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Cearachelys, a New Side-Necked Turtle (Pelomedusoides: Bothremydidae) from the Early Cretaceous of Brazil

EUGENE S. GAFFNEY,[1] DIOGENES DE ALMEIDA CAMPOS,[2] AND REN HIRAYAMA[3]

ABSTRACT

The early Cretaceous Santana Formation exposed on the Chapada do Araripe in Ceará State, northeastern Brazil, has yielded remains of a side-necked turtle, *Cearachelys placidoi*, new genus and species. *Cearachelys* is based on two skeletons, each consisting of articulated shell, associated skull, and postcrania in varying degrees of completeness. *Cearachelys* is a pelomedusoid pleurodire belonging to the family Bothremydidae Baur, 1891, based on these bothremydid characters: (1) precolumellar fossa absent, (2) occipital condyle consisting only of exoccipitals, (3) foramen stapedio-temporale anteriorly facing, and (4) exoccipital contacts quadrate. Within the Bothremydidae, *Cearachelys* is best resolved as the sister group of *Bothremys*, *Rosasia*, *Foxemys*, *Zolhafah*, and *Polysternon*. *Cearachelys* differs from the other two pleurodires in the Santana Formation in the bothremydid characters listed above and in having a quadrate-basioccipital contact, a prootic completely covered in ventral view, and a high lingual ridge on the lower jaw.

INTRODUCTION

First recognized as a group of extinct side-necked turtles in 1891 by George Baur on the basis of the skull of *Bothremys cooki* Leidy, 1865, the Bothremydidae is now thought to consist of more than a dozen skull-based genera, more than half still undescribed. The purpose of this paper is to name and describe a new bothremydid that is represented by two nearly complete skel-

[1] Curator, Division of Paleontology, American Museum of Natural History.
[2] Departamento Nacional da Produçao Mineral, Divisao de Mineraçao, Av. Pasteur 404, Rio de Janeiro 22290–240, Brazil.
[3] Teikyo Heisei University, 2289 Uruido, Ichihara, Chiba 290–01, Japan.

etons. It is one of the oldest members of the family.

The Bothremydidae extend from the early Cretaceous to the Miocene and are found on all the continents except Antarctica and Australia. Adult bothremydids range in size from less than 25 cm to more than 150 cm in length. Throughout their record, bothremydids occur as fossils in near-shore marine sediments as well as terrestrial freshwater units. Bothremydid cranial diversity also suggests a reinterpretation of pleurodire history. This family was a widespread, relatively diverse group adapted to many habitats, rather than a conservative group occupying a few restricted niches. The original misconception arose from the fact that the more commonly preserved shells are unusually conservative in pelomedusoids when compared with the skull; the diversity of this group has gone unappreciated.

Although the Bothremydidae was named as early as 1891 by George Baur, the term fell into disuse for most of this century, and the few included taxa, particularly *Bothremys* and *Taphrosphys,* were simply included in the Pelomedusidae. Broin in Antunes and Broin (1988) and Broin (1988) revived Bothremydidae, provided a new diagnosis, and added taxa, such as *Rosasia,* based on skulls and shells. Recent papers on fossil pleurodires, such as Meylan (1996), Lapparent de Broin and Werner (1998), and Tong et al. (1998), use the Antunes and Broin (1988) terminology, in which Bothremydidae, Podocnemididae, and Pelomedusidae (restricted to *Pelusios* and *Pelomedusa*) are contained in the Pelomedusoides (which equals Pelomedusidae in the classic sense). Bothremydids are now recognized as a far more widespread and diverse group than previously considered.

Useful reviews of the literature on bothremydids can be found in Broin (1988) and Antunes and Broin (1988). Information in varying degrees of completeness on previously described bothremydid skulls are as follows: *Bothremys* (Gaffney and Zangerl, 1968; Gaffney, 1977), *Taphrosphys* (Gaffney, 1975), *Rosasia* (Antunes and Broin, 1988), *Foxemys* (Tong et al., 1998), *Zolhafah* (Lapparent de Broin and Werner, 1998), *Arenila* (Lapparent de Broin and Werner, 1998), and *Nigeremys* (Bergounioux and Crouzel, 1968; Lapparent de Broin and Werner, 1998). Other pelomedusoid skulls are *Araripemys* (Meylan, 1996), *Hamadachelys* (Tong and Buffetaut, 1996), and an unnamed Santana genus (represented by FR 4922, Gaffney and Meylan, 1991). A general treatment and description of pleurodire skulls, turtle-skull morphology and terminology, and a literature review is in Gaffney (1979).

We use Lapparent de Broin and Werner's (1998) reference to a *Bothremys* Group and a *Nigeremys* Group (which includes *Taphrosphys* in our usage), as these continue to form monophyletic taxa in most of our current analyses. Our contents of these groups are as follows: *Bothremys* Group—*Bothremys, Rosasia, Zolhafah, Foxemys*; *Nigeremys* Group—*Nigeremys, Arenila,* and *Taphrosphys.*

The Santana Formation is most famous for its early Cretaceous fishes (Maisey 1991), but it also has a very important turtle fauna consisting of the following:

Cryptodira
- Protostegidae
  - *Santanachelys gaffneyi* (Hirayama, 1998)

Pleurodira
- Araripemydidae
  - *Araripemys barretoi* (Meylan, 1996)
- Unnamed family
  - Unnamed genus, FR 4922 (Gaffney and Meylan, 1991)
- Bothremydidae
  - *Cearachelys placidoi* (new genus and species described here)

Institutional Abbreviations

MPSC	Museu Paleontolgico de Santana do Cariri, Ceará State, Brazil
TUTg	Teikyo Heisei University, Chiba, Japan
FR	Forschungsinstitut Senckenburg, Frankfurt, Germany
YPM	Yale Peabody Museum, New Haven, CT, USA
USNM	United States National Museum, Washington DC, USA

Anatomical Abbreviations

bo	basioccipital
bs	basisphenoid

ex	exoccipital
fpcci	foramen posterius canalis carotici interni
fr	frontal
ju	jugal
mx	maxilla
na	nasal
op	opisthotic
pa	parietal
pal	palatine
pf	prefrontal
pm	premaxilla
po	postorbital
pr	prootic
pt	pterygoid
qj	quadratojugal
qu	quadrate
so	supraoccipital
sq	squamosal
vo	vomer

SYSTEMATICS

ORDER TESTUDINES LINNAEUS, 1758

MEGAORDER PLEURODIRA COPE, 1864 (FIDE GAFFNEY AND MEYLAN, 1988)

HYPERFAMILY PELOMEDUSOIDES COPE, 1868

FAMILY BOTHREMYDIDAE BAUR, 1891

Cearachelys, new genus

TYPE SPECIES: *Cearachelys placidoi,* new genus and new species.

DISTRIBUTION: Aptian or Albian (early Cretaceous) of Brazil.

ETYMOLOGY: In allusion to the type locality that is in Ceará State, Brazil; and *chelys,* turtle.

DIAGNOSIS

Skull triangular, orbits dorsolaterally placed, not dorsally as in *Bothremys* and *Foxemys*; jugal separated from orbital margin in contrast to most bothremydids; jugal entering triturating surface, but not to the extent seen in *Bothremys*; triturating surfaces triangular and expanded posteriorly, but not to the extent seen in *Bothremys* and *Foxemys*; triturating surfaces smooth, no pits as in *Bothremys* and *Rosasia*; broad maxilla-quadratojugal contact; antrum postoticum moderate as in *Podocnemis,* not small as in *Bothremys*; eustachian tube and stapes not separated by bone in incisura columellae auris; quadrate-basioccipital contact present; foramen posterius canalis carotici interni formed by basisphenoid and pterygoid as in *Rosasia*; supraoccipital-quadrate contact present as in *Bothremys, Rosasia,* and *Foxemys*; condylus occipitalis formed only by exoccipitals as in *Zolhafah*; foramen stapediotemporale facing anteriorly.

Carapace moderately domed as in *Pelomedusa,* oval in outline, with eight neurals completely separating all eight costals in contrast to at least one pair of costals meeting in midline as in most other bothremydids; second neural does not contact first costals. Plastron with anterior lobe rounded and broader than in other Santana pelomedusoids; pectoral scales do not extend anteriorly onto entoplastron, but do extend posteriorly onto mesoplastra; mesoplastron small and laterally placed as in *Podocnemis.*

Cearachelys placidoi, new species

TYPE SPECIMEN: MPSC (figs. 2, 3, 6, 7), a partial skull, shell, cervicals, and limb elements.

TYPE LOCALITY: Probably Santana do Cariri, Ceará, Brazil.

HORIZON: (?) Romualdo Member of the Santana Formation, probably Albian in age (ca. 110 mya; Maisey, 1990, 1991).

DIAGNOSIS: Same as for genus.

ETYMOLOGY: In honor of Dr. Placido Nuvens, Director of the Museu Paleontologico de Santana do Cariri, Ceará, Brazil; and *chelys,* turtle.

REFERRED MATERIAL: TUTg 1798—Nearly complete skeleton with skull, lower jaw, shell, cervicals, and limb elements (figs. 4, 5, 8, 9), near Santana do Cariri, Romualdo Member, Santana Formation. Purchased from von Leonhardt, 1993.

