Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY

CENTRAL PARK WEST AT 79TH STREET NEW YORK, N.Y. 10024 U.S.A.

NUMBER 2574

MAY 9, 1975

EUGENE S. GAFFNEY

A Taxonomic Revision of the Jurassic Turtles Portlandemys and Plesiochelys

Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024Number 2574, pp. 1-19, figs. 1-15, tables 1, 2May 9, 1975

A Taxonomic Revision of the Jurassic Turtles Portlandemys and Plesiochelys

EUGENE S. GAFFNEY¹

ABSTRACT

A taxonomic revision of the Jurassic chelonian family Plesiochelyidae recognizes two valid genera: Plesiochelys Rütimeyer and Portlandemys, new. The genera Craspedochelys Rütimeyer and Stegochelys Lydekker are junior synonyms of Plesiochelys, whereas Plesiochelys jaccardi, P. solodurensis, and P. sanctaeverenae are synonymized with Plesiochelys etalloni. The British Plesiochelys planiceps and the central European Plesiochelys etalloni, both represented by cranial material, are the only species of this genus recognized here. Portlandemys mcdowelli, new genus and species, is proposed for the specimens referred to by Parsons and Williams as the "Portland skulls."

INTRODUCTION

The present paper is the first in a series concerned with the cranial morphology and relationships of the plesiochelyid turtles. These turtles are from the Late Jurassic of Europe and have traditionally been considered as typical members of the "Amphichelydia," a "wastebasket" taxon characterized by antiquity and a generally primitive appearance. Elsewhere (Gaffney, In press) I have developed a theory of chelonian relationships in which I have rejected the "Amphichelydia" in favor of monophyletic taxa. Most of my categories rely on cranial characters for their recognition and I have begun a study of a number of skulls previously referred to the "Amphichelydia" with the intention of developing ideas about their relationships using shared derived characters.

In this first paper I intend to deal with the systematics of the taxa within the Plesiochelyidae, whereas in later papers I will present the cranial morphology and ideas about relationships of the Plesiochelyidae within the Chelonioidea.

I refer the reader to a paper (Gaffney, 1975) dealing with the relationships of the "Solnhofen skull" of Parsons and Williams. This paper includes a summary comparison of *Portlandemys* and the "Solnhofen skull." A more extensive comparison may be found in the paper by Parsons and Williams (1961). The anatomical terms used here are discussed in a glossary (Gaffney, 1972).

¹ Department of Vertebrate Paleontology, the American Museum of Natural History; Adjunct Assistant Professor, Department of Geological Sciences, Columbia University.

ACKNOWLEDGMENTS

My greatest debt of gratitude is to the individuals who allowed me to borrow and prepare specimens in their care. Most of the specimens were borrowed from the Solothurn Museum where Dr. H. Ledermann, in charge of the Geology-Mineralogy collections, kindly gave me access to the Jurassic turtle material and generously allowed me to borrow the skulls. Mr. H. P. Powell, Assistant Curator of the Oxford University Museum, Geological Collections, spent much time helping me and facilitating the loan of Owen's "Stegochelys" planiceps. Dr. Alan Charig and Mr. Cyril Walker of the Department of Palaeontology, British Museum (Natural History) helped me a great deal during my stay in London and lent me specimens of Portlandemys. I am very grateful to Dr. Günter Viohl, who kindly took me to see Jurassic turtles in private collections in the Eichstätt-Solnhofen area and also showed me the quarries and geology of that region. He and Prof. Dr. Franz Mayr both aided my work with the Eichstätt material. Dr. Peter Wellnhofer and Prof. Dr. Richard Dehm helped me examine the Munich collection. The figures are the work of Ms. Lorraine Meeker, Mrs. Jennifer Emry, and Ms. Robin Ingle.

ABBREVIATIONS

Institutions

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

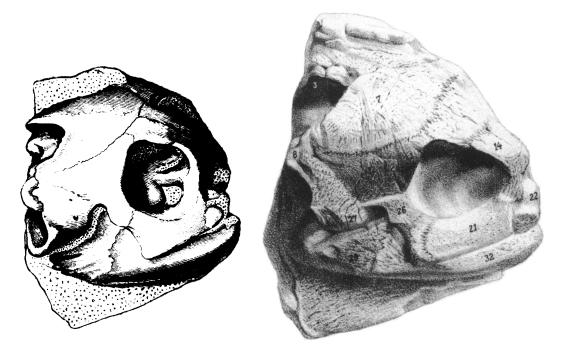


FIG. 1. *Plesiochelys etalloni*, SM 134, Late Jurassic, Switzerland. Right lateral view of skull as figured by previous authors. *Left*: from Cuvier (1824, pl. 15, fig. 7); this appears to be the oldest identifiable figure of a fossil turtle skull. *Right*: from Rütimeyer (1873, pl. 14, fig. 5).

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

PREVIOUS WORK

The skulls used in this study have had a relatively long scientific history. The first mention of a plesiochelyid skull was made by Cuvier in 1824 (p. 230). He also figured the specimen, apparently the earliest figure of a fossil turtle skull (*ibid.*, pl. 15, fig. 7) and it is quite easily identified as SM 134, sent to Cuvier by Prof. F. J. Hugi of Solothurn, Switzerland. Hugi (see Bräm, 1965, p. 5) was largely responsible for the magnificent Jurassic turtle collection at Solothurn, the largest such collection I am aware of. Cuvier indicated that the skull was similar to "....les émydes les plus ordinaires" (*ibid.*). Rütimeyer (1873, pp. 94-101, pl. XIV) described and figured this and two other *Plesiochelys* skulls in his large monograph on the Solothurn collection. He questionably (because no shells were associated) identified them as: *Thalassemys* (pl. XIV, fig. 5; SM 134, the Cuvier specimen), *Plesiochelys* (pl. XIV, figs. 1, 2; SM 136) and *Platychelys* (pl. XIV, figs. 3, 4; SM 135). Rütimeyer classified his Jurassic material as either cryptodires ("Emydidae") or pleurodires ("Chelydidae"), and *Plesiochelys* was considered a pleurodire, and the other two cryptodires.

