Redescription of the Skull of Ummulisani rutgersensis Gaffney, Tong, and Meylan, 2006, a Bothremydid Side-Necked Turtle from the Eocene of Morocco

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Redescription of the Skull of *Ummulisani rutgersensis* Gaffney, Tong, and Meylan, 2006, a Bothremydid Side-Necked Turtle from the Eocene of Morocco

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ABSTRACT

Three skulls of *Ummulisani rutgersensis* are described here as an addendum to the descriptions and analyses presented in Gaffney et al. (2006a). The present paper is essentially a replacement for the *Ummulisani* cranial morphology text in that paper (Gaffney et al. 2006a: 447–457). The original description was based primarily on one skull, AMNH 30563, the type of *Ummulisani rutgersensis*. Because two previously undescribed skulls, AMNH 30569 and AMNH 30562, are more complete, they add significantly to our understanding of this taxon. However, it does not alter the results of the phylogenetic analysis by Gaffney et al. (2006a), in that *Ummulisani rutgersensis* remains the sister taxon to *Phosphatochelys tedfordi*.

INTRODUCTION

The Bothremydidae is an extinct group of side-necked turtles recently reviewed and expanded in content by Gaffney et al. (2006a). The purpose of the present paper is to modify and expand the description of one taxon named in that paper, *Ummulisani rutgersensis*, by adding two specimens to the description. The skull description follows the outline and formatting of Gaffney et al. (2006a: appendix 1) for ease of comparison with other bothremydids. Based on the phylogenetic analysis of Gaffney et al. (2006a), *Ummulisani rutgersensis* is a member of the tribe Taphrosphyini as characterized in Gaffney et al. (2006a). Figures, descriptions, and references to all of the bothremydid taxa referred to in this paper can be found in Gaffney et al. (2006a). The taxonomy also follows that reference. *Ummulisani rutgersensis* is included in the data set of Gaffney et al.

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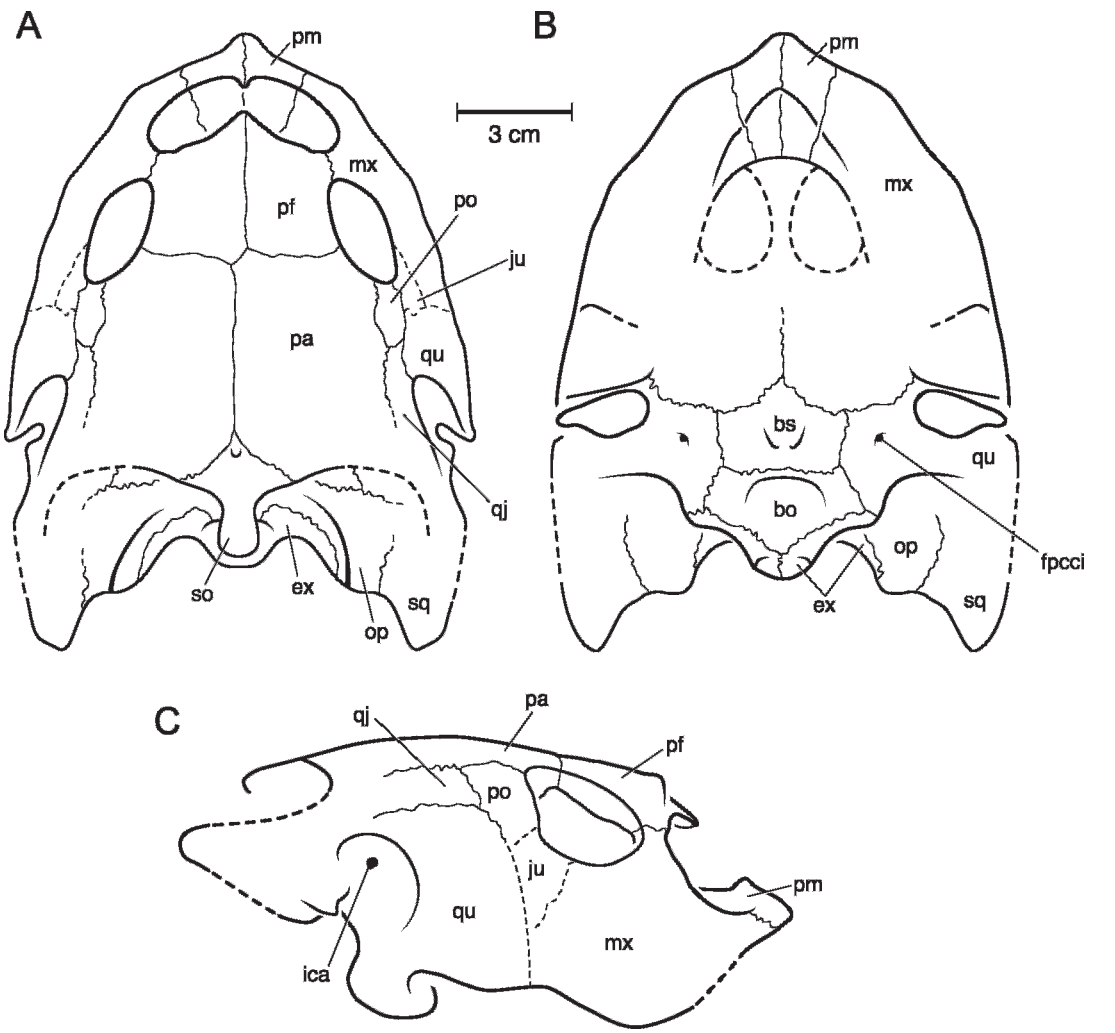