DESCRIPTION

PREFRONTAL

The prefrontal is preserved on both sides of TUTg 1798. It is similar to that bone in living Pelomedusidae, but differs from species such as *Pelomedusa subrufa* in projecting anteriorly to a greater extent, so that the dorsal margin of the apertura narium externa is more anterior than the ventral margin. The prefrontal in *Cearachelys* is dorsally convex, rather than flat as in some Pelomedusidae. The resultant morphology gives *Cearachelys* a prominent and projecting preorbital aspect comparable to

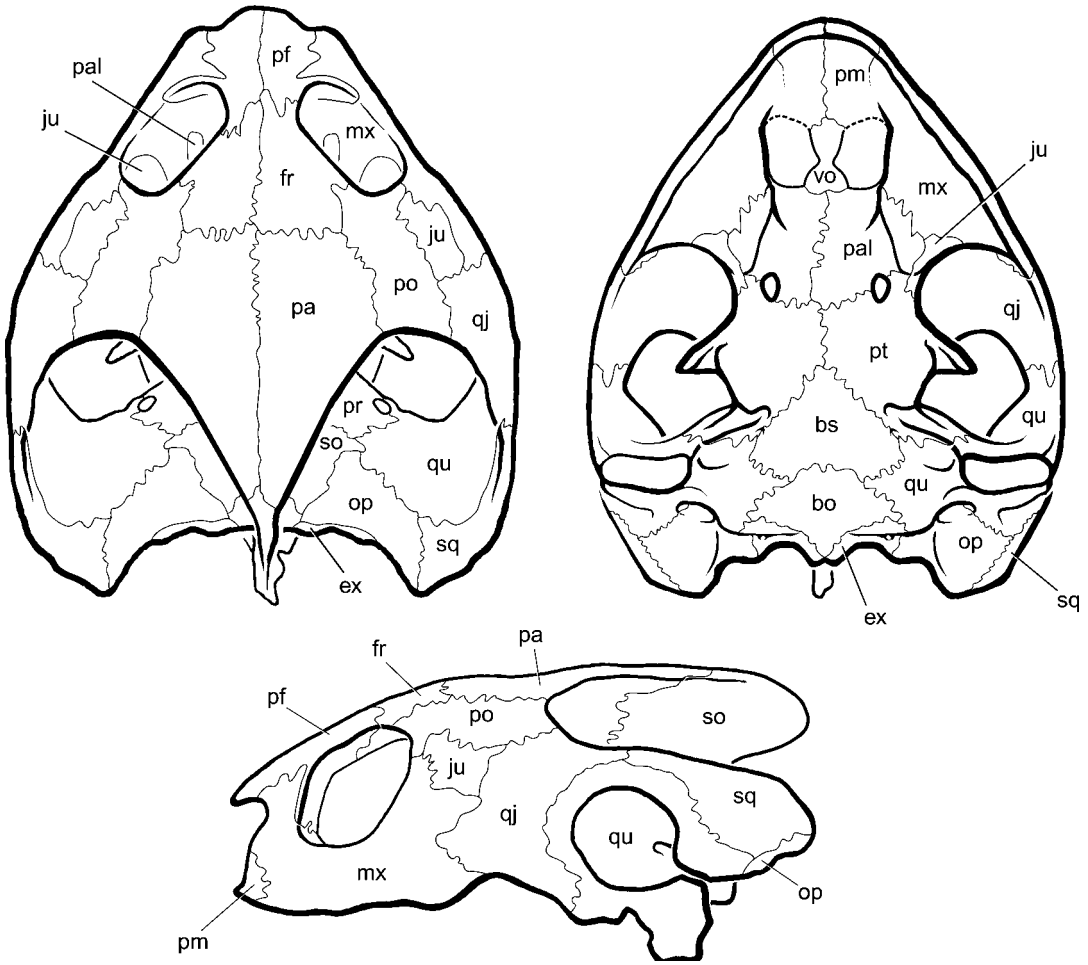

Fig. 1. *Cearachelys placidoi*, n. gen. & sp., Santana Formation, early Cretaceous, Ceará State, Brazil. Restoration of skull based on MPSC specimen and TUTg 1798. Dorsal (left), ventral (right), and lateral (center) views.

some Pelomedusidae, such as *Pelusios subniger*.

The prefrontal in *Cearachelys* has the usual pelomedusoid contacts: maxilla anterolaterally, frontal posteriorly. It borders the orbit laterally and the apertura narium externa anteriorly. The ventral surface of the prefrontal in *Cearachelys* is smooth, concave ventrally in its anterior portion, but bears the parasagittal ridge for the sulcus olfactorius more posteriorly. The prefrontal sends a process ventrally along the anterior margin of the fossa orbitalis comparable in size and extent to that in Recent Pelomedusidae. It contacts the maxilla for most of its length and does not reach other elements.

FRONTAL

The frontal of *Cearachelys* is preserved on both sides in TUTg 1798. It is similar in size, shape, and contacts to living Pelomedusidae. The frontal contacts are with the prefrontal anteriorly, orbit laterally, postorbital posterolaterally, parietal posteriorly, and the other frontal medially. Anteriorly the frontal projects on the midline to a considerable extent on the ventral surface, but only slightly on the dorsal surface.

The frontal forms the well-developed sulcus olfactorius on the ventral surface. In *Cearachelys* the sulcus is very similar to the living Pelomedusidae. The frontal in *Cearachelys* does

not have a ventral process along the edge of the processus inferior parietalis, although the frontal does reach the processus as in recent Pelomedusidae.

PARIETAL

The parietal is preserved on both sides in TUTg 1798 and the MPSC specimen, although it is not entirely complete in either skull. The parietal of *Cearachelys* is nonetheless completely known through both specimens.

The dorsal plate of the parietal in *Cearachelys* contacts the frontal anteriorly and is excluded from the orbit as in other Bothremydidae and the Pelomedusidae. Laterally the parietal contacts the postorbital, but not the quadratojugal, as in FR 4922. The temporal emargination in *Cearachelys* is more extensive than in living Podocnemididae and *Foxemys*, but not as extensive as in Pelomedusidae. The otic chamber is completely uncovered, but there is a relatively long suture between the parietal and the postorbital relative to that seen in the Pelomedusidae.

The ventral process of the parietal, the processus inferior parietalis, is well preserved in both skulls. It has relations similar to those in Pelomedusidae. Anteriorly it contacts the pterygoid and forms most of the side wall of the braincase. Posteriorly the parietal forms the anterodorsal margin of the foramen nervi trigemini (the ventral margin is formed by the pterygoid and the posterodorsal margin by the prootic). Posterior to the foramen nervi trigemini, the parietal contacts the prootic and then the supraoccipital in a suture that rises dorsally to the skull roof.

JUGAL

The jugal is preserved completely on the left side and in part on the right side of the MPSC specimen. In TUTg 1798 the left jugal is complete, but only part of the right jugal is preserved.

The jugal is a complex element that can be described as having three areas: lateral, ventral, and posterior (with two exposure surfaces, anterior and posterior). The lateral exposure of the jugal in *Cearachelys* is unusual among bothremydids. The jugal lies just posterior to the orbit as in all bothremydids; however, in most bothremydids the jugal enters the orbit. In *Cearachelys* a very narrow process of the postorbital runs ventrally along the orbital margin to reach or nearly reach the maxilla and prevent jugal exposure. On the left side of the MPSC specimen there is some breakage along the orbital margin in this area, but it is clear that the postorbital contacts the maxilla in a narrow area of sutural interdigitation. In TUTg 1798 both sides show the contact. In Lapparent de Broin and Werner (1998) an unnamed Moroccan skull is figured, which shows a broad contact of postorbital and maxilla, and this condition is similar to *Cearachelys*. No other bothremydid shows this retraction of the jugal from the orbit. Ventrally the jugal of *Cearachelys* is exposed on the palate to a limited extent, not to as great an extent as seen in *Bothremys* and *Rosasia*.

The jugal is exposed in the floor and posterior wall of the orbit in *Cearachelys* as in most pelomedusoids. In the orbital floor the jugal contacts the postorbital dorsally and posteriorly, the maxilla laterally and anteriorly, and the palatine medially. The limited postorbital-maxilla contact barely separates the orbital floor exposure of the jugal from the cheek exposure of the jugal, a condition unique to *Cearachelys*. The postorbital wall of *Cearachelys* shows the jugal forming the more ventral portion, contacting the maxilla ventrolaterally, the quadratojugal laterally, the postorbital dorsally, and the pterygoid posteromedially.

QUADRATOJUGAL

The quadratojugal is preserved on the left side of the MPSC specimen and on both sides of TUTg 1798.

