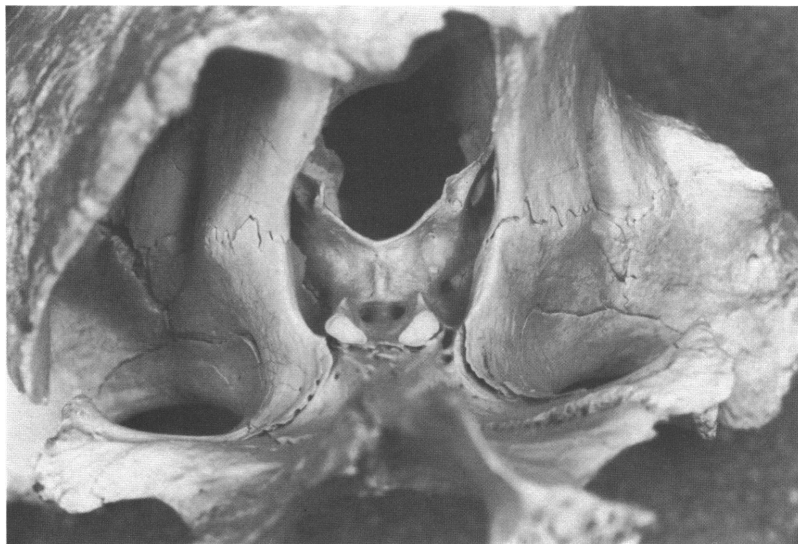


FIG. 36. *Plesiochelys etalloni*, SM 134. Anterior view of basisphenoid and surrounding area. See figures 33-35.

lateral to the sella turcica and form the margins of that structure, and, although the trabeculae may be fused anteriorly as in pleurodires, they

are separated posteriorly. In testudinoid, trionychoid, and baenoid turtles the foramen anterior canalis carotici interni usually lies in the postero-

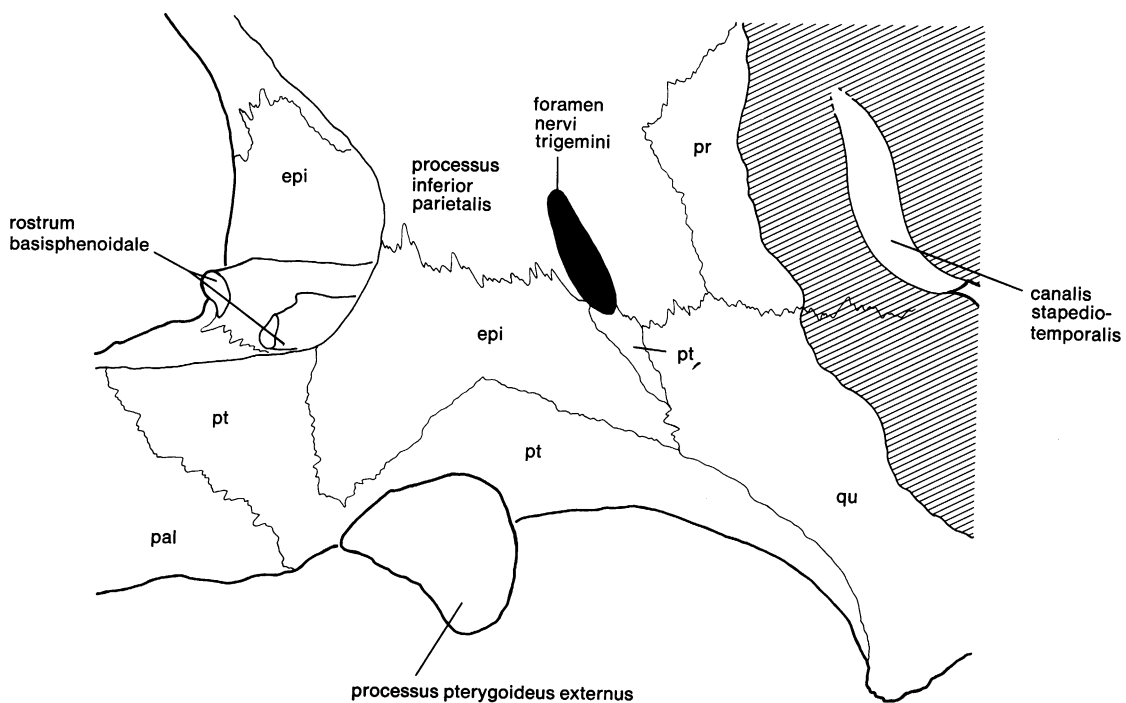


FIG. 37. *Plesiochelys etalloni*, SM 134. Lateral view of left ethmoid region.

lateral margin of the sella turcica. The foramen in cheloniids, however, is separated from its mate only by a thin bar of bone and in most forms they may appear to be a common opening.

The embryology of the basisphenoidal region has also been investigated (Nick, 1912; Pehrson, 1945) and emphasizes the distinctive nature of the chelonioid basisphenoid. In turtles the basi-

sphenoid actually consists of a dermal parasphenoid portion and an endochondral "true" basisphenoid that fuse together in the adult but are distinguishable in the embryo. According to Pehrson (1945) nonchelonioid turtles have an anterior and posterior parasphenoid rudiment but only the posterior one ossifies. In chelonioids there is a new element in the chondrocranium in

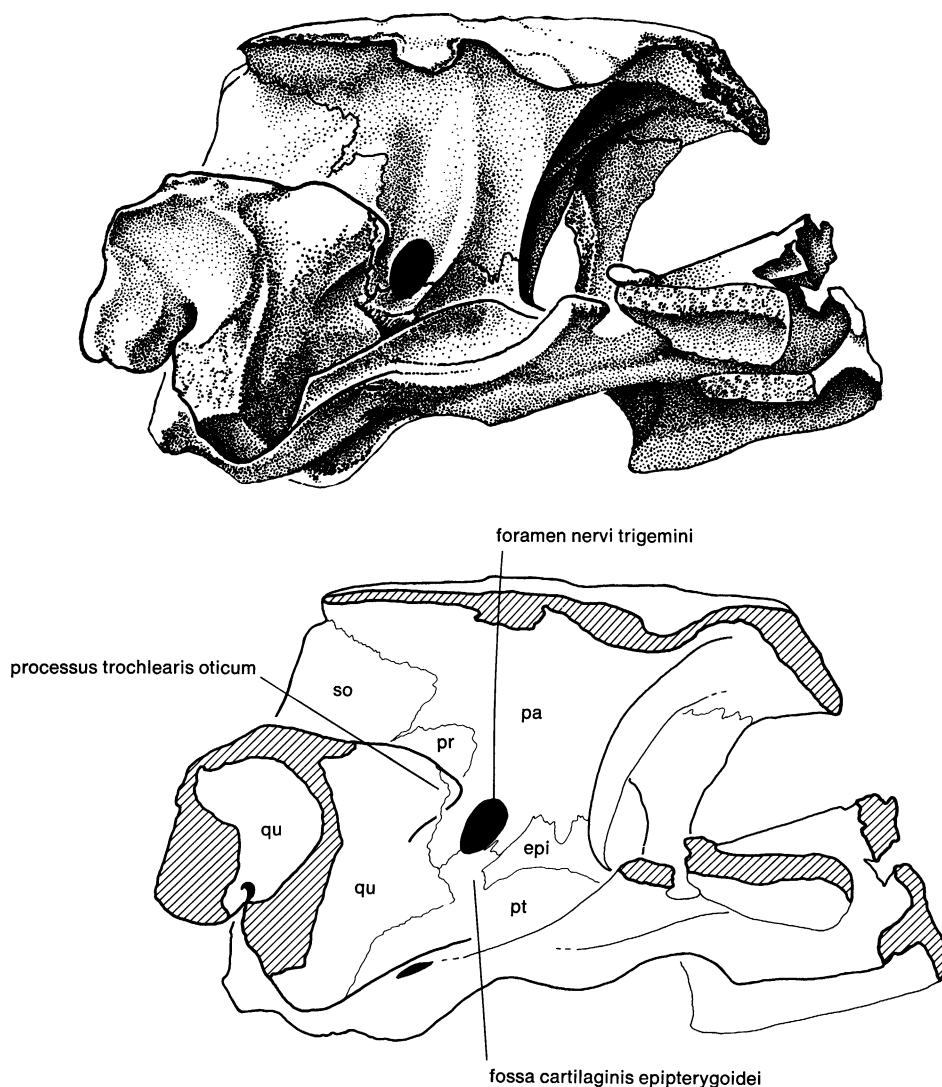


FIG. 38. *Portlandemys mcdowelli*, BM(NH) R3164. Lateral view of right ethmoid region (stippled drawing modified from Parsons and Williams, 1961).