The most recent work on the Swiss *Plesiochelys* specimens is by Bräm (1965). He has completely reviewed and described the Solothurn Jurassic turtle collection including the skulls. Bräm referred all the Swiss skulls to *Plesiochelys*, correctly, I believe. Unfortunately, his figures are highly stylized and difficult to use for comparative work. Furthermore, the descriptions contain important errors (e.g., secondary palate is pres-

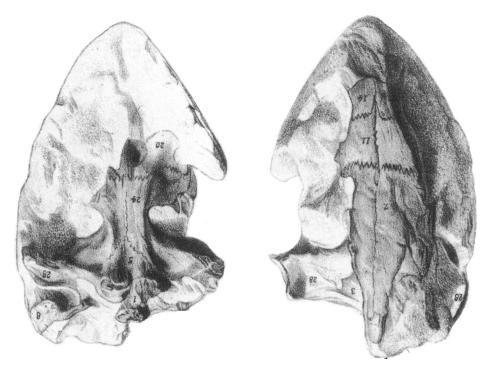


FIG. 2. *Plesiochelys etalloni*, SM 135, Late Jurassic, Switzerland. Figures from Rütimeyer (1873, pl. 14, figs. 3, 4). *Left*: ventral view. *Right*: dorsal view. Figures reoriented so that light is in upper left corner.

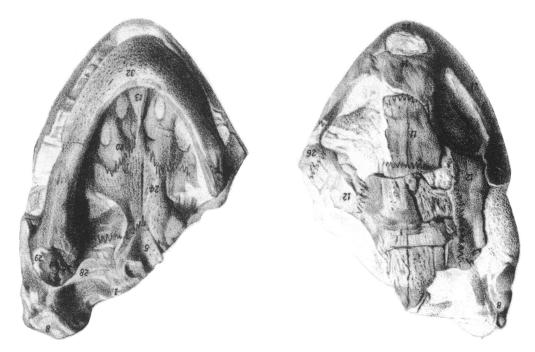


FIG. 3. *Plesiochelys etalloni*, SM 136, Late Jurassic, Switzerland. Figures from Rütimeyer (1873, pl. 14, figs. 1, 2). *Left*: ventral view. *Right*: dorsal view. Figures are reoriented so that light is in upper left corner.

ent, nasals are absent). Nonetheless, Bräm has concluded that *Plesiochelys* is related to the Cheloniidae and in this I agree.

Meanwhile, on the other side of the English Channel, the history of the British plesiochelyid specimens begins with Owen's (1842) announcement of *Chelone planiceps* from the Portland Stone. In 1884 he figured the skull but gave no further description. Lydekker (1889a, p. 233) indicated that the skull was lost and later, Parsons and Williams (1961) also mentioned it as lost. Delair (1958, p. 55), however, assembled a useful list of Dorset fossil reptiles and indicated the Oxford University Museum as the repository of the type specimen. As far as I can determine, however, literature citations of *Stegochelys planiceps* have relied almost entirely on the Owen plate and not on examination of the specimen.

The three skulls studied by Parsons and Williams (1961) and here referred to as *Portlandemys* have not been figured nor specifically mentioned, as far as I am aware, prior to their work. They tentatively referred these skulls to *Stego*- *chelys planiceps* on the basis of the Owen (1884) figures.

SYSTEMATICS

DIVISION TETRAPODA

COHORT AMNIOTA

SUPERORDER SAUROPSIDA

ORDER TESTUDINES LINNAEUS, 1758

SUBORDER CASICHELYDIA, NEW¹

INFRAORDER CRYPTODIRA (COPE, 1868)

PARVORDER EUCRYPTODIRA, NEW¹

SUPERFAMILY CHELONIOIDEA BAUR, 1893

FAMILY PLESIOCHELYIDAE RÜTIMEYER, 1873

Type. Plesiochelys Rütimeyer, 1873.

Known Distribution. Late Jurassic of western Europe.

¹These taxa are diagnosed and discussed in Gaffney (In press).

Diagnosis. Skull roof: Temporal emargination better developed than in most Chelonioidea except Desmatochelys and Corsochelys; parietal, quadratojugal, and squamosal exposed along temporal margin, parietal-squamosal suture absent. Frontal entering orbital margin. Maxilla and quadratojugal not in contact. Parietals small in contrast to Recent Cheloniidae. Postorbital about intermediate in size between Toxochelys and Recent Cheloniidae. Cheek emargination more extensive than in other Chelonioidea. Jugal relatively small in contrast to living Cheloniidae. Nasals present. Prefrontals meeting in midline. Prefrontal-frontal suture transverse.

Palate: Primary palate present. High labial ridge and strong lingual ridge directly bordering apertura narium interna. Ventral margin of labial ridge convex in lateral view. Processus pterygoideus externus developed as in most Testudinoidea and not reduced as in Cheloniidae. Foramen palatinum posterius present (but open posterolaterally in *Plesiochelys*). Foramen praepalatinum present. Vomer completely separating palatines in ventral view but lacking lateral expansion seen in most cryptodires. Basisphenoid and basioccipital of equal width in ventral view. Prominent transverse ridge on posterior surface of processus articularis of quadrate with trough on ventral side.