The quadratojugal of *Cearachelys* forms the posterior part of the cheek. There is only a slight dorsal curve to the lower margin of the quadratojugal to suggest a cheek emargination; nothing like the emargination seen in Pelomedusidae is present. The quadratojugal of *Cearachelys* extends from the anterior limit of the upper temporal emargination to the ventral margin of the cheek. In contrast to members of the Pelomedusidae, which have a well-developed cheek emargination and no jugal-maxilla contact, *Cearachelys* has a broad maxilla-quadratojugal contact, as in *Foxemys*, *Nigeremys*, *Polysternon*, an unnamed Moroccan form

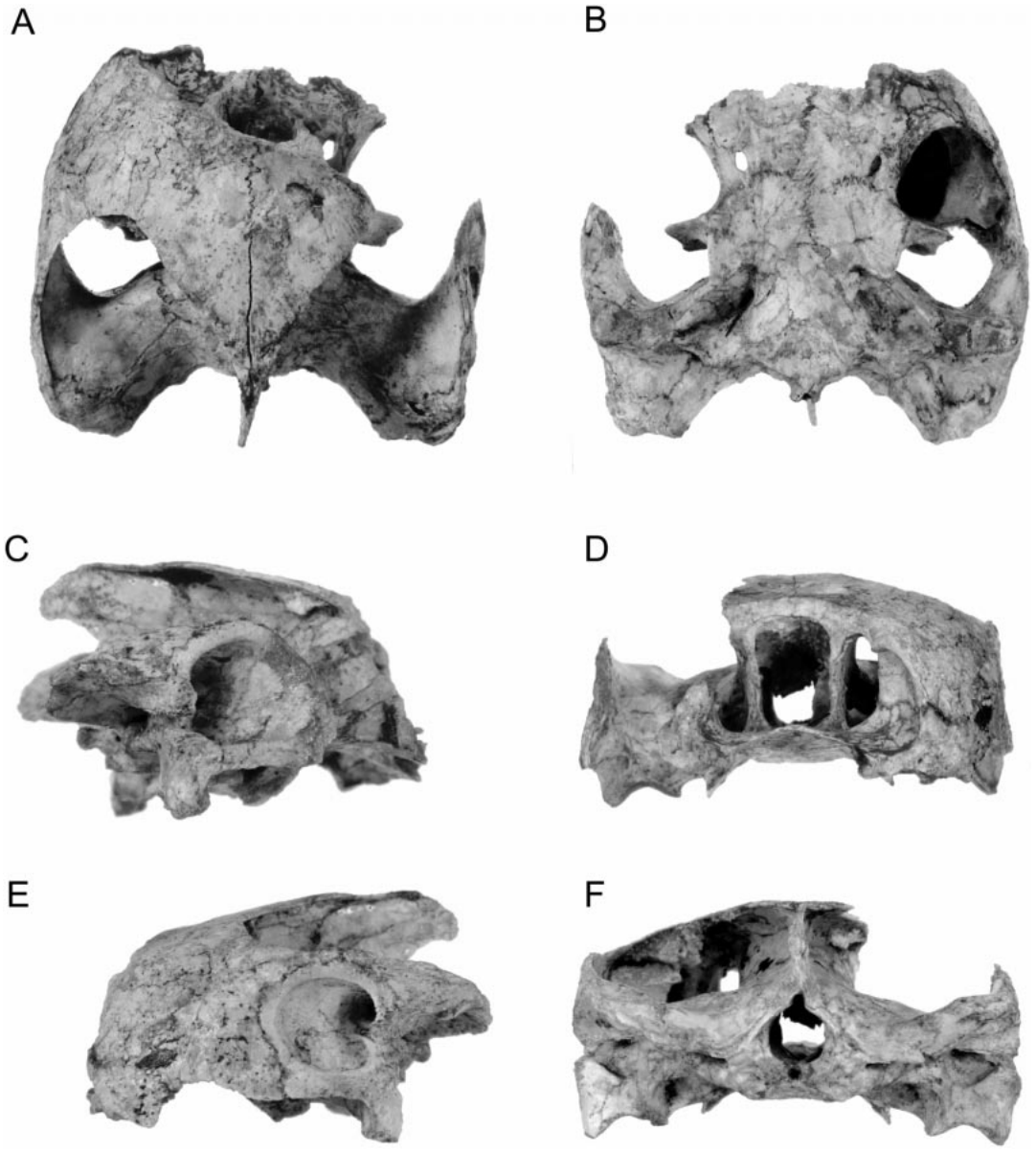

Fig. 2. *Cearachelys placidoi*, n. gen. & sp., MPSC specimen, holotype, Santana Formation, Santana do Cariri, Brazil. A, dorsal; B, ventral; C, right lateral; D, anterior; E, left lateral; F, posterior. See fig. 3 for key.

(Lapparent de Broin and Werner, 1998), and *Rosasia*. It is likely that this is a Bothremydidae synapomorphy.

In *Cearachelys* the anterior contacts of the quadratojugal are with the maxilla anteroventrally, the jugal anterodorsally, and the postorbital dorsally. Posteriorly there is a long curved contact with the quadrate. Posterodorsally a very narrow process of the quadratojugal contacts the squamosal.

SQUAMOSAL

The squamosal is preserved in both *Cearachelys* specimens.

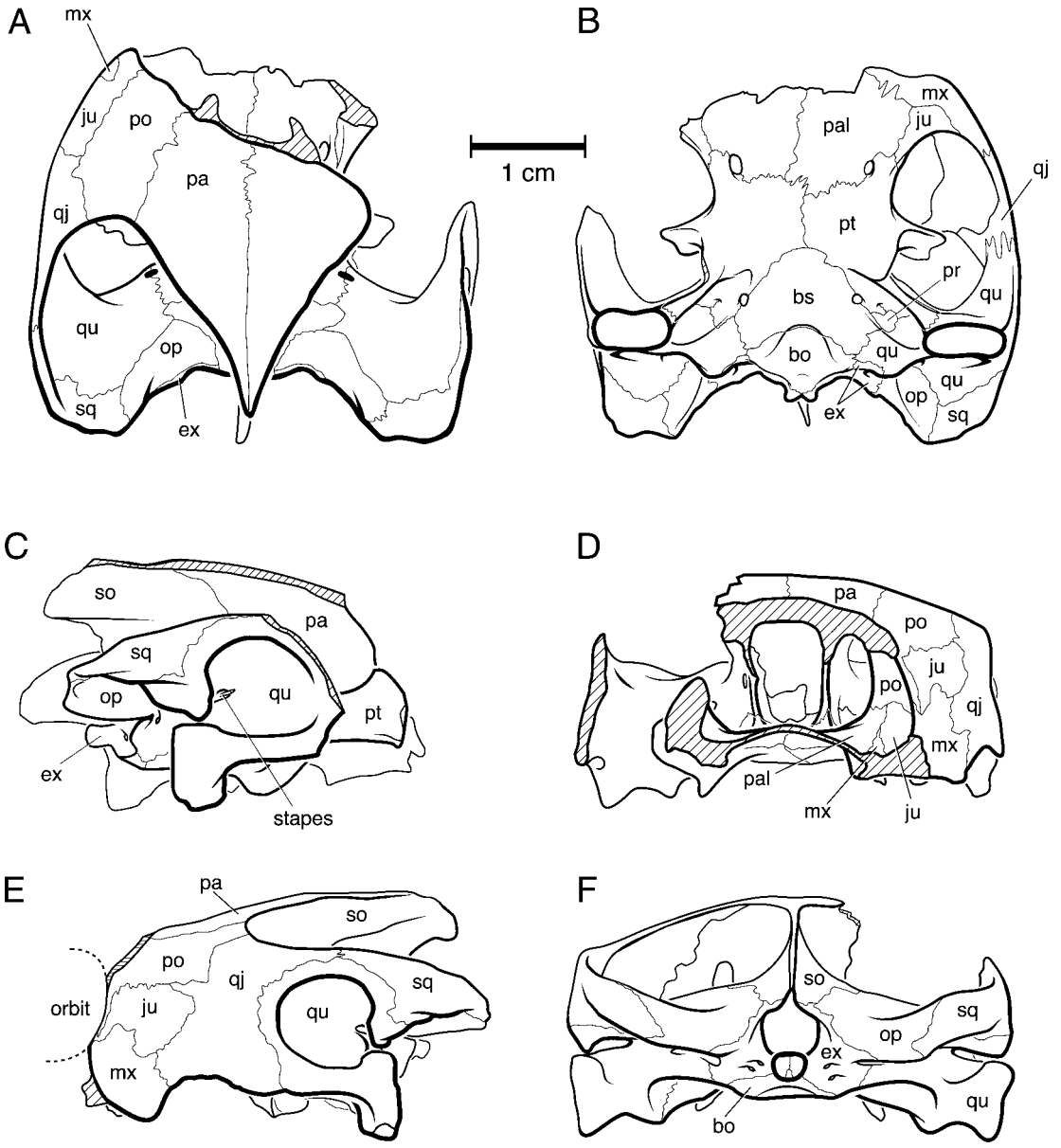

Fig. 3. Key to fig. 2.

The squamosal is a cone-shaped bone that sits on the posterodorsal corner of the quadrate and contains much of the antrum postoticum. The antrum of *Cearachelys* is moderately well developed relative to other pelomedusoids. *Bothremys* and *Taphrosphys* have an antrum that is very small, merely an elongate canal, while members of the Pelomedusidae have an antrum that is quite large. *Cearachelys* has an antrum postoticum intermediate in size between these, comparable to that in *Foxemys.*

The complete squamosal is not known for other bothremydids, such as *Arenila, Zolhafah, Rosasia,* or *Bothremys.* But in *Foxemys* the posterior part of the squamosal is developed into a flat plate. In *Taphrosphys*