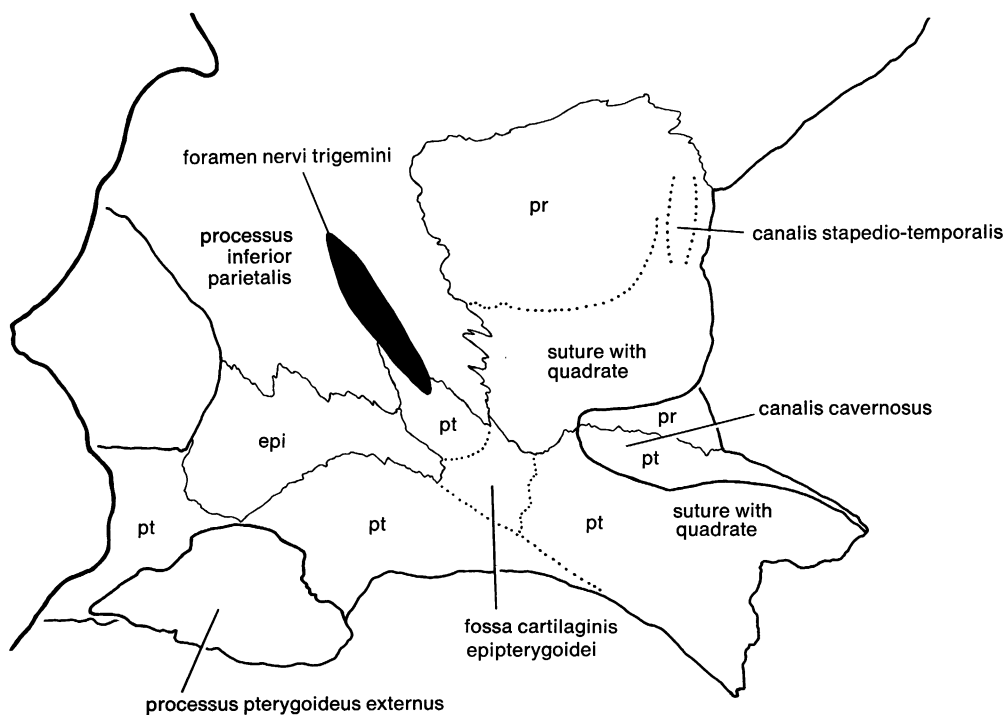


FIG. 39. *Plesiochelys etalloni*, MH 435. Lateral view of left ethmoid region with quadrate removed. This specimen may possibly be juvenile, compare with figure 37, a presumed adult. See Gaffney (1975a, fig. 4) for view of whole skull.

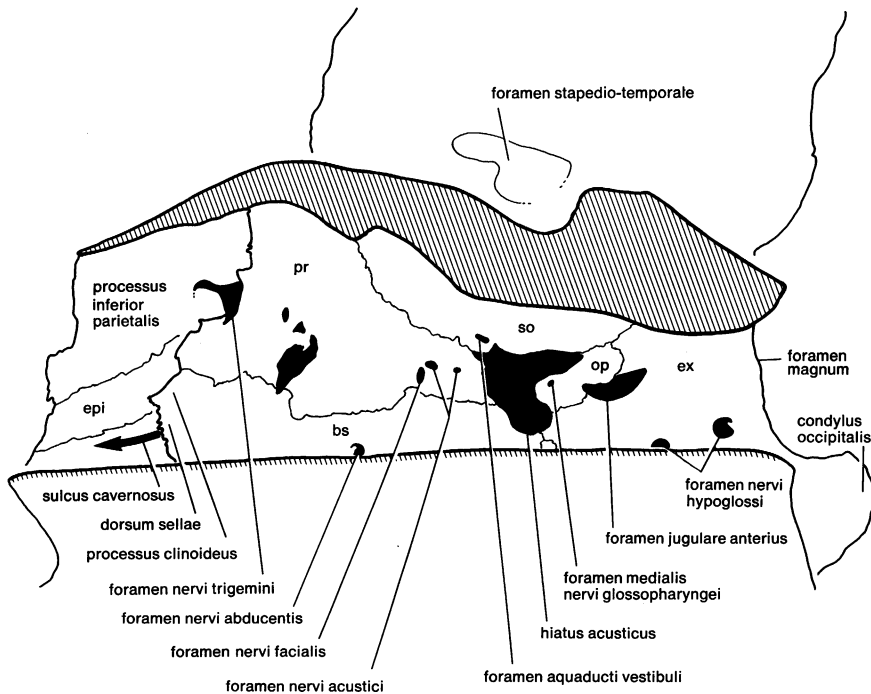


FIG. 40. *Plesiochelys etalloni*, SM 135. Oblique view of the medial surface of the braincase wall. Skull roof removed from specimen (see Gaffney, 1975a, fig. 7); this figure is an attempt to illustrate the features that would be seen in a sagittal section. Anterior is to the left and the hatched areas indicate cut surfaces. Note the unusual development of a process from the prootic that extends anteroventrally to the processus clinoides and obscures much of the foramen nervi trigemini.



FIG. 41. *Plesiochelys etalloni*, SM 134. Right and left stapes (unfortunately the original orientation relative to each other and to the skull is unknown).

addition to the parasphenoid rudiment and this is the taenia intertrabecularis, a sagittal bar lying in the sella turcica between the trabeculae (see Nick, 1912, figs. 32, 40). It is the ossification of this bar and the medial movement of the trabeculae that results in the obliteration of the sella turcica and the formation of a rodlike rostrum basisphenoidale. Some testudinoids (e.g., *Macroclermys*) also may have the trabeculae lying relatively close together but a distinct sella turcica is usually present and the taenia intertrabecularis (although difficult to identify in the dried skull of an adult) is absent.

The dorsum sellae of baenoids, testudinoids, trionychoids, and pleurodires usually overhangs part of the sella turcica. That is, the bone surface curves posteroventrally and a cavity is usually present directly beneath the dorsum sellae. This feature, however, is not found in all members of the above groups; *Dermatemys*, for example, is an exception. Cheloniids, however, do not have an overhanging dorsum sellae because of the anterior movement of the foramen anterior

canalis carotici interni and the development of a vertical or anteriorly sloping surface anterior to the dorsum sellae. This anteriorly sloping surface often has a median ridge developed between the dorsum sellae and the foramina anterius canalis carotici interni. Although the above features may occur in other groups, the combination of features characterizes the chelonioids:

1. Ossified trabeculae of basisphenoid usually lie close together for all their length or are fused into a rodlike rostrum basisphenoidale.
2. Paired foramina anterius canalis carotici interni lie close together.
3. Sella turcica reduced or obliterated due to approximation of trabeculae and/or development of taenia intertrabecularis.
4. Dorsum sellae high and separated from sella turcica and foramina anterius canalis carotici interni by prominent bone surface that usually has a sagittal ridge.
5. Posterior portion of sella turcica not concealed by overhanging dorsum sellae.

With regard to the above characters, *Toxochelys moorevillensis*, described by Zangerl (1953, pl. 9) is about intermediate between *Chelydra* and Recent cheloniids, whereas *Ctenochelys* (*ibid.*, fig. 100, and p. 152) is closer to cheloniids. Another toxochelyid braincase (AMNH 1042, referred to *Toxochelys latiremis* by Zangerl, 1953) has a partially overhanging dorsum sellae but agrees with the other features. Again, it should be emphasized that these comparisons should be made with the testudinoid, baenoid, and trionychoid conditions in mind as they necessarily involve degrees of development and not an all or none situation.