Braincase: Trabeculae of rostrum basisphenoidale not fused or closely apposed. Sella turcica somewhat reduced in comparison with Chelvdra but not so reduced as in most other Che-Paired foramina anterius canalis lonioidea. carotici interni not lying close together as in Toxochelys or Cheloniidae but not placed far laterally as in Chelvdra and most Testudinoidea. Dorsum sellae high and separated from sella turcica and foramina anterius canalis carotici interni by prominent bone surface having sagittal ridge. Posterior portion of sella turcica not concealed by overhanging dorsum sellae. Canalis caroticus internus not entering sulcus cavernosus as in Recent Cheloniidae. Processus inferior parietalis reduced in anteroposterior extent in comparison to Chelydra and Testudinoidea but not so reduced as in Recent Cheloniidae. Foramen nervi trigemini relatively smaller in Chelydra and conspicuously smaller than in Recent Cheloniidae. Processus trochlearis oticum moderately well developed, as in *Chelydra*. Parietal extending ventrally to meet pterygoid along posterior margin of foramen nervi trigemini, as in many batagurine testudinids. Epipterygoid large and broadly entering margin of foramen interorbitale; entering or not margin of foramen nervi trigemini. Anterior opening of foramen nervi abducentis posteroventral to base of processus clinoideus in contrast to Recent Cheloniidae and most turtles.

Lower Jaw: Triturating surface narrow in contrast to Recent Cheloniidae. High labial and subequal or lower (but distinct) lingual ridge; welldeveloped trough between labial and lingual ridges for reception of lingual ridge of skull; no accessory ridges present. Symphyseal hook present or absent. Processus coronoideus higher than in Recent Cheloniidae. Surangular exposed posteriorly in contrast to Chelydra but not so exposed as in Caretta. Surangular bearing variable portion of area articularis mandibularis as in Recent Cheloniidae. Splenial present and large in contrast to nearly all other cryptodires. Fossa meckelii and most of sulcus (canalis) cartilaginis meckelii closed medially by splenial and prearticular.

PLESIOCHELYS RÜTIMEYER, 1873

Chelone: Owen, 1842, p. 168. Emys: Pictet and Humbert, 1857, p. 1. Stylemys: Maack, 1869, p. 320. Craspedochelys Rütimeyer, 1873, p. 86. Stegochelys Lydekker, 1889b, p. 229.

Type Species. Plesiochelys solodurensis Rütimeyer, 1873. Although Rütimeyer did not designate a type species for this genus, Lydekker (1889a, p. 197) did.

Known Distribution. Late Jurassic of western Europe. Species have been reported from China (Young and Chow, 1953; Yeh, 1963; Yeh, 1973) but the specimens consist only of partial shells that I do not believe are sufficiently diagnostic for generic identification.

Diagnosis. Member of the Plesiochelyidae (sensu Gaffney, present paper) known from skull, shell, and appendicular elements; foramen palatinum posterius open posteroventrally due to absence of medial process of jugal, anteroposterior length of premaxillae shorter than in Portlandemys, angle between labial ridges (of max-

AMERICAN MUSEUM NOVITATES

| Characters | Plesiochelys | Portlandemys |
|---|--------------|--------------|
| Foramen palatinum posterius | Open | Closed |
| Anteroposterior length of premaxilla | Short | Long |
| Angle between labial ridges of maxillae and lower jaw | More obtuse | More acute |
| Median channel between lingual ridges | Wide | Narrow |
| Length of lower jaw symphysis | Short | Long |
| Symphyseal "hook" on lower jaw | Absent | Present |
| Processus clinoideus expanded dorsolaterally to meet process of prootic | Yes | No |

TABLE 1 Characters Differentiating Plesiochelys from Portlandemys

illae and lower jaws) more obtuse than in *Portlandemys*, median channel between lingual ridges of palate wider in comparison with *Portlandemys*; length of lower jaw symphysis shorter than in *Portlandemys*, symphyseal hook absent; prootic process extending anteroventrally to meet expanded processus clinoideus.

Carapace oval, nuchal bone indented anteriorly, pygal bone without posterior indentation seen in Eurysternum, two suprapygal bones and six to eight neural bones present; pair of small accessory scutes usually lateral to nuchal (cervical) scute, vertebral scutes wider than in Tropidemys, supramarginal scutes absent. Plastron with or without one or two median fontanelles, mesoplastral bones absent; paired intergular scutes usually extending onto entoplastron, completely separating gular scutes and sometimes partially separating humeral scutes; four or five inframarginal scutes present. Dorsal surface of xiphiplastron with facet for seemingly movable articulation with pubis, sutural attachment between shell and pelvis absent; scapula with neck and coracoid moderately enlarged as in other chelonioids, angle between head and shaft of humerus 117-128 degrees (Bräm, 1965).

Discussion. The genus Plesiochelys has been essentially a "form genus" primarily because of its Jurassic age and fully ossified shell lacking mesoplastra. Even a more restricted shell diagnosis, such as the one I have presented here, does not serve as a satisfactory set of identifying criteria. This diagnosis is really a morphotype for a primitive eucryptodiran shell and one could expect to find this assemblage of shell features in any primitive eucryptodire. The only derived character differentiating this shell type from baenoids (Paracryptodira) is the loss of mesoplastra, a feature that characterizes most eucryptodirans (but possibly not all of them) as well as cheliid pleurodires. The movable pubic-xiphiplastron articulation can also be seen in the baenoids as well as in *Plesiochelys* and appears to be a primitive character for cryptodires. It is possible that the shell morphology in this case is common to a number of different taxa that might be placed in different families or superfamilies if more adequate morphologic information were available. For example, I am here referring Plesiochelvs and the Plesiochelvidae to the Chelonioidea on the basis of the derived characters in the skull, but this does not imply that all specimens with this type of shell morphology can also be referred to the Chelonioidea.

Plesiochelys planiceps (Owen)

Chelone planiceps Owen, 1842, p. 168. Stegochelys planiceps (Owen), Lydekker, 1889b, p. 229.