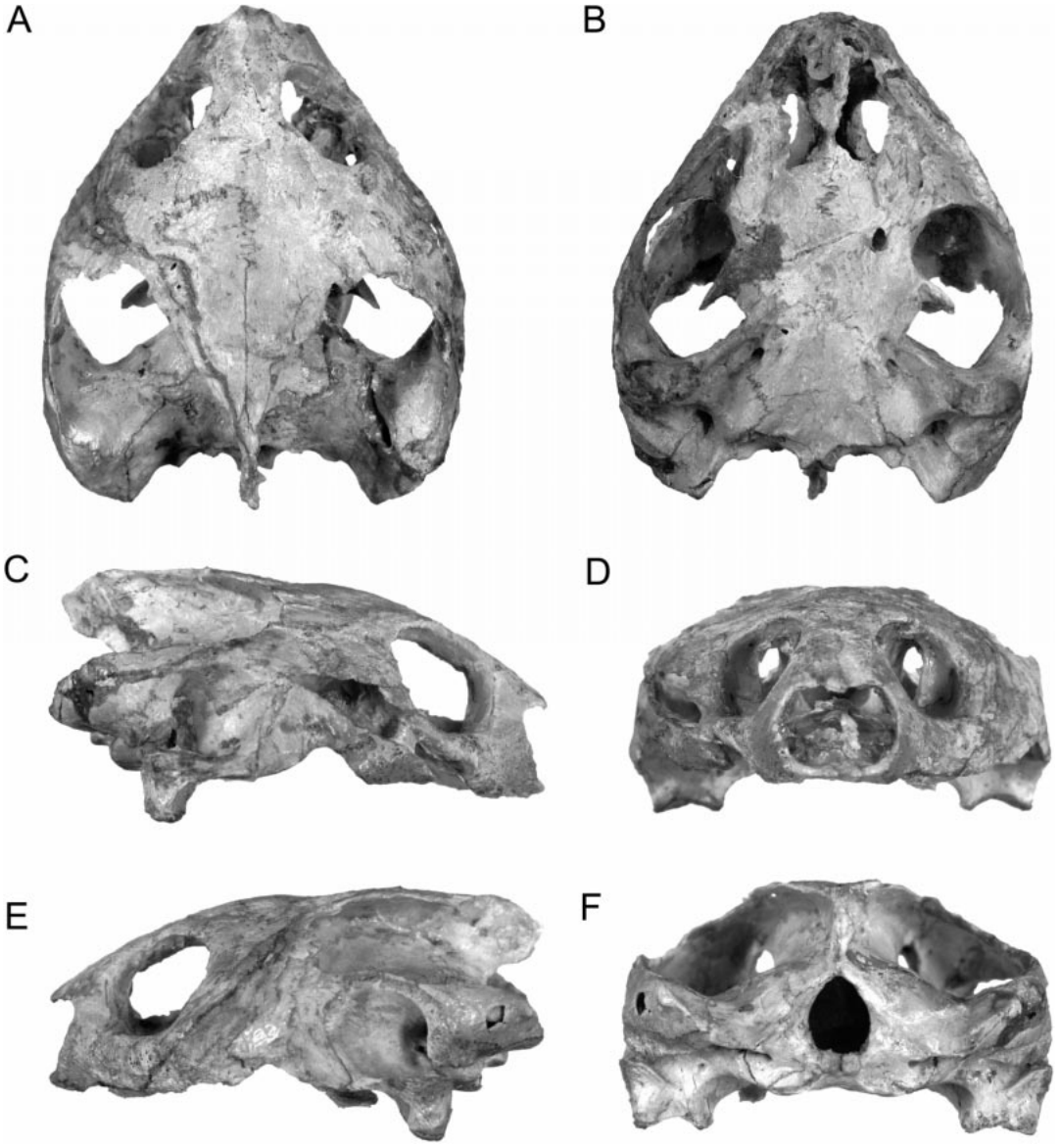

Fig. 4. *Cearachelys placidoi*, n. gen. & sp., TUTg 1798, Santana Formation, Santana do Cariri, Brazil. A, dorsal; B, ventral; C, right lateral; D, anterior; E, left lateral; F, posterior. See fig. 5 for key.

there is a more vertical flange extending ventrally. *Cearachelys* lacks these posterior processes and ends in a curved edge with only a slight horizontal component continuous with the posterior extension of the opisthotic. It is similar to the condition in Pelomedusidae.

POSTORBITAL

Both postorbitals are preserved in TUTg 1798, but there is some damage and sutures are not entirely clear. However, by using information from both sides, the postorbital in this specimen can be fully restored. The

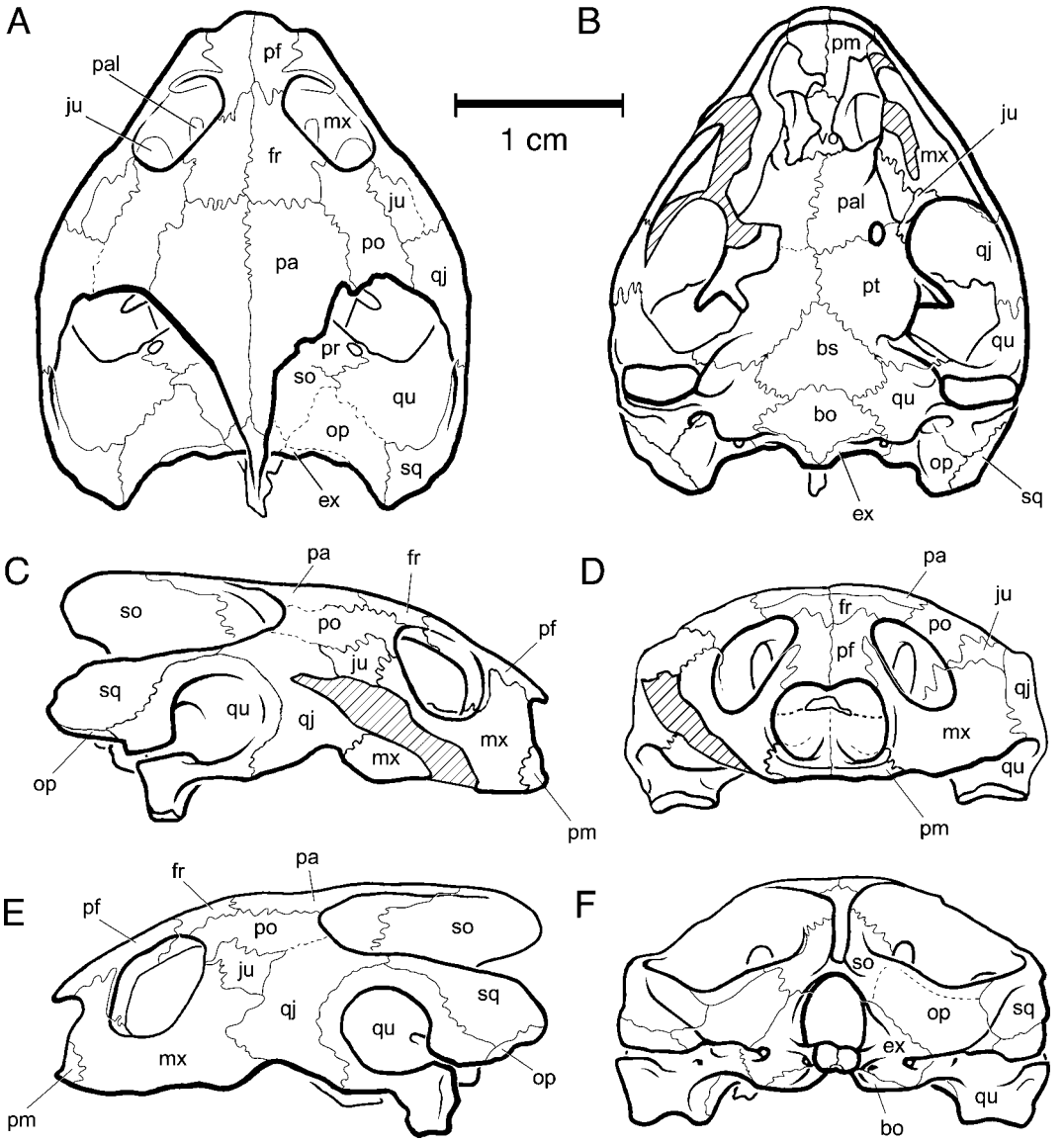

Fig. 5. Key to fig. 4.

MPSC specimen has only the left postorbital and that is missing part of its anterior edge.

The postorbital in *Cearachelys* is a long element extending from the orbit to the temporal skull roof margin, much as in *Foxemys.* The postorbital of *Cearachelys* is larger than in *Araripemys,* Pelomedusidae, and Podocnemididae. A very narrow ventral process of the postorbital in *Cearachelys* contacts the maxilla in the orbital margin, barely preventing jugal exposure in the orbital margin. Anteroventrally the postorbital contacts the jugal, and posteroventrally it contacts the quadratojugal. Anteromedially the postorbital contacts the frontal, and posteromedially the parietal.

PREMAXILLA

Both premaxillae are present, but damaged, in TUTg 1798. They are absent in the MPSC specimen.

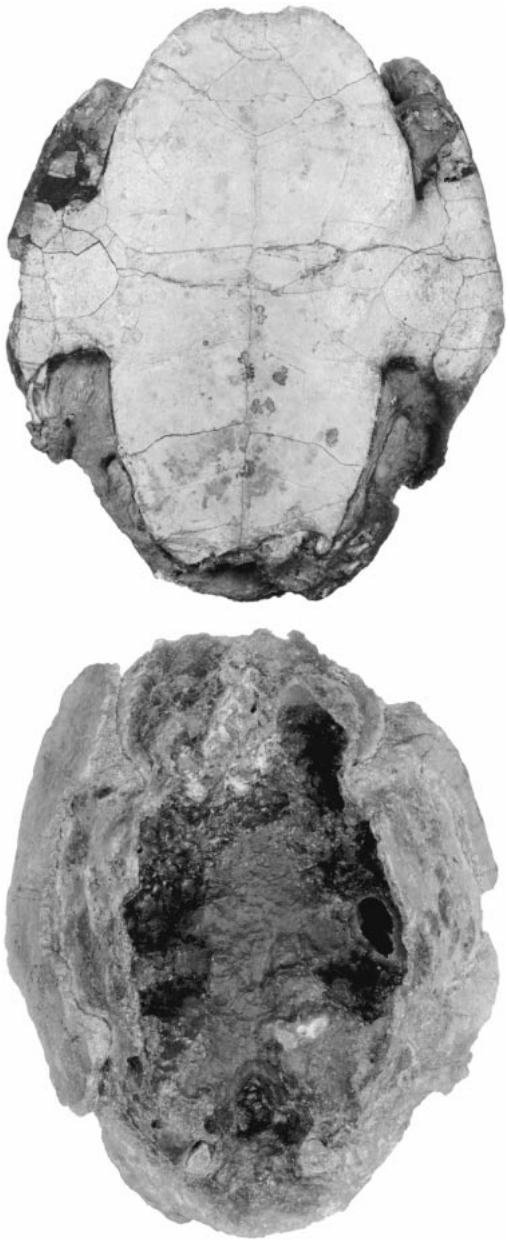

Fig. 6. *Cearachelys placidoi,* n. gen. & sp., MPSC specimen, holotype, shell in ventral (upper) and dorsal (lower) views. (See fig. 7).