Finally, we may compare the plesiochelyids to other turtles using this character complex. Both *Portlandemys* and *Plesiochelys* are primitive with regard to characters (1) and (3); that is, the trabeculae are not closely apposed and the sella turcica is not largely obliterated. Nonetheless, in comparison with the baenoid condition the sella turcica is somewhat reduced, particularly in *Portlandemys*. There is some variation among the skull characters (2). *Portlandemys* and SM 134 have a very narrow bar of bone separating the foramina anterius canalis carotici interni, whereas SM 135 has a broader bar. The other specimens (SM 136, MH 435, OU J1582) are intermediate



but closer to the SM 134 condition. Nonetheless, most of the specimens are chelonoid in this respect.

The most pronounced similarity to the chelonid basicranium is in characters (4) and (5), involving the structure of the dorsum sellae. *Portlandemys* and *Plesiochelys* are both advanced in these characters and in all the specimens, except SM 135, a sagittal ridge is also present.

**Prootic.** The prootic is present in all six *Plesiochelys* skulls but useful information is most easily obtained from three: MH 435, in which the lateral and posterior sutural faces are exposed; SM 135, in which the skull roof is removed revealing the medial surface of the prootic; and SM 134, in which the sutures are particularly well preserved and determinable.

The prootic of turtles is a complex element involved in forming parts of the cavum acusticojugulare and cavum labyrinthicum. The prootic of *Plesiochelys* agrees with the prootic of *Portlandemys*, with the following exceptions, and the reader is referred to Parsons and Williams (1961, pp. 72-74, 77-81) for more extensive description.

The most striking difference between the prootic of plesiochelyids and other turtles is in the sutural area near the foramen nervi trigemini. As described elsewhere (see parietal and pterygoid) the parietal sends a process ventrally that reaches the quadrate and prevents the prootic from entering the margin of the foramen nervi trigemini. This condition is, as far as I am aware, peculiar to *Plesiochelys*, *Portlandemys*, and *Corsochelys*. *Corsochelys* (see discussion under parietal) appears to have a ventral process of the parietal preventing exposure of the prootic in the foramen nervi trigemini as in plesiochelyids, but this cannot be determined with certainty. A trough on the prootic having the appearance of a sutural face is the only indication of a parietal process.

As described under basisphenoid, *Plesiochelys* has an enlarged processus clinoides that extends dorsolaterally to the prootic. The prootic has an anteroventral process that meets the processus clinoides and both processes appear to be ossifications in the pila prootica of the chondrocranium. The prootic contribution partly prevents observation of the foramen nervi trigemini from inside the skull.

**Opisthotic.** The opisthotic is present in all six

*Plesiochelys* skulls but best seen in SM 134 and MH 435.

As far as I can tell, the opisthotic of *Plesiochelys* agrees with that bone in *Portlandemys* with the following exceptions and the reader is referred to Parsons and Williams (1961, pp. 70-72, 77-81) for more extensive description.

As in most turtles the processus interferentialis of *Plesiochelys* is involved in the formation of the fenestra perilymphatica on its medial edge and the hiatus postlagenum on its ventral edge. The hiatus is a quite small opening completely formed in bone and bordered dorsally by the opisthotic and ventrally by the basioccipital.

The ventral end of the processus interferentialis has variable contacts among the plesiochelyid specimens. In *Portlandemys* (BM[NH] 2914) the processus has a well-developed contact with the exoccipital and basioccipital but in *Portlandemys* (BM[NH] 3164) the contact is primarily with the pterygoid and basioccipital. In *Plesiochelys* (SM 134) most of the processus is sutured to the basioccipital, whereas in SM 135 most of the contact is with the pterygoid.

**Quadrate.** The quadrate is present in all six *Plesiochelys* skulls, it is partially disarticulated in MH 435, and the following description is based largely on that specimen, SM 134, and OU J1582. The quadrate is very nearly the same in *Portlandemys* and *Plesiochelys* and the description of Parsons and Williams (1961, pp. 74-76) will suffice, with the following additions.

The quadrate contacts with the skull roof are not clear in *Portlandemys* but they can be determined in *Plesiochelys* by using MH 435 and SM 594. There is a curved, anterolateral suture with the quadratojugal and a posterodorsal one with the squamosal. This is the condition in most turtles having moderate temporal emargination.

The cavum tympani has features of both chelonoids and testudinoids. The incisura columellae auris is open posteroventrally as in living chelonids and *Toxochelys*, presumably a primitive condition, but one that is characteristic of the chelonoids. As is the case in most eucryptodires, the incisura tends to constrict the stapelial region and separate it from the eustachian tube as opposed to the baenid condition in which the stapes and eustachian tube tend to be enclosed together. Testudinoids and trionychoids typically have the incisura closed, or nearly

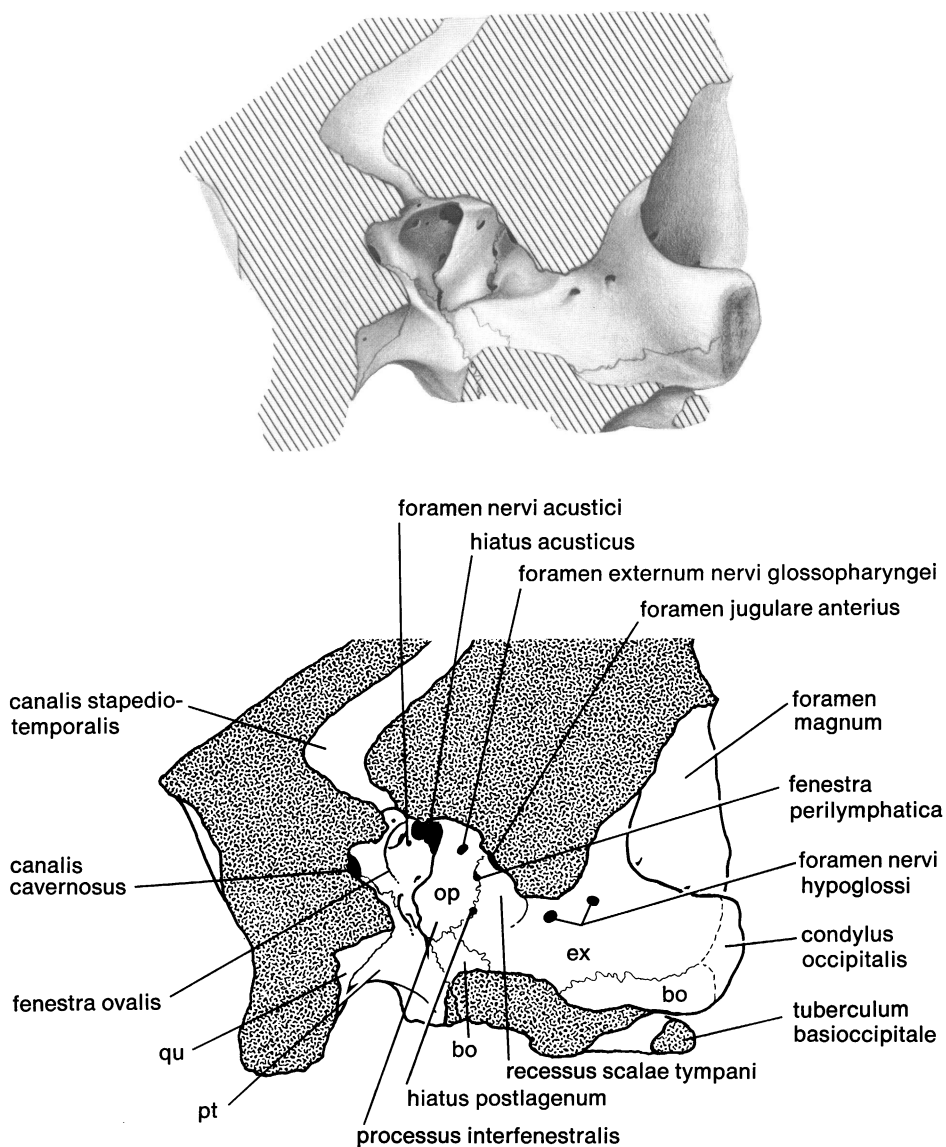


FIG. 42. *Plesiochelys etalloni*, SM 134. Lateral view (anterior to the left) of the cavum acustico-jugulare and associated structures in a skull that has most of the left quadrate eroded away. As an aid to orientation see figure 6 in Gaffney, 1975a. The label leader identifying the fenestra ovalis ends at the anteroventral margin of the structure, the posterior border of it is formed by the processus interfenestralis. The irregular stipple pattern indicates the broken surface parallel to the page but is inclined with dorsal portion farther from the viewer and ventral portion closer.