Fig. 1. *Ummulisani rutgersensis* Gaffney, Meylan, and Tong, 2006. AMNH 30563 holotype. Partially restored views of skull. **A**, dorsal; **B**, ventral; **C**, lateral. (from Gaffney et al., 2006a) (C. Blik del.)

(2006a: appendix 3) and is shown in cladograms in figures 288–314. The reader should consult this work for further discussion of this phylogenetic analysis, which concluded that *Ummulisani* is the sister taxon to *Phosphatochelys* within the subtribe Taphrosphyina.

Ummulisani was first named and described in 2006 by Gaffney (Gaffney et al., 2006a). Although three skulls of this taxon were known at that time, only one was sufficiently prepared to fully describe and figure. Unfortunately, that skull, the holotype and figured skull, AMNH 30563, is the least complete of the three, although complete enough to serve as the type. It is the purpose of this paper to redescribe *Ummulisani* on the basis of all three skulls, particularly incorporating information from the more complete skulls. This present paper is essentially a replacement for the *Ummulisani* cranial morphology text in Gaffney et al. (2006a: 447–457) and should be considered an addendum to that paper.

Other additions to Gaffney et al. (2006a) are Gaffney et al. (2006b), describing *Acleistochelys* and Gaffney et al. (in prep.), describing new *Bothremys* and *Chedighaii* material from North America.