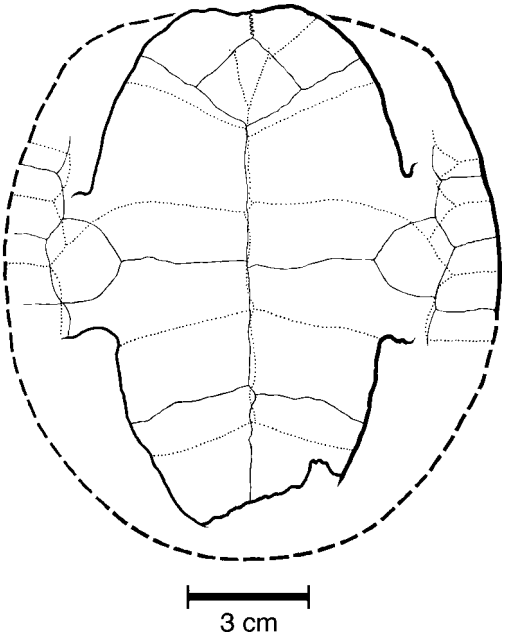

Fig. 7. *Cearachelys placidoi,* n. gen. & sp., MPSC specimen, holotype, shell in ventral view.

The premaxilla of *Cearachelys* bears a distinct labial ridge anteriorly with a flat plate posteriorly. The labial ridge, however, is relatively thin in *Cearachelys* in anterior view, in contrast to the deeper ridge of *Foxemys.* Posterior to the labial ridge on the palatal surface, the premaxilla rises in a shallow, smooth arch to the vomer contact. In *Foxemys, Bothremys, Zolhafah,* and *Polysternon* there is a step on the triturating surface between the labial ridge and vomer. The premaxilla of *Cearachelys* is triangular, being broadest anteriorly and narrowing posteriorly. The lateral limits, however, are represented by broken edges and the precise position of sutures is not clear.

The dorsal surface of the premaxilla forms the anterior floor of the fossa nasalis and the margin of the apertura narium externa. As on the ventral surface, the dorsal surface slopes posterodorsally to meet the vomer. The apertura ventral margin is nearly straight in *Cearachelys,* with only a slight dorsal curve on the midline, similar to *Foxemys* but in contrast to the apertura margin in *Bothremys,* which has a sharp dorsal curve at the midline. Nuances of shape of the apertura narium externa, however, are variable even among species of living *Pelusios.*

MAXILLA

The posterior portion of the left maxilla is preserved in the MPSC specimen. Most of

both maxillae are present in TUTg 1798, but both are damaged to the extent that the anteromedial edges and contacts are not known.

Ventrally the maxilla of *Cearachelys* forms most of the upper triturating surfaces. The labial ridge is relatively narrow, comparable to *Pelomedusa,* in contrast to the thick labial ridge in *Bothremys* and *Rosasia.* The labial ridge in *Cearachelys,* however, is low, not deep as in *Taphrosphys.* The triturating surface of *Cearachelys,* to the extent preserved, is smooth, with complete absence of the pits seen in *Bothremys, Rosasia,* and *Zolhafah.* The triturating surface, however, agrees with these taxa and *Polysternon* and *Foxemys* in being widened posteriorly to form a triangular area. On the left side of TUTg 1798 the triangular triturating area is clearly visible. On the right side much of the surface is damaged and the medial limits eroded.

The maxilla in *Cearachelys* contacts the premaxilla anteriorly and the palatine posteromedially. Between the two contacts the maxilla limits are represented by broken edges, and the margin of the apertura narium interna is not definite. However, by using the bone edges as preserved on both sides, limits of the apertura are determinable. The apertura narium interna of *Cearachelys* is placed relatively close to the midline. Posteriorly the maxilla in *Cearachelys* contacts the jugal. The more medial part of this contact is on the palatal surface, and more laterally it curves dorsally onto the posterior surface of the postorbital wall.

In lateral view the vertical plate of the maxilla in *Cearachelys* forms the posterior margin of the apertura narium externa, the ventral margin of the orbit, and the anterior portion of the cheek wall. The lateral margin of the apertura narium externa slopes posterodorsally as in nearly all other bothremydids. The orbit is larger than in *Bothremys* and smaller than in *Pelomedusa.* The posterior cheek contacts of the maxilla are with the quadratojugal more ventrally and with the jugal dorsally. A very thin ventral process of the postorbital contacts the maxilla along the orbital margin. The exposure of the maxilla in the orbital floor is bordered by the jugal posteriorly and the palatine posteromedially. The palatine sends a narrow process anterolaterally into the maxilla, giving the sutural contact an interdigitating shape.

VOMER

The vomer is preserved only in TUTg 1798. Its lateral margins are represented by broken edges.

The vomer of *Cearachelys* is roughly dumbbell shaped, the presumed primitive condition for pleurodires and pelomedusoids. The anterior end is swollen and contacts the paired premaxilla, a contact preserved only on the left side. The posterior end, also swollen, contacts the palatine bones. The anterior end of the vomer lies ventral to the posterior end, and between them is a narrow bar separating the paired apertura narium interna. The vomer of *Cearachelys* is quite similar in shape and proportions to that in FR 4922 and lacks the larger anterior end of *Bothremys* or the stout central bar of *Nigeremys.*

PALATINE

Palatines are preserved on both sides of both specimens. In the MPSC specimen the left palatine is nearly complete, while the right one lacks part of its anterior edge. Preservation and sutures are clear. In TUTg 1798 the right palatine is nearly complete, but the left one lacks its posterolateral portion and is poorly preserved, missing some of its ventral surface.

On the ventral surface, the palatine in *Cearachelys* contacts the maxilla anterolaterally, the jugal laterally, the pterygoid posteriorly, the other palatine medially, and the vomer anteromedially. In such forms as *Bothremys* the palatine makes up a significant portion of the large triturating surface, but in *Cearachelys* this contribution is no more than in Pelomedusidae and FR 4922. In forms such as *Bothremys* the palatine is deeply curved to form a choanal trough leading to the apertura narium interna. In *Cearachelys* the palatine surface leading into the apertura is much flatter and not strongly curved.

The dorsal surface of the palatine is well preserved and easily seen in the MPSC specimen. There is a low dorsal ridge that contacts the processus inferior parietalis and forms the lower margin of the foramen in-

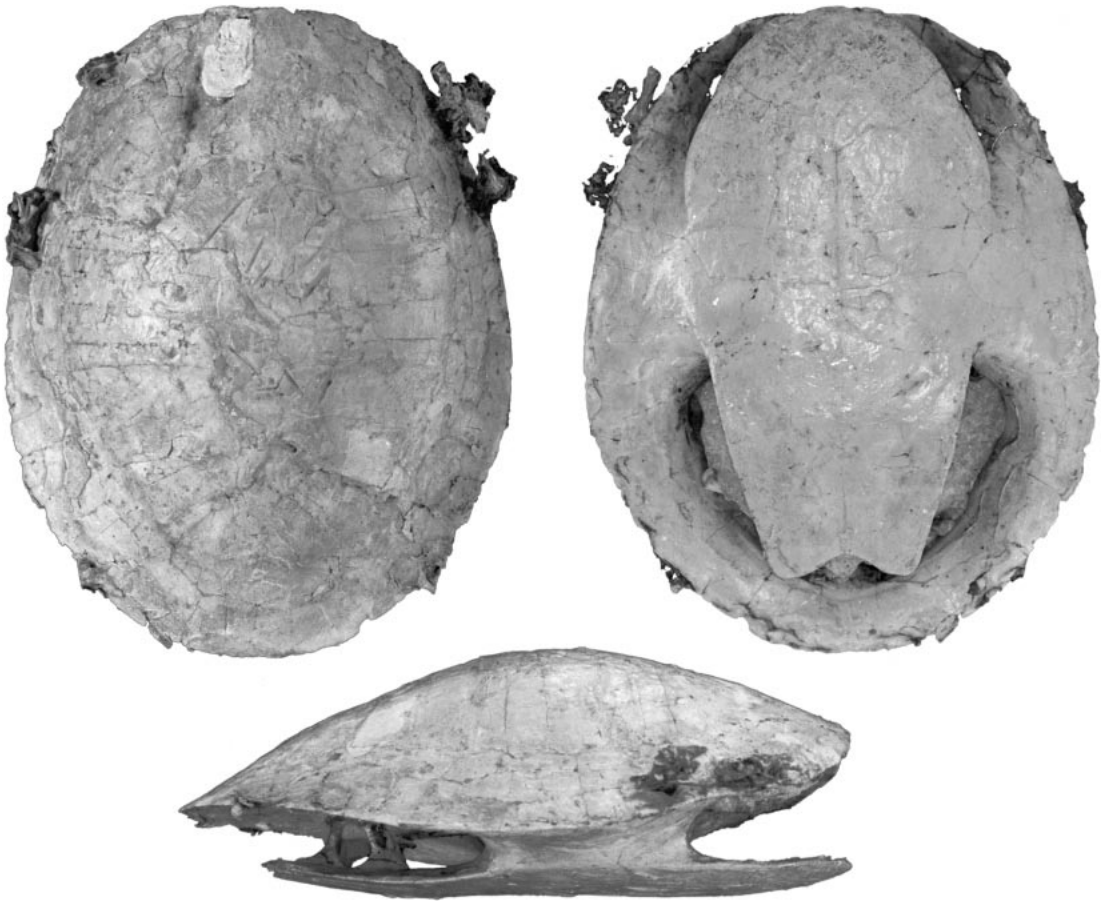

Fig. 8. *Cearachelys placidoi,* n. gen. & sp., TUTg 1798, dorsal (left), ventral (right), and lateral (bottom) views of carapace. See fig. 9.