closed, behind the stapes. The antrum postoticum of *Plesiochelys*, however, is larger than in living cheloniids. This is also probably primitive,

at least for eucryptodires, because baenids have the antrum developed to a degree quite comparable with *Plesiochelys*, whereas most eucrypto-

dires have a larger antrum postoticum, therefore suggesting that the cheloniid condition is owing to reduction.

Both *Portlandemys* and *Plesiochelys* have a prominent ridge on the posterior face of the processus articularis ventral to the incisura columellae auris and dorsal to the condylus mandibularis. This ridge appears to be the dorso-lateral margin of the M. depressor mandibulae or possibly the M. pterygoideus portio ventralis, which Schumacher (1954, 1955a, 1955b) described as extending onto the posterior surface of the quadrate in cheloniids, but not in other turtles. Less distinct rugosities appear on a number of turtles in this region and these seem to be related to eustachian tube attachment or the M. depressor mandibulae. The ridge as developed in *Plesiochelys* and *Portlandemys* with a troughlike infolding on its ventral side, can also be found in *Solnhofia* (Gaffney, 1975b).

The passage of the chorda tympani branch of the facial (VII) nerve can usually be seen as a canal in the quadrate. *Eretmochelys* and *Chelonia* lack the chorda tympani (Soliman, 1964) but *Caretta* retains it (Poglayen-Neuwall, 1953). I have been unable to find evidence of the chorda tympani in the quadrate of either *Portlandemys* or *Plesiochelys*, but the passage of this nerve can be seen in the lower jaw of OU J1582 (see articulation).

**Basioccipital.** The basioccipital is completely absent only in MH 435 but is best seen in SM 134 and SM 135. The description by Parsons and Williams (1961, pp. 65-66) of the basioccipital in *Portlandemys* is again largely sufficient for *Plesiochelys* with a few additions.

The extent to which the ventral end of the processus interfenestralis contacts the basioccipital is variable in turtles but in most turtles there is a well-developed contact. The Emydinae of McDowell (1964), however, are characterized by a reduction of this contact caused by a loss of the lateral margin of the basioccipital. McDowell hypothesized that the loss of this lateral tuberosity (the batagurine process) is a derived character uniting the Emydinae and that in the Batagurinae the reduction has not taken place. The batagurine process can be identified by the following characteristics listed in their order of importance as I interpret this from McDowell:

extends lateral to lagena (this can only be roughly determined from the bony skull), forms floor of recessus scalae tympani, and is in contact with paracapsular sac (this is also difficult to determine definitively from the dried skull). In *Plesiochelys* and *Portlandemys* the batagurine process appears to be present. Comparison of the two Jurassic forms with batagurines and especially emydines is difficult because the Recent groups tend to have less bone in the floor of the cavum acustico-jugulare. The pterygoid and basioccipital completely cover the processus interfenestralis from ventral exposure in *Portlandemys* and *Plesiochelys* and the emydine condition is not really approached.

**Exoccipital.** The exoccipital is poorly preserved or absent in SM 136, MH 435, and SM 594 but OU J1582 and SM 134 have the bone well preserved with distinct sutures.

The exoccipital of *Plesiochelys* does not contact the pterygoid but in *Portlandemys* it does. This feature is variable in Recent turtles (the contact is absent in pleurodires because of the lack of a posterior pterygoid flange) with trionychids and cheloniids tending to have the contact well developed and testudinoids tending to have it reduced or absent. Baenids have the contact well developed and as its absence in emydids seems related to a general loss of ossification in this group the presence of a contact would seem to be primitive for the Cryptodira. The contact is absent in *Dermochelys* among Recent chelonioids but fossil chelonioids are not sufficiently well known to determine the condition of this feature.

There are two foramina nervi hypoglossi in each exoccipital in *Plesiochelys* and *Portlandemys* as in many Recent turtles. The exoccipital often forms a closed foramen jugulare posterius on the medial edge of the fenestra postotica of Recent turtles. Chelonioids, however, characteristically have this structure open laterally and this is the condition in *Plesiochelys* and *Portlandemys*. Baenids also have the foramen jugulare posterius open laterally and this condition is probably primitive for all turtles.

The exoccipitals characteristically form the anterolateral portions of the condylus occipitalis and in *Plesiochelys* and *Portlandemys* they do so, meeting sagittally on the ventral margin of the

foramen magnum thereby preventing exposure of the basioccipital in the foramen magnum.

*Supraoccipital.* Some of the supraoccipital is preserved in all six *Plesiochelys* specimens but it is complete in only one skull, OU J1582. The supraoccipital is complete in none of the *Portlandemys* specimens.

The supraoccipital is roughly divisible into two main portions: the posterodorsal crista supraoccipitalis and the anteroventral contribution to the cavum labyrinthicum and cavum cranii. The anteroventral portion forms the crus communis and dorsal part of the cavum labyrinthicum and part of the braincase roof. This area

is relatively constant in all turtles and no particularly interesting features were noted in the two Jurassic genera.

The crista supraoccipitalis is usually long in post-Jurassic turtles but the living chelonioids characteristically have relatively poorly developed ones. *Plesiochelys* has a crista that is relatively shorter than in living cheloniids but it is about comparable in length with that in *Dermochelys*. Baenids also have a short crista supraoccipitalis and as this structure is short in other reptiles as well, this would appear to be the primitive condition.

## LOWER JAW ELEMENTS

*Dentary.* The lower jaw is preserved in four *Plesiochelys* specimens: OU J1582, MH 435, SM 134, and SM 136. In *Portlandemys* only one specimen, BM(NH) R2914, has the lower jaws preserved and the posterior portions are missing.

A comparison of the four *Plesiochelys* jaws is somewhat difficult because they are variably preserved. OU J1582 is not broken or distorted and is the best preserved. MH 435 and SM 136 appear undistorted but are abraded, somewhat broken, and lack fine preservation of surficial details. SM 134 has well-preserved bone and yields information on sutures and foramina not readily seen in the other Swiss jaws, but it is distinctly distorted. I have decided to recognize two species of *Plesiochelys*: *P. etalloni* (SM 134, SM 136, MH 435) and *P. planiceps* (OU J1582), primarily on the basis of lower jaw features (see Gaffney, 1975a). In *P. etalloni* the lingual ridge of each ramus curves anteriorly at the symphysis so that the ridge is pointing more anteriorly than medially and the lingual ridges do not meet at the symphysis. In *P. planiceps*, however, the anterior portion of the lingual ridge curves medially, paralleling the labial ridge, and meets the other lingual ridge at the symphysis. The Swiss jaws also have a slight symphyseal ridge that the British specimen lacks. The splenial bone in SM 134 (the other Swiss specimens are not well preserved in this area) appears to be more extensive than in the British jaw but this region is eroded in the latter specimen and the sutures could have

been the same. In addition the labial ridge is higher in the British specimen than in the Swiss ones. It is impossible to develop any satisfactory criteria for determining whether these differences represent variation between biologic species or not, in view of the very limited sample size. How-