Type Specimen. OU-J1582, nearly complete skull lacking nasals, anterior margins of apertura narium externa, and most of posterolateral skull roof (i.e., jugal preserved only on right side, quadratojugals and nearly all postorbitals missing). Posterior edges of pterygoids missing. Lower jaw nearly complete, lacking only parts of right surangular. Portions of the anterior cervicals and hyoid elements also present. Figured by Owen (1884, first pl. 8, figs. 1-3).

Locality and Horizon. "Prof. Buckland possesses....a beautiful specimen of the skull of a chelonian from the Portland sandstone..." (Owen, 1842, p. 169). No further information is

GAFFNEY: JURASSIC TURTLES

| Characters | P. planiceps | P. etalloni Variable from low to high, but not so high as in P. planiceps Curves anteriorly | |
|---|-------------------------------------|--|--|
| Lingual ridge of maxilla | Slightly higher than in P. etalloni | | |
| Anterior portion of lingual ridge on lower jaw | Curves medially | | |
| Distance between lingual ridges of maxillae at level of vomer- premaxillae suture | Wide | Narrow | |

TABLE 2 A Comparison of *Plesiochelys* Species

available but presumably the specimen is Late Jurassic in age and from the Isle of Portland, Great Britain.

Diagnosis. Member of the Plesiochelyidae (sensu Gaffney, present paper) known only from the skull; distinguishable from *Plesiochelys etalloni* by the following features: lingual ridge of maxilla higher than in *P. etalloni*, anterior portion of lingual ridge on lower jaw curving medially (as opposed to anteriorly in *P. etalloni*), at level of vomer-premaxilla suture the distance between lingual ridges of maxillae being wider than in *P. etalloni*.

Hypodigm. The type specimen.

Plesiochelys etalloni (Pictet and Humbert)¹

Emys Etalloni Pictet and Humbert, 1857, p. 1.

Emys jaccardi Pictet, 1860, p. 15.

Stylemys lindensis Maack, 1869, p. 320.

Plesiochelys solodurensis Rütimeyer, 1873, p. 50. Plesiochelys Jaccardi (Pictet) [non] Rütimeyer,

1873, p. 68. Plesiochelys Etalloni (Pictet and Humbert)

[non] Rütimeyer, 1873, p. 72.

Plesiochelys Sanctae Verenae Rütimeyer, 1873, p. 80.

Craspedochelys Picteti Rütimeyer, 1873, p. 89. Craspedochelys crassa Rütimeyer, 1873, p. 90.

Type Specimen. Apparently lost (H. Bräm, personal commun.).

Locality. "... dans la forêt de Lect, près de Moirans (département du Jura" and "... des en-

¹Bräm (1965, p. 60) indicated Pictet as sole author but figure captions and title page in the original paper, although possibly written by Pictet alone, indicate both individuals as authors: "*Emys Etalloni*, Pictet et Humbert" (Pictet and Humbert, 1857, p. 10, pls. I, II). virons de St. Claude..." (Pictet and Humbert, 1857, p. 1). Eastern part of France, near Swiss border.

Horizon. "... terrain jurassique supérieur (Portlandien?)" (Pictet and Humbert, 1857, p. 2).

Diagnosis. Member of the Plesiochelyidae (sensu Gaffney, present paper) known from nearly all the skeleton, distinguishable from *Plesi*ochelys planiceps by the following features: lingual ridge of maxilla usually lower than in *P.* planiceps, anterior portion of lingual ridge on lower jaw curving anteriorly (as opposed to medially in *P. planiceps*), at level of vomerpremaxilla suture the distance between lingual ridges of maxillae is narrower than in *P. planiceps*.

Hypodigm. Bräm (1965) listed and described the known Swiss specimens. The skulls used in this paper are listed below with comments on the state of preservation.

MH 435, skull, jaws, shell, and some appendicular elements. This is one of the two skull-shell associations for Plesiochelys etalloni. Unfortunately the shell (on exhibit in Basel) is not completely prepared but I have examined it and believe that the shell features as determinable at this time are consistent with my concept of Plesiochelys etalloni. Furthermore, Bräm (1965, p. 62, pl. 4, figs. 1-4) also identified this specimen as P. etalloni. The skull is well preserved and only slightly distorted around the nasal area. All the sutures are open and readily visible. Most of the right cheek area, the basioccipital, exoccipital, and most of the right quadrate are missing. Only a portion of the left squamosal remains but none of the right. The posterior braincase elements were disarticulated and lost presumably before burial, allowing an excellent view into the skull.



FIG. 4. Plesiochelys etalloni, MH 435, Late Jurassic, Switzerland. Left: dorsal view of skull. Right: ventral view of skull. Bottom: left lateral view of skull. Midline length of specimen as preserved, 56 mm.

Unfortunately the specimen was mounted by drilling a hole horizontally into the cavum cranii destroying part of the dorsum sellae. Nonetheless, this is the best preserved skull externally and has been used as the basis for the principal restorations (figs. 8-12).

Locality: Northeast of Glovelier, between Glovelier and Boécourt, in the District of Delemont, Canton Berne, Switzerland (personal commun. J. Hürzeler, 1971). Horizon: "Kimmeridge" (Bräm, 1965, pl. 4), Late Jurassic.

SM 134, partially disarticulated skull, jaws, hyoid elements, and shell fragment. Cuvier (1824, p. 230, pl. 15, fig. 7) and Rütimeyer (1873, pl. 14, fig. 5) figured this skull (see history of previous work). Preparation in acetic acid has allowed the disarticulation of the anterior skull elements (vomer, maxillae, jugals) and an unobscured view of the anterior part of the braincase. The skull has been subjected to oblique pressure that has distorted features by moving them ventrally and to the left. Minute fractures can be seen in some areas but for the most part the deformation does not seem to have affected the strength of the bone. The posteroventral surface of the basicranium and occiput is particularly well preserved in this skull, and it has been the source of information on this area in the principal restorations (figs. 11, 12).