terorbitale. This is in contrast to the condition in *Emydura* (and some *Pelusios,* i.e., USNM 42144), in which the palatine does not contact the parietal. However, in other *Pelusios* (YPM 5429) there is a very similar condition. In the posterior suture with the pterygoid both bones form the foramen palatinum posterius. The palatine has an anterolateral extension meeting the jugal and the foramen lies in the suture along this extension.

QUADRATE

Both quadrates are well preserved in both specimens. The right quadrate of the MPSC specimen lacks its anterior edge along the cavum tympani.

The quadrate of *Cearachelys* has a long, C-shaped anterior contact with the quadratojugal. Posteriorly the cone-shaped squamosal fits onto the posterodorsal corner of the quadrate. The narrow quadratojugal-squamosal contact prevents exposure of the quadrate along the temporal emargination. Most of the quadrate is involved in the formation of the cavum tympani. *Cearachelys* lacks any precollumellar fossa, as is the case in nearly all bothremydids, but in contrast to most other pelomedusoids and chelids. The antrum postoticum of *Cearachelys* is not extremely small as in *Bothremys* and *Taphrosphys,* but it is significantly smaller than in pelomedusids and FR 4922.

The cavum tympani of most bothremydids is a hemispherical depression, with a canal in the center for the stapes, a small or absent

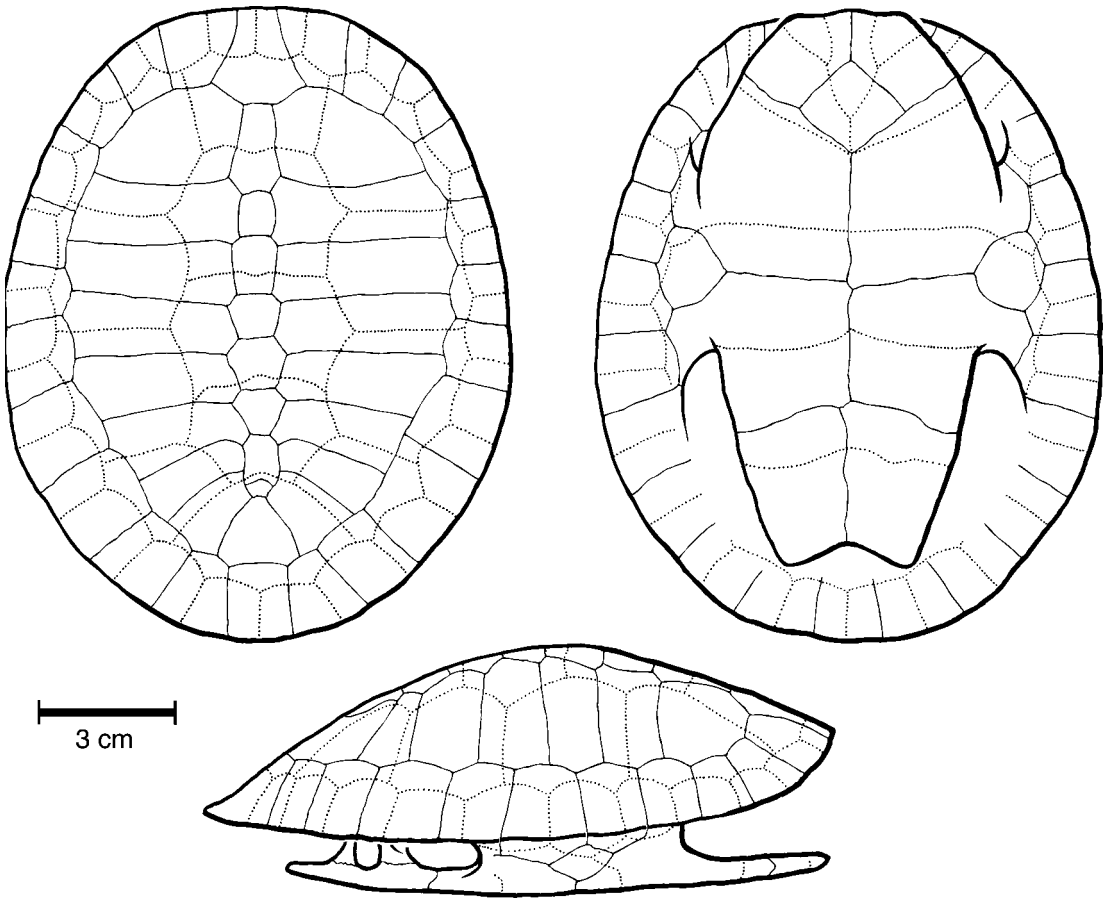

Fig. 9. *Cearachelys placidoi,* n. gen. & sp., TUTg 1798, dorsal (left), ventral (right), and lateral (bottom) views.

antrum postoticum, and a shallow groove for the eustachian tube that is separated from the stapes by a wall of bone. This is the condition in *Bothremys, Taphrosphys, Nigeremys, Arenila, Rosasia,* and *Zolhafah.* However, *Cearachelys,* like *Foxemys,* has an open incisura columellae auris, so that there is no bony separation posteriorly between the eustachian tube and the stapes. In the MPSC specimen there is a small bar of bone on the left side that closes the incisura at its most distal portion. On the right side the incisura is completely open but a broken surface suggests that it was also probably closed originally. TUTg 1798, however, is open on both sides and looks as if that was the original condition. The MPSC specimen is larger, and this difference may be due to TUTg 1798 being younger and generally less ossified.

Cearachelys and *Foxemys* differ slightly in the shape of the incisura columellae auris. In *Cearachelys* the incisura is oval in shape, much as in pelomedusids, so that, clearly, the eustachian tube was contained in it, and this is demonstrated by examination of the living species. In *Foxemys* the right incisura is complete in both available skulls, and it seems to show that the incisura widens laterally and is quite narrow for most of its length in contrast to *Cearachelys.* It is possible that the eustachian tube is excluded from the incisura in *Foxemys.* In *Cearachelys* the oval-shaped incisura is continuous posteriorly with a groove and lateral ridge on the

TABLE 1
Comparison of Santana Pleurodire Shells

	Cearachelys	*Araripemys*	FR 4922
Nuchal embayment	absent	present	absent
First costals reach shell margin between nuchal and peripherals	no	yes	no
Carapacial and plastral fontanelles	no	yes	no
Shell height	moderately domed	strongly flattened	moderately domed
Neural number	8	9	8
Neural 2 contacts costal 1	no	no	yes
Anterior peripherals unusually narrow	no	yes	no
Vertebra 1 on shell margin	no	yes	no
Anterior marginals unusually narrow	no	yes	no
Neural 8 contacts costal 7	slightly–none	widely	widely
Plastral fontanelles	absent	present	absent
Epiplastra very narrow	no	yes	no
Anterior plastral lobe	broad, semicircular	narrow, tapering to a point	narrow, semicircular
Entoplastron	trapezoidal	V-shaped	trapezoidal
Mesoplastra	present	absent	present
Scales anterior to humerals	3	2	3
Pectoral scales on entoplastron	no	no	yes
Abdominal scales meet on midline	yes	no	yes

posterior face of the ventral part of the quadrate. This ridge seems to form an outer limit for the continuing path of a eustachian tube. A similar groove and ridge occurs in some pelomedusids, and is associated with the eustachian tube. *Foxemys* also has this ridge, and it substantiates the presumption that the eustachian tube is included in the incisura of *Foxemys.*

The medial contacts of the quadrate in *Cearachelys* on the dorsal surface of the otic chamber are with the prootic anteromedially, the supraoccipital medially, and the opisthotic posteromedially. The prootic and opisthotic contacts are found in all pleurodires, but the quadrate and supraoccipital contact occurs only within the *Bothremys* subgroup of bothremydids.

On the ventral surface the quadrate contacts the pterygoid anteromedially, the basisphenoid medially, and the exoccipital posteromedially. Between the basisphenoid and exoccipital contacts there is a narrow contact with the basioccipital. The basioccipital contact occurs in all bothremydids and podocnemidids. The basisphenoid-quadrate contact occurs in pelomedusids, podocnemidids, and all bothremydids.