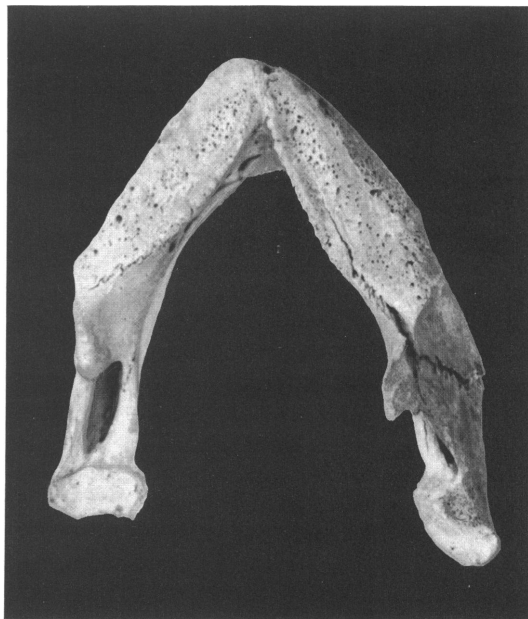


FIG. 43. *Plesiochelys etalloni*, SM 134. Dorsal view of lower jaw, see figure 45 (right) for reconstruction, also figure 48.

ever, I have chosen to retain the two named species in preference to leaving the specimens undesignated as to species. Some differences exist among the Swiss lower jaws. MH 435 is thinner, shallower, and has less pronounced features than the other two, whereas SM 134 is deeper than the others.

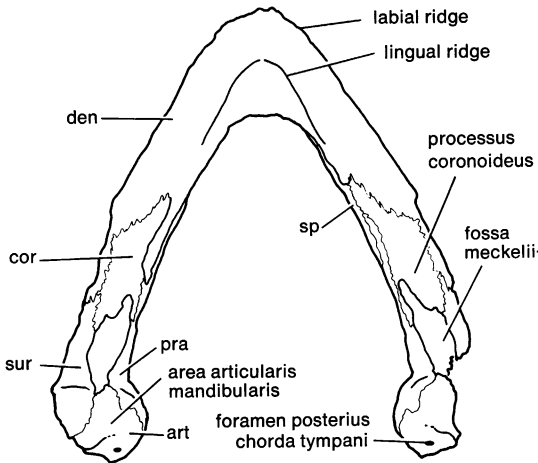


FIG. 44. *Plesiochelys planiceps*, OU J1582. Diagram of lower jaw (see figure 46, right, for shaded drawing, see also figures 47, 49) showing labeled structures useful for the following figures as well.

The triturating surfaces in *Portlandemys* and *Plesiochelys* have a high labial ridge and a sub-equal or lower lingual ridge. The trough formed between the ridges is well developed and usually deeper medially where the lingual ridge of the skull fits into it. In the Swiss specimens of *Plesiochelys* the lingual ridge turns anterolaterally near the symphysis. In *Portlandemys* this feature is more developed and the lingual ridges form a trough as the symphysis.

**Splenial.** The splenial bone is present in only a few living turtles (cheliids; it is reported in some testudinoids but this has not been substantiated) but more often in Mesozoic forms and its presence may be considered a primitive character for turtles. In the Swiss *Plesiochelys etalloni* the splenial is quite large and extends farther anteriorly than in *Plesiochelys planiceps*, at least as preserved (see dentary). Parsons and Williams (1961) should be consulted for a description of the splenial in *Portlandemys*.

The following description of the splenial is based on SM 134 as it is best preserved in this specimen. The splenial is roughly trapezoidal (as in *Portlandemys*) and has the following contacts: dorsally with the coronoid (and with the dentary at the extreme anterodorsal corner), posteriorly with the prearticular, posteroventrally with the



FIG. 45. *Plesiochelys etalloni*, dorsal views of lower jaws. Left, SM 136, specimen somewhat eroded, particularly posteriorly, the limits of which are indicated in outline only; SM 134 (see figures 43, 48), restoration of left ramus.

angular, and anteroventrally with the dentary. The anterior edge has an indentation which is the margin of the foramen intermandibularis medius. Ventral to the foramen the splenial sends a process anteriorly on the medial surface of the dentary which reaches the symphysis on the left side but not on the right.

About midway along the ventral dentary-splenial suture is a foramen contained in the splenial bone. This foramen is not strictly comparable with anything in living cryptodires but is roughly similar in position (ventral to the foramen intermandibularis medius) to the foramen intermandibularis oralis. This foramen appears absent in OU J1582 but the area of the

splenial forming its dorsal and anterior margins has been eroded in this specimen.

*Prearticular.* The prearticular of *Plesiochelys* is smaller in size in comparison with most eucryptodires because of the large size of the splenial in *Plesiochelys*. In later turtles the prearticular extends anteriorly as the splenial is reduced and finally lost. The contacts of the prearticular are quite comparable with other eucryptodires: coronoid dorsally, articular postero-medially, and angular ventrally; in addition, however, there is an anterior contact with the splenial.

The foramen intermandibular caudalis lies in the prearticular-angular suture as in other crypto-

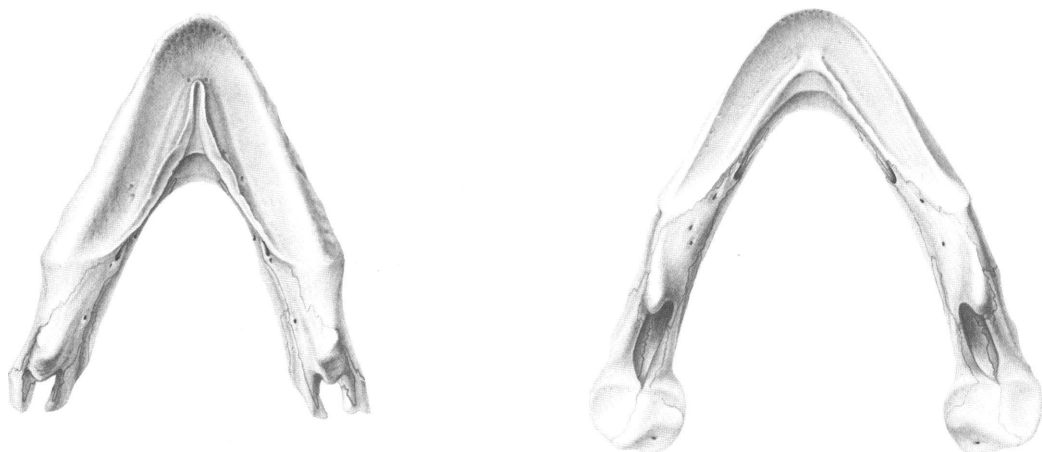


FIG. 46. Left, *Portlandemys mcdowellii*, BM(NH) R2914, dorsal view of lower jaw, see also figure 50; right, *Plesiochelys planiceps*, OU J1582, dorsal view of lower jaw, see also figures 44, 47, 49. Both views partially restored by the assumption of bilateral symmetry.

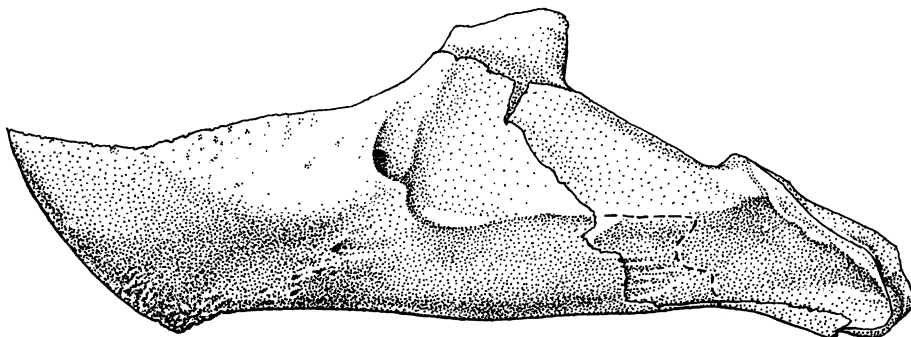


FIG. 47. *Plesiochelys planiceps*, OU J1582, lateral view of lower jaw, see also figures 44, 46, 49.