Locality: Quarries near Solothurn, Switzerland (label, also Rütimeyer, 1873). Although Bräm (1965) and Rütimeyer (1873) gave no detailed information on locality or stratigraphy, Lang and Rütimeyer (1866) published detailed maps and sections of the area around Solothurn. One of the maps (pl. 1, fig. 2) indicates 11 numbered quarries that appear to have yielded turtle remains. I visited this area in 1971 and many of them are still recognizable and a few are currently being worked. Unfortunately neither Rütimeyer (1873) nor Bräm (1965) have used quarry numbers to indicate specimen localities and I have been unable to find information of this sort in the Solothurn Museum catalogue. Rütimeyer and Bräm both said, however, that many of the specimens were found by quarry workmen who brought the specimens to the museum, and it is quite possible that the specific quarry data was not retained.

Horizon: "Kimmeridge, *Pseudomutabilis* zone" (label), Late Jurassic.

SM 135, a frontally sectioned skull. This specimen was figured by Rütimeyer (1873, pl. 14, figs. 3, 4) and Bräm (1965, pl. 6, fig. 1). The external surface is somewhat damaged (as are most of the Solothurn specimens) by manual preparation. Acetic acid dissolved the remaining matrix revealing a well-preserved braincase that was further exposed by removing the braincase roof.

Locality and Horizon: Same as SM 134.



FIG. 5. *Plesiochelys etalloni*, SM 136, Late Jurassic, Switzerland. *Left*: dorsal view of skull. *Right*: ventral view of skull. Midline length of specimen as preserved, 71 mm.



FIG. 6. *Plesiochelys etalloni*, SM 134, Late Jurassic, Switzerland. Dorsal view of skull. Midline length of specimen as preserved, 62 mm.

SM 136, a skull and jaws. Rütimeyer (1873, pl. 14, figs. 1, 2) and Bräm (1965, pl. 6, fig. 2) illustrated this specimen. Dorsoventral compression and external surface damage limit the usefulness of the skull but many palatal and basicranial features are nonetheless visible.

Locality and Horizon: Same as SM 134.

SM 594, a partial skull, partial shell, and appendicular material. The shell material is described by Bräm (1965, p. 66) and he has identified it as *Plesiochelys etalloni*. As this is one of the two skull-shell associations, the identification is of some importance. I have examined the shell material, and although it requires further preparation, I agree with the determination. Bräm (1965, fig. 9; pl. 4, fig. 6) also described and figured the skull but in this case I have interpreted the sutures somewhat differently. Further preparation of the skull by acetic acid and air abrasive methods (the skull is too badly fractured for complete development in acid in contrast to most other Solothurn skulls) has allowed exposure of the basicranium and better understanding of the skull roof. This specimen is the only *Plesi*ochelys skull that appears to have most of the posterior parietal margin preserved as well as part of the squamosal-quadratojugal region. The principal restorations (figs. 8, 9) rely on this specimen for the posterior temporal roof margin.

Locality and Horizon: Same as SM 134.

Discussion. Although my synonymy list for Plesiochelys etalloni may look like rampant lumpism in comparison with that of another student of this group (Bräm, 1965), I have carefully considered his arguments and examined the specimens in question. Basically our differences involve the degree of individual variation we will accept in one biologic species. This is a difficult problem to deal with for fossil forms and there is certainly a considerable amount of subjectivity involved. The type and degree of variation is apparently specific to a particular population (Mayr, 1965) and comparing variation in a Recent turtle population with a postulated population of *Plesiochelys* may not be a satisfactory method of determining species boundaries. Nonetheless, I have some knowledge (however subjective) of the type and degree of variation seen in Recent turtle species and have applied this to the specimens in question.

Bräm's criteria for differentiating the species of Plesiochelys may be separated into two categories: features probably due to postmortem deformation and features due to biologic variation. Although Bräm recognized the fact that the Solothurn turtles are variably deformed and distorted, he nonetheless used some criteria that, in my opinion, are better ascribed to diagenetic rather than biologic processes. The carapace outline of P. jaccardi is broader than in other species (a width/length ratio of 101% versus 89% for P. etalloni and 84% for P. solodurensis) but the specimens involved seem to be flattened dorsoventrally by postmortem compression resulting in a relatively wider shape. Bräm also uses the angle at which the anterior thoracic ribs meet the vertebral column. This area is available for examination in only a few specimens and one of them, SM 101, the only measured specimen of P. jaccardi, is compressed and distorted. It is also the most extreme of the measurements. The other

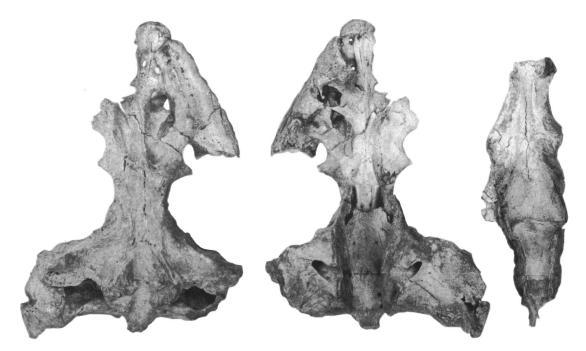


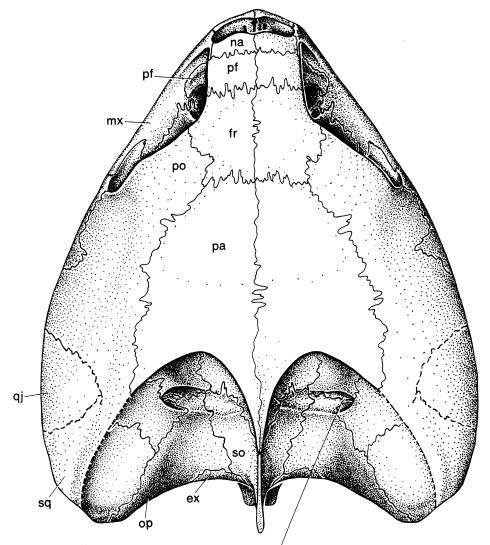
FIG. 7. Plesiochelys etalloni, SM 135, Late Jurassic, Switzerland. Left: ventral view of skull. Center: dorsal view of skull with skull roof removed. Right: ventral view of skull roof. Condyle-premaxilla length, 78 mm.

specimens are less compressed but, in my opinion, the published angles are within the range of measurement error even without invoking compression.