Medially the foramen stapedio-temporale is formed in the quadrate-prootic suture. As in nearly all other bothremydids, the foramen is on the anterior surface of the otic chamber in *Cearachelys.* The canalis stapedio-temporale is well preserved and open on the left side of TUTg 1798. Although barely visible in dorsal view, the foramen in *Cearachelys* is not very close to the foramen nervi trigemini as in *Bothremys.*

PTERYGOID

In the MPSC specimen, both pterygoids are complete and well preserved, except for the distal margins of the pterygoid flange. In TUTg 1798, the left pterygoid is nearly com-

plete, but the right one lacks a significant portion anteriorly and is damaged by erosion on its ventral surface. The dorsal structures of the pterygoid are visible and well preserved in the MPSC specimen.

On the ventral surface, the pterygoid of *Cearachelys* has a roughly transverse suture with the palatine that trends anterolaterally to meet the jugal. The foramen palatinum posterius is formed in the palatine-pterygoid suture as in most pleurodires. Medially the pterygoids meet on the midline for about half their length. The basisphenoid separates them posteriorly. As in all pleurodires, there is a laterally projecting processus trochlearis pterygoidei. In *Cearachelys* the processus lies at a less acute angle to the midline in contrast to the more acute angle seen in pelomedusids, chelids, FR 4922, and *Araripemys*. The flange of the pterygoid that extends ventrally from the base of the processus trochlearis pterygoidei along the quadrate process in all pleurodires is often broken in fossils, because it is so thin and fragile. It is partially preserved in both *Cearachelys* specimens and seems to be developed to about the extent seen in pelomedusids.

The posterolaterally extended quadrate process of the pterygoid in *Cearachelys* is distinctly narrower and longer than in FR 4922, *Araripemys,* pelomedusids, or chelids. In the latter groups the processus is relatively flat and more horizontal, while in *Cearachelys* it is narrower and more vertical. This is related to the presence in *Cearachelys* of a ventrally concave depression in the posterolateral part of the pterygoid. This depression has a sharp anterolateral margin that extends posterolaterally along the processus articularis of the quadrate, and has a barely perceptible margin medially on the basisphenoid. The depression is not as deep as in *Foxemys* nor much deeper as in *Nigeremys,* but it is obviously present in contrast to *Bothremys* and *Taphrosphys,* which lack it. This pterygoid depression differs from the podocnemidid pterygoid chamber, seen in its primitive condition in *Hamadachelys,* by not having any development of an overhang by the basisphenoid or pterygoid.

The foramen posterius canalis carotici interni in *Cearachelys* lies in the basisphenoid-pterygoid suture, just anterior to the quadrate contact. Its position is similar to that in *Rosasia* and *Foxemys.* It differs from the pterygoid-quadrate formation of the foramen seen in *Bothremys* and the pterygoid-quadrate-basisphenoid formation seen in *Taphrosphys, Zolhafah,* and *Arenila.* The lateral margin and most of the ventral margin of the foramen posterius canalis carotici interni in *Cearachelys* are formed by pterygoid. The medial edge is formed by the basisphenoid. The dorsal roof of the foramen has both the basisphenoid and pterygoid making it up. As in most of the other bothremydids the foramen leads into the canalis carotici interni, lying in a nearly horizontal plane, so that the ventral margin of the foramen and canalis are quite thin. This is in contrast to the condition in pelomedusids, where the canalis is much more vertical.

There is some variability in the structures around the foramen posterius canalis carotici interni in *Cearachelys.* The MPSC specimen shows very little damage of the thin bones in this region, but TUTg 1798 is eroded to a varying extent on both sides. In the MPSC specimen the posterior flange of the pterygoid just posterolateral to the foramen posterius canalis carotici interni has a foramen opening out of a canal that parallels the canalis carotici interni and is just lateral to it. This foramen and canal is probably for the facial branch of VII and probably leads into the prootic, where this nerve goes dorsally. On the left side of the MPSC specimen a small hole in the floor of the canal allows determination of its size and location, but the opening into the prootic is not visible on either side of this specimen. In TUTg 1798, however, the prootic and the foramen nervi facialis are visible. Due to either erosion or less ossification in life (perhaps related to the smaller size of TUTg 1798), the pterygoid in TUTg 1798 lacks the canal for the facial nerve seen in the MPSC specimen. On the right side of TUTg 1798, the prootic is exposed in a narrow band leading out of the canalis carotici interni and forming part of the roof of the foramen posterius canalis carotici interni, between the pterygoid and basisphenoid. In the anterior part of the prootic exposure is a dorsally extending foramen and canal, the foramen nervi facialis. On the left side of TUTg 1798 more of the pterygoid is present, covering the foramen nervi facialis

ventrally. The foramen can still be seen by looking along the length of the canalis carotici interni.

The dorsal surface of the pterygoid is visible in the MPSC specimen. The crista pterygoidea is quite low, there is a low dorsal area on the outside of the crista anteriorly, and it rises again to form the ventral margin of the foramen nervi trigemini. The anterodorsal margin of this foramen is formed by the parietal, and the posterodorsal margin by the prootic.

Supraoccipital

The supraoccipital is complete in both skulls. In the MPSC specimen a small part of the ventral edge of the crista supraoccipitalis is missing, and in TUTg 1798 part of the crista on the right side is gone near its base.

The supraoccipital of turtles is Y-shaped in posterior view, with paired lateral projections that contain the medial part of the cavum labyrinthicum, the recessus labyrinthicus supraoccipitalis. In cryptodires and most pleurodires the supraoccipital has a tripartite suture, with the prootic and opisthotic visible on the dorsal surface of the otic chamber. In *Cearachelys* the supraoccipital has a lateral projection that separates the prootic and opisthotic and contacts the quadrate. This contact is well preserved on both sides of the MPSC specimen and on the left side of TUTg 1798. On the right side of TUTg 1798 the area is damaged and not determinable.

The supraoccipital-quadrate contact also occurs in *Bothremys, Rosasia,* and *Foxemys,* but not in *Taphrosphys*. In *Cearachelys* the degree of contact is less than in the other bothremydids.

The crista supraoccipitalis is shorter in bothremydids than it is in most podocnemidids. In *Cearachelys* the crista extends posteriorly about as far as the posterior end of the squamosals. It is similar in length to most *Pelomedusa* and shorter than in most *Pelusios.* The crista in *Cearachelys* is slightly longer than in FR 4922.

Exoccipital

The exoccipitals are complete and well preserved in both the MPSC specimen and TUTg 1798.

The exoccipital in *Cearachelys* contacts the supraoccipital dorsally (the exoccipitals do not meet in the midline above the foramen magnum as in some chelids), and the opisthotic laterally and anteriorly. Dorsomedially the exoccipital forms the lateral and ventral margin of the foramen magnum, a structure that varies little in pelomedusoids. Ventromedially the two exoccipitals form the condylus occipitalis, with no contribution from the basioccipital, a condition found in *Bothremys, Zolhafah, Taphrosphys,* and *Arenila.* Nonetheless, the basioccipital in *Cearachelys* does completely separate the exoccipitals in ventral view in both skulls. In *Taphrosphys* the exoccipitals are in contact ventrally as well and make up the neck of the condylus occipitalis.

Laterally the exoccipital in *Cearachelys* forms the medial portion of the foramen jugulare posterius, contacting the opisthotic dorsally and the quadrate ventrally. In *Cearachelys* the foramen jugulare posterius is open laterally as in *Foxemys,* not closed as in *Bothremys, Taphrosphys,* pelomedusids, and chelids. In *Cearachelys,* however, the foramen jugulare posterius is partially closed or restricted laterally in comparison to the more open condition in *Araripemys* and FR 4922. In *Cearachelys* there are two foramina nervi hypoglossi, as in all the other pelomedusoids. As in *Taphrosphys* and *Bothremys, Cearachelys* has an extensive quadrate-exoccipital contact below the fenestra postotica. This contact is absent in chelids, podocnemidids, pelomedusids, and FR 4922.

Basioccipital

The basioccipital is preserved intact in both TUTg 1798 and the MPSC skull.

The basioccipital of *Cearachelys,* as in other bothremydids, is relatively shorter than in chelids and pelomedusids, but the width is about the same. The basioccipital has a wide contact with the basisphenoid anteriorly and a narrow contact with the quadrate at its lateral limit. Posterolaterally and posteriorly the basioccipital contacts the exoccipital.

Prootic

The prootic in the MPSC specimen is present and well preserved on both sides, but in

TUTg 1798 only the left prootic is well preserved, although both are present.

The prootic is exposed on the dorsal and anterior surface of the otic chamber, contacting the parietal medially, the quadrate laterally, the supraoccipital posteriorly, and the pterygoid ventrally. The foramen stapedio-temporale is formed in the prootic-quadrate suture and the foramen nervi trigemini is formed between the parietal, pterygoid, and prootic.

The foramen stapedio-temporale in *Cearachelys* is situated on the anterior face of the otic chamber as in other bothremydids, and in contrast to the primitive position in chelids and pelomedusids, where it is more posterior and faces dorsally. In *Cearachelys* and other bothremydids the foramen stapedio-temporale faces anteriorly and is barely visible in dorsal view. In chelids and pelomedusids the foramen lies on the dorsal surface of the otic chamber and opens more dorsally. Although *Cearachelys* has the anterior-facing foramen stapedio-temporalis, the foramen is not in close proximity to the foramen nervi trigemini as in *Taphrosphys, Bothremys, Rosasia,* and *Foxemys.* As described under Supraoccipital, the prootic does not contact the opisthotic in *Cearachelys,* due to a supraoccipital-quadrate contact. This contact is found in *Bothremys, Rosasia,* and *Foxemys.*

The prootic in *Cearachelys* forms the posterodorsal margin of the foramen nervi trigemini, similar to the condition in pelomedusids, and FR 4922. On the ventral surface a narrow band of the prootic is exposed in the roof of the foramen posterius canalis carotici interni in TUTg 1798. The prootic is exposed on the left side in the basisphenoid-pterygoid-quadrate suture of the MPSC specimen.