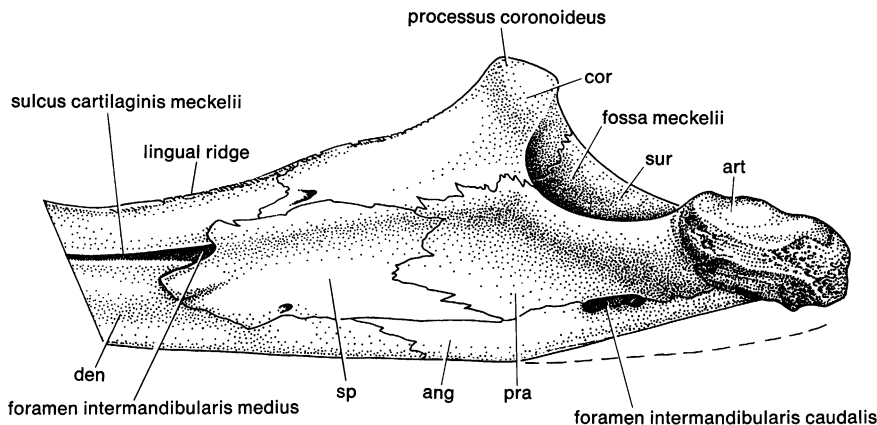


FIG. 48. *Plesiochelys etalloni*, SM 134, medial view of right lower jaw ramus. Dashed line indicates presumed extent of jaw before erosive damage. See also figures 43, 45 (right).

dire but its position is somewhat posterior in comparison with *Chelydra*. The posterodorsal margin of the prearticular forms the medial edge of the fossa meckelii also as in most other turtles.

**Angular.** The angular is a long, slender bone somewhat smaller in *Plesiochelys* than in other eucryptodires. It does not reach the dentary anteriorly, but there is a long anterodorsal contact with the splenial and a posterodorsal one with the prearticular. The angular is exposed mostly along the ventral surface of the jaw but is partially visible medially and the posterior end of the bone wraps around the jaw to reach the articular posteriorly and the surangular postero-laterally.

**Articular.** The articular has the usual cryptodire form with a low, median ridge separating two concavities. In contrast to many turtles, the area articularis mandibularis is borne to a consid-

erable extent by the surangular laterally and the prearticular medially, although the articular does form the largest part of the area. A modest but distinct depression occurs just posterior to the area articularis mandibularis for the attachment of the *M. depressor mandibulae*. In this depression is the foramen posterius chorda tympani.

**Coronoid.** The coronoid contacts are: dentary anteriorly and laterally; surangular postero-laterally, prearticular posteroventromedially. The processus coronoideus is well developed and higher than in chelydrids and most chelonoids.

**Surangular.** The surangular is a sheetlike element that lies between the dentary and articular in the lateral side of the jaws. It also contacts the coronoid anterodorsally and the angular posteroventrally. The surangular in *Plesiochelys* is quite comparable with that bone in most other turtles.

#### RELATIONSHIPS OF *PORTLANDEMYS* AND *PLESIOCHELYS*

I have developed (Gaffney, 1975c) a theory of relationships for the turtles and proposed criteria for identifying members of certain categories. By these criteria the Plesiochelyidae can be identified as members of the following taxa. The Plesiochelyidae are cryptodires (Infraorder Cryptodira) because they have these characters:

1. Skull with trochlear surface for cartilago transiliens developed on processus trochlearis oticum.
2. Pterygoid extends posteriorly between quadrate and braincase.
3. Epipterygoid present.
4. No development of hemispherical articulation on lower jaw.
5. Foramen palatinum posterius in floor of fossa orbitalis.
6. Foramen supramaxillare present.
7. Descending process of prefrontal meets vomer ventromedially.



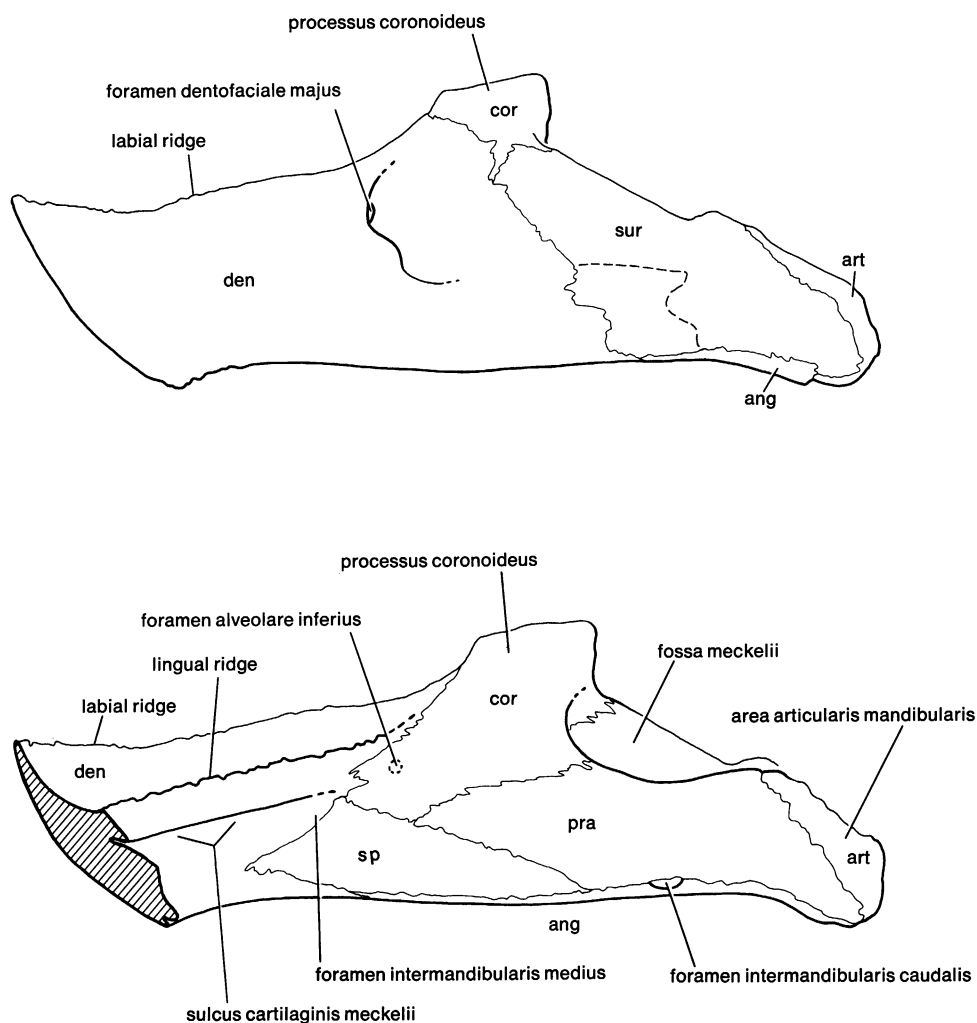


FIG. 49. *Plesiochelys planiceps*, OU J1582. Upper, lateral view of left lower jaw ramus, dashed line indicates probable former extent of dentary, see figure 47; lower, medial view of right lower jaw ramus, bone extent in vicinity of splenial, lower portion of coronoid, and anterior portion of prearticular has been eroded.

Characters 1 and 2 are particularly important shared derived characters and sufficiently diagnostic for cryptodires. Plesiochelyids can also be identified as members of the Parvorder Eucryptodira (see Gaffney, *ibid.*) by possessing this derived character:

1. Foramen posterius canalis carotici interni lying at posterior edge of pterygoid and formed mostly by the pterygoid.

In most features of the skull the plesiochelyids are primitive with respect to other eucryptodires. Nonetheless, some diagnostic basicranial features of the Chelonioidea do occur in the plesiochelyids and I am presenting here a hypothesis that they are members of the Chelonioidea based on the possession of the following shared derived characters of chelonoids:

1. Dorsum sellae high and separated from

sella turcica and foramina antierus canalis carotici interni by prominent bone surface that usually has a sagittal ridge (see basisphenoid).