The existence of the following features as biologic variation is not disputed, but on the basis of my subjectively determined limits I consider them to be within the range of a biologic species: degree of nuchal emargination, plastron outline, posterior carapace outline, width of neural scutes, and degree of sulcus definition.

One particularly important (perhaps the most important to Bräm) feature due to biologic variation is the development of fontanelles in the plastron. Bräm noted that juvenile *Plesiochelys* had fontanelles and has used the persistence or loss of them in the presumed adult to differentiate *P. etalloni* and *P. jaccardi* (present in adults) from *P. solodurensis* (absent in adults). Bräm seems to use this feature for specimen identification more than others. For example, SM 606 is broad, has an evenly rounded nuchal indentation, and is small in size; all features of *P. jaccardi*. But there are no plastral fontanelles and Bräm identifies it as *P. solodurensis*. Wood (MS, personal commun.) has observed that the retention of a plastral fontanelle in the living *Pelomedusa subrufa* is variable; some adults have one and some do not. I suspect that this is the case in *Plesiochelys*. There is certainly variability in the size and age of individuals at the time of fontanelle closure in other living turtles but few recent species retain a small (rather than large as in cheloniids) plastral fontanelle as adults. From these considerations, I advance the hypothesis that *Plesiochelys solodurensis*, *P. jaccardi*, and *P. etalloni* as defined by Bräm are referable to one biologic species.

Plesiochelys sanctaeverenae consists of one large, partial carapace. None of the features used by Bräm, either individually or in concert, differentiate this form from other *Plesiochelys* specimens. In fact, Bräm's diagnosis of *P. sanctae*verenae agrees with his own diagnosis of *Plesio*chelys etalloni in all but one feature: the sulci



foramen stapedio-temporale

FIG. 8. *Plesiochelys etalloni*, Late Jurassic. Restored dorsal view of skull based primarily on MH 435 with additions from SM 594. Posterolateral region of skull roof conjectural and indicated by dashed lines. See Abbreviations.

grooves are supposedly deeper in *P. sanctaevere*nae. This feature seems quite variable in all turtles, however.

The principle feature differentiating *Craspe*dochelys from *Plesiochelys* according to Bräm is the free first thoracic rib and the "stronger" second rib connected only to the second thoracic vertebrae (the shell outline features are clearly the result of deformation). The ribs are visible in only one specimen, SM 608, and their condition is ambiguous due to incomplete preparation and postmortem damage. I am hesitantly synonymizing this form with *Plesiochelys*, although the rib criteria may prove to be biologically consistent after further preparation.

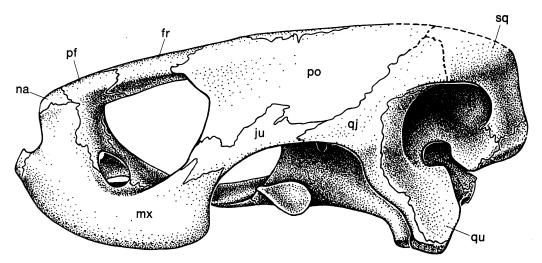


FIG. 9. *Plesiochelys etalloni*, Late Jurassic. Restored lateral view of skull based primarily on MH 435 with additions from SM 594. Posterodorsal region conjectural and indicated by dashed lines. see Abbreviations.

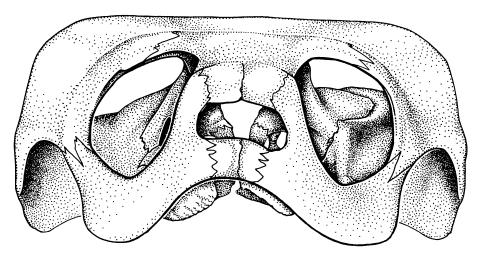


FIG. 10. *Plesiochelys etalloni*, MH 435, Late Jurassic, Switzerland. Anterior view of skull restored along right cheek and otic chamber, but otherwise drawn from the specimen as preserved.

PORTLANDEMYS,¹ NEW GENUS

Type Species. Portlandemys mcdowelli, new species.

¹The specimens constituting this genus have been referred to by Parsons and Williams (1961) as "the Portland skulls"; the type locality is the Island of Portland.

Known Distribution. Late Jurassic of Great Britain.

Diagnosis. Member of the Plesiochelyidae (sensu Gaffney, present paper) known only from skull; foramen palatinum posterius enclosed by bone as in most other turtles, anteroposterior length of premaxillae longer than in Plesiochelys, angle between labial ridges (of max-