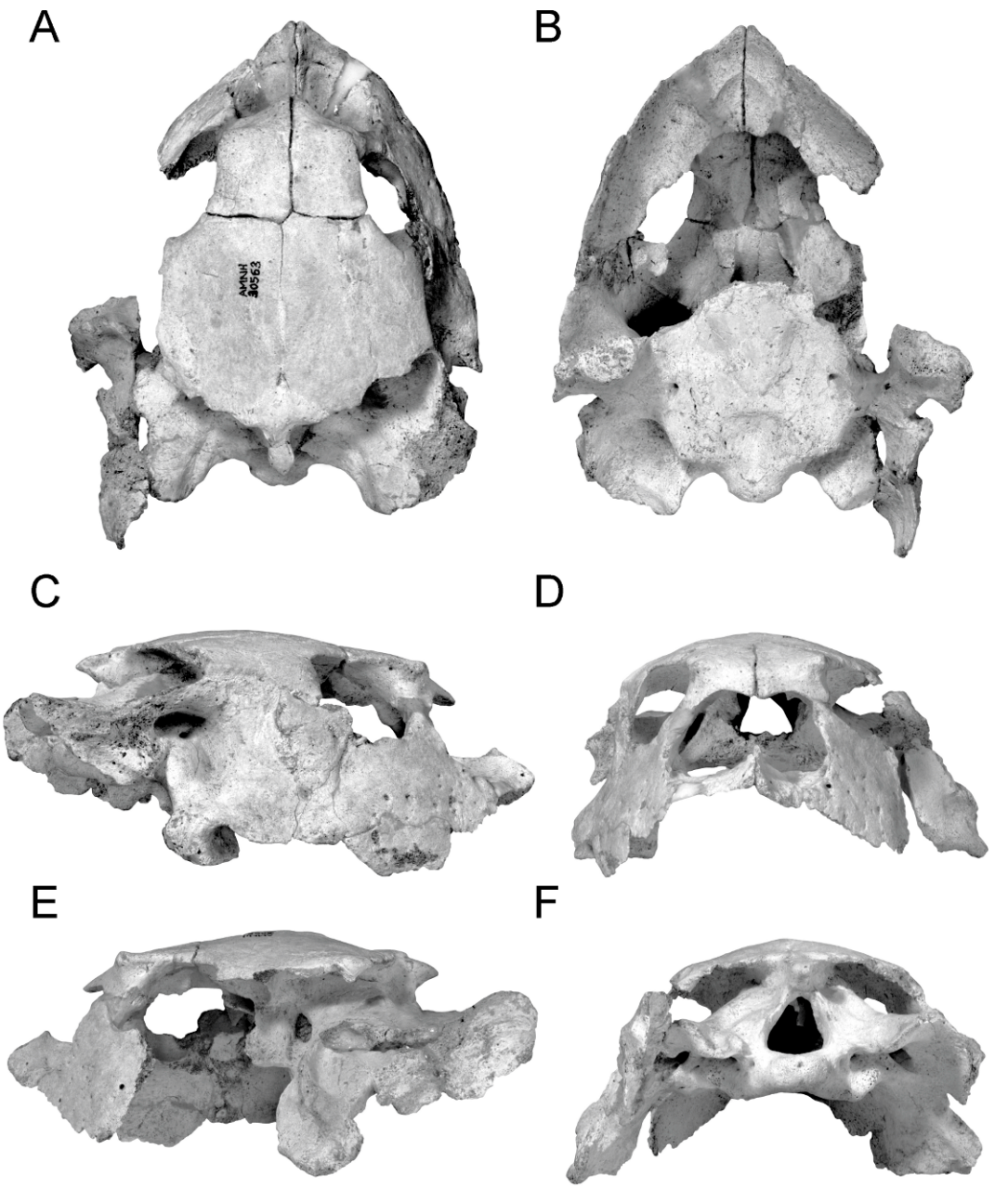

Fig. 2. *Ummulisani rutgersensis* Gaffney, Meylan, and Tong, 2006. AMNH 30563 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. (from Gaffney et al., 2006a) (C. Blik del.)

The type specimen of *Ummulisani rutgersensis*, AMNH 30563 (figs. 1–3), was one of the few purchased specimens from the Moroccan phosphates that has the original information about the locality and the stratigraphy, which is "Marah Iaresh, 20 km south east of Ouled Ouali" (Gaffney et al. 2006a), although no shark-teeth dating is available. Two additional

specimens, AMNH 30569 (figs. 4–6), a skull and plastron also from Marah Iaresh, and AMNH 30562 (figs.7, 8), an isolated skull without precise locality information, contained the original matrix, which is the white, soft, sandy phosphate. The shark teeth found in the matrix indicates a Ypresian (Early Eocene) age for both (Cappetta, personal commun.), which agrees with the type specimen.

Ummulisani Gaffney, Tong, and Meylan, 2006

TYPE AND ONLY INCLUDED SPECIES: *Ummulisani rutgersensis* Gaffney, Tong, and Meylan, 2006.

DISTRIBUTION: Eocene of Morocco.

ETYMOLOGY: *Ummu-'lIhsan*, Arabic, "mother of integrity" is the originally (Gaffney et al., 2006:103) intended etymology. According to our present editor (M. Knight, personal commun.), this was transliterated in error when the "h" was dropped from the genus name, so that it may be translated as "the mother of the tongue" or "the mother of language" (*Ummu 'l-lisan*).