Opisthotic

Both opisthotics are present and complete in both the TUTg 1798 and MPSC specimens.

In dorsal view the opisthotic contacts the supraoccipital anteromedially, the quadrate anterolaterally, the squamosal laterally, and the exoccipital posteromedially. The opisthotic in *Cearachelys* ends posteriorly at about the same level as the squamosal; it does not extend posterolaterally beyond the squamosal as in pelomedusids, *Araripemys,* and FR 4922.

Ventrally the opisthotic forms the roof and some subdivisions of the fenestra postotica. In *Cearachelys* the foramen jugulare posterius is open laterally and is continuous with the fenestra postotica. Laterally the fenestra postotica is bordered by the quadrate, which also forms most of the floor. The exoccipital contacts the quadrate and forms the more medial part of the floor. In *Bothremys* and *Taphrosphys* the fenestra postotica is completely separated from the foramen jugulare posterius by a bar of bone formed by the opisthotic and quadrate. This bar is absent in *Cearachelys.* However, the fenestra postotica in *Cearachelys* is nonetheless smaller and more restricted than in chelids, pelomedusids, and *Araripemys.* The medial part of the fenestra postotica in *Cearachelys* is a narrow horizontal slit where the opisthotic and quadrate nearly meet. In neither the TUTg 1798 nor the MPSC skull is there any contact here. The more lateral part of the fenestra postotica is figure-8-shaped, because it is partially divided by low ridges into a more lateral portion for the lateral head vein and a more medial portion for the stapedial artery.

The processus interfenestralis of the opisthotic is completely covered in *Cearachelys* as in all other bothremydids and podocnemidids. The fenestra postotica is so small that the fenestra ovalis is only barely visible in TUTg 1798.

Basisphenoid

The basisphenoid is present and complete in both skulls, but in TUTg 1798 it is slightly eroded. Most of the dorsal surface is visible in TUTg 1798.

In ventral view the contacts of the basisphenoid in *Cearachelys* are with the pterygoid anterolaterally, the quadrate posterolaterally, and the basioccipital posteriorly. The basisphenoid is roughly triangular in shape, its apex separating the pterygoids for about half their length. The basisphenoid forms the medial margin of the foramen posterius canalis carotici interni, but the foramen is close to the pterygoid-quadrate suture. The ventral surface of the basisphenoid in *Cearachelys* is

broadly convex and does not participate in the pterygoideus muscle concavity.

The dorsal surface of the basisphenoid in *Cearachelys* shows the oval sella turcica, low dorsum sellae, and fused rostrum basisphenoidale as seen in *Pelusios, Podocnemis,* and *Bothremys.* The long, narrow rostrum and only barely overhanging dorsum are more similar to *Bothremys.* The paired foramen anterius canalis carotici interni lie close together as in *Podocnemis* and *Bothremys.* There is no foramen caroticum laterale. The foramen nervi abducentis is posterior to the base of the processus clinoideus as in *Pelusios* and *Podocnemis.*

Carapace

The carapace of *Cearachelys* is nearly complete in TUTg 1798, but only fragments of the left and right bridge peripherals are present in the MPSC specimen.

The carapace of *Cearachelys* is moderately domed, much as in recent *Pelomedusa.* The carapace is composed of a nuchal, 8 neurals, 8 pairs of costals, 11 pairs of peripherals, a single suprapygal, and a single pygal. There are no fontanelles as in *Araripemys,* and all the bones are tightly sutured as in FR 4922 and most pleurodires. The principal distinguishing features of the carapace in *Cearachelys* lie in the neural bones. The first neural in most pelomedusoids is four sided and contacts only the nuchal, first costals, and second neural. In *Cearachelys* the first neural is six sided and has short, paired contacts with the second costals. The second neural is four sided, rather than six as in most pelomedusoids, and as a consequence does not contact the first costals. In *Araripemys* the second neural also does not contact the first costals. Neurals 3 to 6 in *Cearachelys* are the usual six-sided, coffin-shaped bones, with short sides facing anteriorly. Neurals 7 and 8 are smaller and more irregular. Neural 7 is six sided, but the two lateral sides converge as in the other neurals. Neurals 7 and 8 occupy the area between costals 7 and 8. A complete neural series is not typical of Pelomedusoides. In most species the posterior costals intervene between the seventh or eighth neural and the suprapygal. The triangular suprapygal contacts the last neural.

The eight costals of *Cearachelys* are similar to those in *Bothremys* and *Taphrosphys* as well as those in FR 4922. The 11 peripherals are also similar to the other bothremydids, being wider posteriorly. The carapacial scales of *Cearachelys* are quite similar to the generalized condition for pelomedusoids seen in *Bothremys, Taphrosphys,* and *Podocnemis.* A cervical scale is absent as in all Pelomedusoides. Because of a complete neural series, the sulcus between vertebrals 4 and 5 falls on the seventh neural in TUTg 1798. As expected, the scales in *Cearachelys* differ from the unique condition in *Araripemys,* in which the first vertebral enters the nuchal emargination and the first two marginals are widely separated.

Plastron

The plastron in *Cearachelys* is known in both specimens. TUTg 1798 is nearly complete, with all sutures and sulci preserved. The MPSC specimen is missing some of the anterior edges of the plastron and the posterior margins of the xiphiplastra are broken off.

The plastron of *Cearachelys* has a broad, semicircular anterior lobe and a tapering posterior lobe with a shallow xiphiplastral notch. The anterior lobe in *Cearachelys* is much broader than in FR 4922 and *Araripemys.* It agrees with FR 4922 and most pleurodires in being rounded and differs strongly from *Araripemys,* which is pointed. The epiplastra in *Cearachelys* meet on the midline for a length that is much more than in *Araripemys,* but less than in FR 4922. The entoplastron in *Cearachelys* is trapezoidal, not V-shaped as in *Araripemys,* and it does not have a curved posterior margin as in FR 4922.

Paired, laterally placed mesoplastra are present in *Cearachelys* in contrast to *Araripemys,* which lacks them, and in common with FR 4922. The mesoplastra of *Cearachelys* are similar in size and shape to *Podocnemis, Taphrosphys* and *Bothremys.* The axillary and inguinal buttress attachments are not visible in any of the specimens at their current stage of preparation. The xiphiplastron has a moderate posterior projection and

a shallow xiphiplastral notch, much as in *Bothremys,* but in contrast to the pointed projections and C-shaped notch in *Taphrosphys.*

The plastral scales in *Cearachelys* are much as in other pelomedusoids. The intergular is elongate and roughly V-shaped. It extends onto the entoplastron, partially separating the humerals as in *Bothremys* and *Podocnemis.* The intergular extends onto the entoplastron slightly more than in FR 4922, but not as much as in *Taphrosphys,* in which the intergular is large and completely separates the humerals. The pectoral-abdominal sulcus crosses the anterior part of the mesoplastron as in *Bothremys* and pelomedusids, but unlike Podocnemididae. The other plastral scales are very similar to *Bothremys.*

RELATIONSHIPS

Cearachelys is a pleurodire because it has these synapomorphies of the group listed by Gaffney and Meylan (1988) as diagnostic for the Pleurodira: (1) processus trochlearis pterygoidei present, (2) quadrate process below cranio-quadrate space, (3) epipterygoid absent, (4) foramen palatinum posterius behind orbit, and (5) pelvis suturally attached to carapace and plastron. The sixth character, hyomandibular nerve in its own canal, cannot be determined in the articulated skull. It is a member of the Pelomedusoides (sensu Broin, 1988; Lapparent de Broin and Werner, 1998; Meylan, 1996; Tong et al., 1998), which is equivalent to the Pelomedusidae in the classical sense (sensu Gaffney and Meylan, 1988) because it has these characters: (1) cervical scale absent, (2) nasal absent, (3) prefrontals meeting on midline, and (4) splenial absent (lower jaws present in TUTg 1798). *Cearachelys* can be identified as a member of the family Bothremydidae based on its possession of the following characters: (1) precolumellar fossa absent, (2) occipital condyle consisting only of exoccipitals (reversal in *Pelusios* and *Pelomedusa*), (3) foramen stapedio-temporale facing anteriorly, (4) fenestra postotica reduced in size relative to pelomedusids, chelids, and podocnemidids, and (5) exoccipital-quadrate contact. Within the Bothremydidae, *Cearachelys* can be allied with *Bothremys, Rosasia, Foxemys,* and *Zolhafah,* (the *Bothremys* Group of Lapparent de Broin and Werner, 1998) on the basis of these characters: (1) triangular triturating surfaces and (2) supraoccipital-quadrate contact.

The other *Bothremys* Group taxa differ from *Cearachelys* and are united by these characters: (1) broad preorbital portion of skull, (2) triturating surfaces very wide, (3) palatine extensively exposed in triturating surfaces, and (4) supraoccipital-quadrate contact extensive.

Some contradictory characters concerning *Cearachelys* are the exposure of the jugal in the palate in *Cearachelys, Rosasia,* and *Bothremys,* but not in *Foxemys, Polysternon,* and *Zolhafah*; the open foramen jugulare posterius in *Cearachelys, Foxemys,* and *Polysternon* (presumed to be primitive), but the closed condition in all the other bothremydids, in which the character is determinable.

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