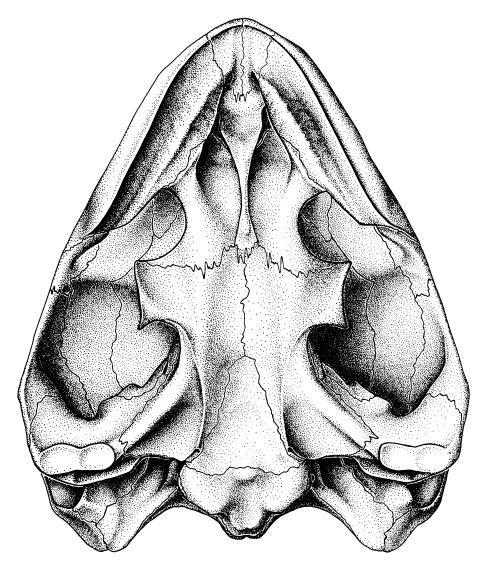
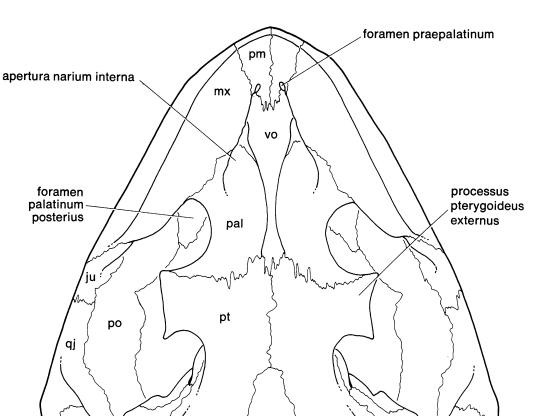


FIG. 11. *Plesiochelys etalloni*, Late Jurassic. Restored ventral view of skull based primarily on MH 435 with additions from SM 134 around the posterior region of the pterygoid and fenestra postotica.

illae and lower jaws) more acute than in *Plesi-ochelys*, median channel between lingual ridges of palate narrower in comparison with *Plesiochelys*; length of lower jaw symphysis longer than in *Plesiochelys*, symphyseal hook developed to the extent seen in *Chelydra*; prootic process seen in *Plesiochelys* absent, not contacting processus clinoideus.

Discussion. The preparation of the type of Stegochelys showed that it is more properly in-

cluded in the genus *Plesiochelys* and that it is quite different in a number of features from the "Portland skulls" referred to *Stegochelys* by Parsons and Williams (1961). As a name for the "Portland skulls" is unavailable, I have thought it best to provide one even though there is no associated shell material. The chief distinguishing characters of *Plesiochelys* and *Portlandemys* are summarized in table 1.



foramen posterius canalis carotici interni

FIG. 12. Key to figure 11. See Abbreviations.

bs

bo

Portlandemys mcdowelli,¹ new species

qo

ėχ

qu

sģ

Type Specimen. BM (NH) R 2914, nearly complete skull lacking both lateral temporal regions and left cheek. Mandible lacking posterior portions. "By exchange with R. Damon,

¹For Dr. Samuel B. McDowell, in recognition of his work on the basicranial morphology and systematics of turtles.

1899. Developed with acetic acid by A. E. Rixon, in Geol. Department workshop, Feb. 1953. Originally identified as *Pleurosternum*" (label). Figured by Parsons and Williams (1961, figs. 1, 3, 4; pls. 1, 2, 3).

Locality and Horizon: Portlandian, Isle of Portland (label); Late Jurassic, Great Britain.

Hypodigm. BM (NH) R 3163, disarticulated partial skull. Largest portion is braincase that has

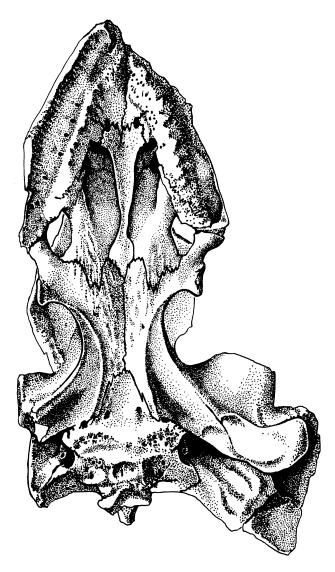
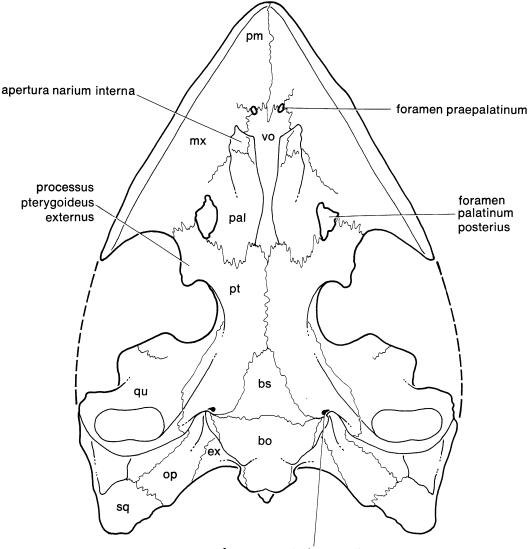


FIG. 13. Portlandemys mcdowelli, new genus and species, BM (NH) R 2914, Late Jurassic, Great Britain. Ventral view of type specimen. From Parsons and Williams, 1961.

been eroded posteroventrally and lacks left otic chamber. Other elements that are present: both parietals lacking posterolateral edges of skull roof (3163a), both frontals, most of left prefrontal, left maxilla, right postorbital, most of both palatines, vomer, right prootic. Figured by Parsons and Williams (1961, fig. 8; pl. 3). "Bought from R. F. Damon, Jan. 1904. Originally identified as *Chelone*. Redetermined by Dr. E. Williams as *Stegochelys planiceps*, 1953. Developed with acetic acid in BM Geol. Dept. by A. E. Rixon, 1953" (label).



foramen posterius canalis carotici interni

FIG. 14. Key to figure 13. See Abbreviations.

Locality and Horizon: Portlandian, Portland (label); Late Jurassic, Great Britain.

BM (NH) R 3164, skull lacking portion anterior to middle of orbits and lateral and posterior portions of skull roof, plus one phalange. Figured by Parsons and Williams (1961, figs. 5, 6). "Bought from R. F. Damon, Jan. 1904. Originally identified as Chelonian ?*Pleurosternum.* Redetermined by Dr. E. Williams, Jan. 1953, as *Stegochelys planiceps.* Developed with acetic acid in BM Geol. Dept. workshop by A. E. Rixon, Jan. 1953" (label).