2. Posterior part of sella turcica not concealed by overhanging dorsum sellae (see basisphenoid).

Other features are suggestive of chelonoids more than the other superfamilies but are somewhat removed from the degree of development seen in most other chelonoids.

1. Paired foramina antierus canalis carotici interni usually lie close together as in *Toxochelys* and are not placed far laterally as in most Testudinoidea and Trionychoidea (see arterial canal section).

2. Processus parietalis inferior narrow antero-posteriorly (see parietal).

3. Dorsal roof of canalis caroticus lateralis apparently open in some individuals of *Plesiochelys* (see arterial canal section).

4. Foramen caroticum laterale and foramen antierus canalis carotici interni equal in diameter (see arterial canal section).

The principal inconsistency with regard to the hypothesis that plesiochelyids are chelonoids is the structure of the shell. The plastron of chelydrids,<sup>1</sup> toxochelyids, and chelonoids is characterized by narrow epiplastra, xiphiplastra and

<sup>1</sup>Except in *Platysternon*, which I included in the Chelydridae, see Gaffney, 1975d.

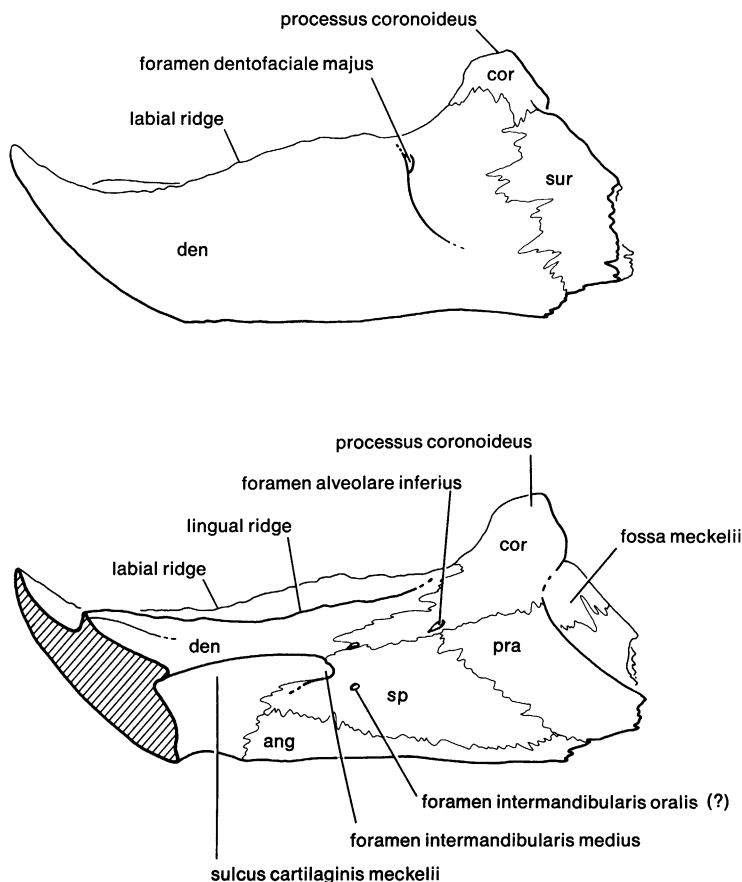


FIG. 50. *Portlandemys mcdowelli*, BM(NH) R2914. Upper, lateral view of left lower jaw ramus; lower, medial view of right lower jaw ramus. See also figures 10, 46 (left).

TABLE 1  
A Comparison of Skull Features among Chelonioidea and Chelydridae  
(See text for further discussion.)

|  | Plesiochelyidae | Chelydridae<br>(including<br><i>Platysternon</i> ) | Toxochelyidae | <i>Dermochelys</i> | Recent Chelonioidea |
|--|-----------------|--|---------------|--------------------|---------------------|
| Nasal lost   | —               | +  | —             | +                  | +                   |
| Squamosal-<br>parietal contact   | —               | —  | —             | +                  | +                   |
| Incisura columella<br>auris closed<br>posteriorly  | —               | +  | —             | —                  | —                   |
| Foramen jugulare<br>posterius separated<br>by bone from<br>fenestra postotica  | —               | +  | —             | —                  | —                   |
| Processus pterygoideus<br>externus reduced   | —               | —  | —             | +                  | +                   |
| Foramen palatinum<br>posterius absent  | —               | —  | —             | +                  | +                   |
| Medial process<br>of jugal   | + and —         | +  | +             | —                  | +                   |
| Dorsum sellae high<br>and separated from<br>sella turcica and<br>foramina anterius<br>canalis carotici<br>interni by prominent<br>bone surface | +               | —  | +             | +                  | +                   |
| Posterior portion<br>of sella turcica<br>not concealed by<br>overhanging dorsum<br>sellae  | +               | —  | +             | +                  | +                   |
| Processus parietalis<br>inferior reduced in<br>anteroposterior<br>extent   | +               | —  | +             | +                  | +                   |
| Parietal extends<br>ventrally to meet<br>pterygoid along<br>posterior margin<br>of foramen nervi<br>trigemini                                  | +               | —  | indet         | —                  | —                   |
| Epipterygoid rela-<br>tively large   | +               | +  | +             | —                  | —                   |
| Splénial lost  | —               | +  | +             | +                  | +                   |
| Palatine artery<br>larger than<br>internal carotid   | —               | —  | —             | +                  | +                   |

entoplastron, the development of midline fontanelles, and the loss of sutural contact with the carapace along the bridge. *Plesiochelys* (the postcranium is unknown in *Portlandemys*) has broad epiplastra, xiphiplastra and entoplastron, limited midline fontanelles, and a sutural contact with the carapace. The plesiochelyid condition is presumably primitive for cryptodires because it occurs in baenoids, pleurodires, and widely within the eucryptodires. My hypothesis of relationships requires independent derivation of the reduced plastral type twice, once in chelydrids and once in chelonioids. Although Bräm (1965) described limb characters of *Plesiochelys* that indicate relationship to cheloniiids, I have not been able to utilize these features in a shared derived character analysis. The most important of the postcranial characters involves the structure of the forelimb, and the single specimen of a *Plesiochelys* forelimb is not well enough preserved to differentiate it from *Chelydra*, let alone show characters in common with cheloniiids.

At the present time it seems most likely that

*Portlandemys* and *Plesiochelys* have an ancestor in common that they do not have in common with other known forms. This hypothesis is based primarily on palatal features. As remarked by Parsons and Williams (1961, p. 90) the presence of a strong lingual ridge at the margin of the apertura narium interna separated from the labial ridge by a trough without any secondary ridges is rare. *Plesiochelys* and *Portlandemys* both have this palatal morphology but so do baenids and the feature may be primitive for cryptodires or eucryptodires. Another feature of the palate is the reduction of the lateral shelf on each side of the vomer. In most turtles the palatines articulate with these processes but in *Plesiochelys* and *Portlandemys* the vomer is reduced and the palatines meet dorsal to the vomer although ventrally the main stem of the vomer reaches the pterygoids. I also interpret this condition as shared derived although it is approached by Recent cheloniiids in which the palatines meet for part of their length but the lateral vomer expansions are still present. In any case, the follow-