Locality and Horizon: Portlandian, Portland (label); Late Jurassic, Great Britain.

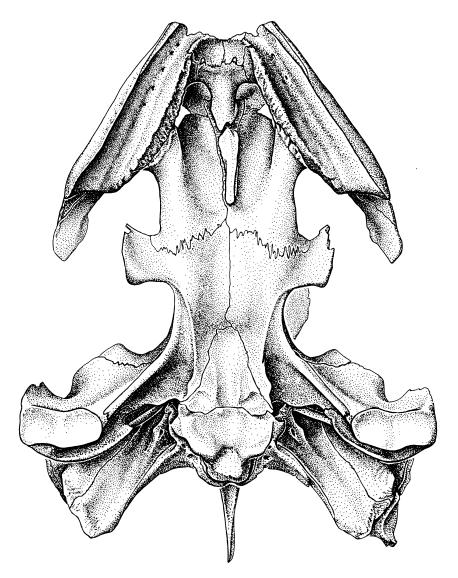


FIG. 15. *Plesiochelys planiceps*, OU-J1582, Late Jurassic, Great Britain. Partially restored ventral view of type specimen. Posterior margin of pterygoid and area surrounding fenestra postotica somewhat eroded.

LITERATURE CITED

Baur, G.

1893. Notes on the classification of the Cryptodira. Amer. Nat., vol. 27, no. 319, pp. 672-675.

Bräm, Heinrich

1965. Die Schildkröten aus dem oberen Jura (Malm) der Gegend von Solothurn. Schweizerische Paläont. Abhandl., vol. 83, pp. 1-190.

- Cope, Edward D.
- 1868. On the origin of genera. Proc. Acad. Nat. Sci. Philadelphia, vol. 20, pp. 242-300.

Cuvier, Georges

1824. Recherches sur les ossements fossiles, où l'on rétablit les caractères de plusiers animaux dont les révolutions du globe ont détruit les espèces. 2nd ed. Paris. vol. 5.

- Delair, J. B.
 - 1958. The Mesozoic reptiles of Dorset (part I). Proc. Dorset Nat. Hist. Archaeol. Soc., vol. 79, pp. 47-72.
- Gaffney, Eugene S.
 - 1972. An illustrated glossary of turtle skull nomenclature. Amer. Mus. Novitates, no. 2486, pp. 1-33.
 - 1975. Solnhofia parsonsi, a new cryptodiran turtle from the Late Jurassic of Europe. Amer. Mus. Novitates, no. 2576.
- [In press.] A phylogeny and classification of the higher categories of turtles. Ibid.
- Lang, F., and L. Rütimever
 - 1866. Die fossilen Schildkröten von Solothurn. Denkschr. Naturf. Gesell. (Schweiz), Jahrgang 22, 47 pp.
- Linnaeus, Carolus
- 1758. Systema naturae. 10th ed. Stockholm, vol. 1, 824 pp.
- Lydekker, Richard
 - 1889a. Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History). Part III. The order Chelonia. London, British Museum (Nat. Hist.), 239 pp.
 - 1889a. On remains of Eocene and Mesozoic Chelonia and a tooth of ?Ornithopsis. Quart. Jour. Geol. Soc. London, vol. 45, pp. 227-246.
- Maack, G. A.
 - 1869. Die bis jetzt bekannten fossilen Schildkröten und die im oberen Jura bei Kehlheim (Bayern) und Hannover neu aufgefundenen ältesten Arten derselben. Palaeontographica, band 18, pp. 193-338.
- Mayr, Ernst
 - 1965. Animal species and evolution. The Belknap Press of Harvard Univ. Press, 797 pp.

Owen. Richard

- 1842. Report on British fossil reptiles. Rept. Brit. Assoc. Adv. Sci., London, vol. 11, pt. 2, pp. 60-204.
- 1884. A history of British fossil reptiles. London, Cassell and Co., Ltd., vol. 2, pls. Parsons, Thomas S., and Ernest Williams
- 1961. Two Jurassic turtle skulls: a morphological study. Bull. Mus. Comp. Zool.,
- vol. 125, pp. 43-107. Pictet, F. J.

 - 1860. Reptiles et poissons fossiles de l'étage virgulien du Jura neuchatelois. Part 2. Description des fossiles. I. Emys jaccardi, Pictet. Matériaux Paléont. Suisse. ser. 3, pp. 15-20.

Pictet, F. J., and A. Humbert

- 1857. Description d'une émyde nouvelle (Emys etalloni) du terrain Jurassique supérieur des environs de St. Claude, Matériaux Paléont. Suisse, ser. 1 (1854-1858), pp. 1-10.
- Rütimever, L.
 - 1873. Die fossilen Schildkröten von Solothurn und der übrigen Jura-formation. Denkschr. Schweizer. Naturf. Gessell., band 25, pp. 1-185.
- Wood, Roger C.
 - [MS.] The fossil Pelomedusidae (Testudines; Pleurodira) of Africa.
- Yeh, Hsiang-K'uei
 - 1963. Fossil turtles of China. Palaeont. Sinica, no. 150, new ser. C, no. 18, pp. 1-112.
 - 1973. Discovery of Plesiochelys from Upper Lefeng Series, Oshan, Yunnan and its stratigraphical significance. [In Chinese.] Vertebrata PalAsiatica, vol. 11, no. 2, pp. 160-163.
- Young, Chung-Chien, and Min-Chen Chow
 - 1953. New fossil reptiles from Szechuan China. Acta Sci. Sinica, vol. 2, no. 3, pp. 216-243.

· · · · ·