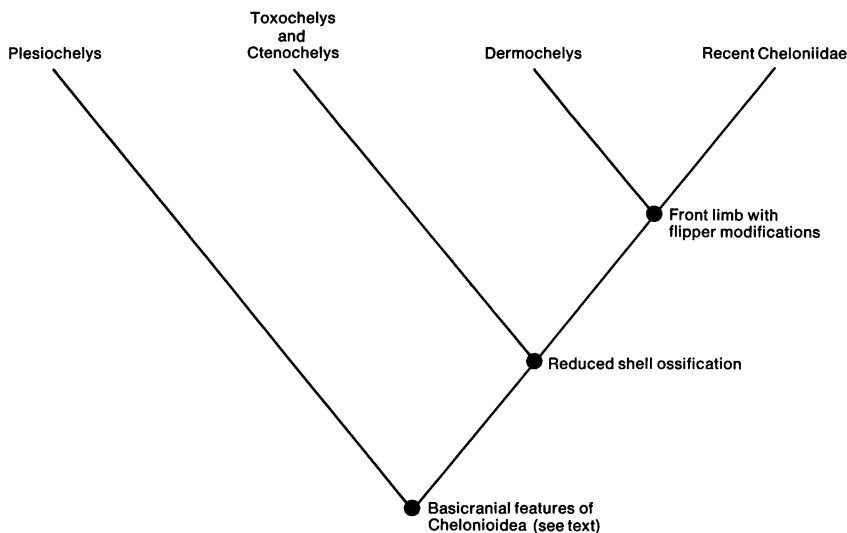


FIG. 51. Cladogram of a hypothesis of relationships involving some chelonioid groups known from skull and postcranial material. This hypothesis relies on postcranial characters suggested by Zangerl and Sloan (1960) for groups within the Chelonioidea; *Portlandemys* is omitted because its postcranium is unknown. Each of the four groups at the top of the page in this diagram and in figure 52 is hypothesized as monophyletic. *Toxochelys* and *Ctenochelys* have a series of shell characters in common, *Dermochelys* is a single species (*D. coriacea*), the Recent cheloniiids have secondary palates (absent in the other forms used here), and *Portlandemys* and *Plesiochelys* are discussed in the text section on relationships.

ing combination of features is unique to these two genera: palatines meet for nearly all of their length dorsal to vomer, lateral extensions of vomer absent, vomer reaches pterygoids and separates palatines in ventral view.

In addition there are some other features held in common by the two genera. The basisphenoid and basioccipital are of equal width in ventral view. This condition is not known in other chelonioids but does occur in other cryptodires, although sporadically (some trionychids, some testudinoids, some chelids). It may be primitive for chelonioids although I suspect that it is derived and the primitive condition is one in which the basioccipital is wider as in baenids.

The anterior opening of the foramen nervi abducentis is posteroventral to the base of the processus clinoides in *Portlandemys* and *Plesiochelys*. This is distinctly different from its position in all other turtles in which this is known. Unfortunately, the position of the foramen is unknown in most fossil chelonioids except *Cosuchelys* and *Rhinochelys*. In these fossil and living forms the foramen is anterior and dorsal as in other turtles. This feature, then, seems to be a good shared derived character for the Plesiochelyidae.

A large epipterygoid is found in *Portland-*

*emys*, *Plesiochelys*, and *Solnhofia*. It is usually assumed that a large epipterygoid is primitive for turtles and the absence of the bone in pleurodires and its fusion in baenids seem to be derived features of those groups. Nonetheless, most cryptodires (particularly Recent cheloniids) have a relatively small epipterygoid and, at present, I do not see that a choice can be made for the primitive size of the bone.

Another feature, which is doubtful as far as primitive and derived states are concerned, is the pterygoid-parietal contact along the posterior margin of the foramen nervi trigemini. This occurs in *Portlandemys*, *Plesiochelys*, and some but not all members of the Batagurinae of McDowell (1964). I would accept this feature as a good shared derived character for plesiochelyids were it not for McDowell's (*ibid.*) persuasive argument that batagurines generally possess primitive testudinoid characters and may be interpreted as the sister group of the other testudinoids. Nonetheless, I am considering this as a derived character for plesiochelyids.

There are, however, some character distributions that contradict the hypothesis that *Portlandemys* and *Plesiochelys* have an ancestor in common that they do not have in common with other turtles. The most important of these is the

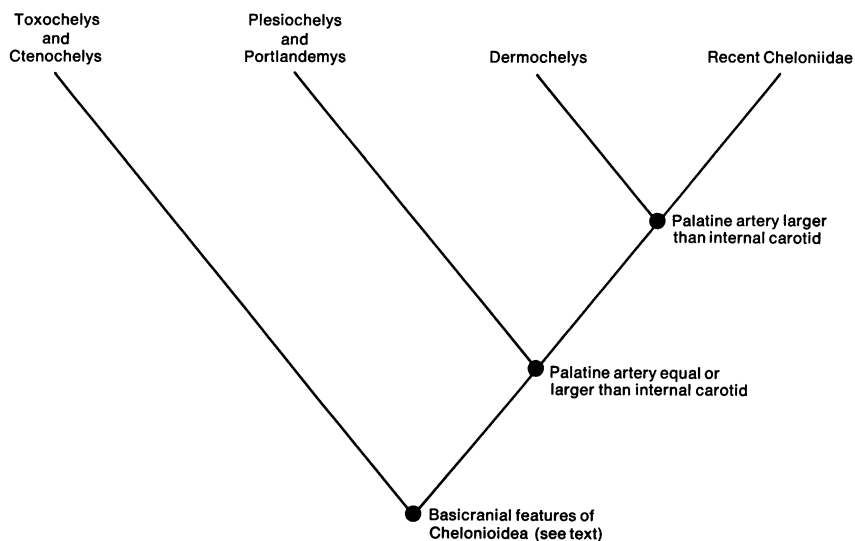


FIG. 52. Cladogram of a hypothesis of relationships involving some chelonioid groups known from skull material. This hypothesis relies on characters found in the basicranium.

open foramen palatinum posterius found in *Plesiochelys*. The posterolateral margin of the foramen is absent due to the loss of the medial process of the jugal (see jugal). The almost universal presence of a fully formed foramen palatinum posterius in turtles and its presence in captorhinomorphs suggests that the open condition is a derived character. *Rhinochelys* also has the foramen open posterolaterally. *Rhinochelys* has a low lingual ridge and the vomer is more reduced (does not reach pterygoid) than in the plesiochelyids but conditions could be considered uniquely derived for *Rhinochelys*. I do not know if the medial process of the jugal is absent in *Rhinochelys* but if so the open foramen palatinum posterius caused by the loss of the medial jugal process would be a good shared derived character linking *Plesiochelys* and *Rhinochelys* but not *Portlandemys*. Furthermore, better knowledge of the palate in *Protostega* and *Archelon* may indicate that the absence of the medial jugal process characterizes the Protostegidae (see jugal). Again, the important ethmoid and palatal areas are not sufficiently well known in advanced protostegids for useful comparisons to be made with *Plesiochelys* and *Portlandemys*.

Therefore it would seem that the Plesiochelyidae as construed here may be abandoned with further understanding of protostegids and other chelonoids. Nonetheless, the hypothesis that *Plesiochelys* and *Portlandemys* are sister taxa is the most parsimonious at the present time.

Although the cranial osteology of plesiochelyids is now known almost as well as in Recent turtles, it is not possible to set up a well-tested

phylogenetic hypothesis including most forms identifiable as chelonoids. The protostegids are not sufficiently understood in the palate and basicranium to test my arterial characters, and the osteopygine toxochelyids are also poorly known in the basicranium. Limbs of plesiochelyids would be useful for comparison with the ideas of Zangerl and Sloan (1960) about chelonoid systematics but information about them is lacking. A host of fossil chelonoids are known from cranial material but it is as yet unprepared.

I will present two hypotheses here in the hope that future work will allow more rigorous testing. The first (fig. 51) suggests plesiochelyids as the sister group of other chelonoids. This hypothesis relies on the reduced shell ossification of toxochelyids, dermochelyids, and chelonoids (particularly the plastron) as a derived character but the occurrence of this same shell morphology in *Chelydra* and *Macrolemys* requires derivation of this morphology twice. The other hypothesis (fig. 52) relies on the palatine artery size as a derived character defining a monophyletic group plesiochelyids, dermochelyids, and chelonoids with toxochelyids as the sister group of other chelonoids. The more ossified "normal" shell of *Plesiochelys* would have to be derived in this case or the reduced shell of toxochelyids versus dermochelyids plus chelonoids would have to be independently derived. Clearly more tests are required but at least here are two explicitly stated phylogenies not invoking gradal evolution or "levels of organization" which, I hope, will stimulate discussion and criticism.

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