REVISED DIAGNOSIS: A member of the tribe Taphrosphyini with the unique feature of a hornlike, anterodorsal process on each prefrontal. Other distinguishing features are a partially open septum orbitotemporale in contrast to other Taphrosphyini such as *Nigeremys* and *Arenila*; apertura narium externa smaller than in *Rhothonemys*, but similar in size to *Phosphatochelys*; preorbital part of skull short, in contrast to *Taphrosphys* and *Labrostochelys*; triturating surface unique in having very deep labial ridge beneath orbit with very low to absent labial ridge beneath apertura narium externa; labial ridge and maxilla very thin, as in *Labrostochelys* and in contrast to *Phosphatochelys* and *Rhothonemys*; wide quadrate-basisphenoid contact, as in *Taphrosphys* and in contrast to all other Taphrosphyini; foramen posterius canalis carotici interni formed entirely by quadrate (in two of three specimens), as in *Labrostochelys*, but in contrast to all other pleurodires.

DISCUSSION: This genus, now known from three skulls, one with a plastron, is one of the more unusual pleurodires. *Ummulisani* has hornlike processes on the prefrontals, and these probably were covered by a hornlike scale that would have been larger than the underlying bony process in life, as in the squamosal horns of meiolaniids. The phylogenetic analysis of Gaffney et al. (2006a) resolves *Ummulisani* as the sister taxon to *Phosphatochelys*.

Ummulisani rutgersensis Gaffney, Tong, and Meylan, 2006

TYPE SPECIMEN: AMNH 30563, skull, lacking palate (figs. 1–3; Gaffney et al., 2006a: figs. 206, 207), purchased from Adam Aaronson.

TYPE LOCALITY: "Mrah Iaresh, 20 km south east of Ouled Boali" (from Adam Aaronson), Ouled Abdoun Basin, Morocco (Gaffney et al., 2006a: figs. 14–16).

HORIZON: "Eocene Phosphates, Upper Ypresian, Couche O" (from Adam Aaronson); see Gaffney et al. (2006a: 73–76, fig. 17, for discussion and references to Moroccan phosphates).

DEPOSITIONAL ENVIRONMENT: Near-shore marine (see Gaffney et al., 2006a: 73–76).

DIAGNOSIS: As for genus.

ETYMOLOGY: For Rutgers, the State University of New Jersey, in gratitude to the faculty of the Department of Geology, Rutgers College, New Brunswick, who from 1961 to 1965 provided the senior author with inspiration, encouragement, and friendship, as well as with an education.

REFERRED MATERIAL: AMNH 30562, skull and plastron (figs. 7, 8; plastron figured in Gaffney et al., 2006a: figs. 268, 269), Couch 0, late Ypresian phosphates (based on shark teeth; Cappetta, personal commun.), Mrah Iahresh, 20 km southeast of Ouled Boali, Ouled Abdoun Basin, Morocco; AMNH 30569 (figs. 4–6), skull, Ypresian phosphates (based on shark teeth; Cappetta, personal commun.), Ouled Abdoun Basin, Morocco.

PREVIOUS WORK: This taxon was first described by Gaffney et al. (2006a), which is the only literature on the taxon to date.

DISCUSSION: See Conclusions below.

ABBREVIATIONS

Institutional Abbreviations

AMNH	American Museum of Natural History

Anatomical Abbreviations

bo	basioccipital
bs	basisphenoid
ex	exoccipital
fjp	foramen jugulare posterius
fpcci	foramen posterius canalis carotici interni
fpo	fenestra postotica
fr	frontal
ica	incisura columellae auris
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
XII	foramen nervi hypoglossi

Cranial Morphology

(see table 1 for measurements)

Prefrontal (figs. 1, 3, 6, 8)

Preservation: Both prefrontals are complete in AMNH 30563 except for a small part of the maxilla contact. The prefrontals in AMNH 30569 and AMNH 30562 are both present and nearly complete. There is some breakage in AMNH 30562 on the right prefrontal.

Contacts: In AMNH 30563, the type specimen, there is a long medial contact with the parietal. In the two other specimens of *Ummulisani*, AMNH 30569 and AMNH 30562, small paired frontals lie in the medial part of this suture and the prefrontal-parietal contact is relatively short. The only other pleurodire or turtle to have a prefrontal-parietal contact is *Phosphatochelys*. *Phosphatochelys* also has small frontals that are separated from the orbital margin by the prefrontal-parietal contact, as in *Ummulisani*. Many other turtles have small frontals, but none combine that with large prefrontals to produce a prefrontal-parietal contact.

In all three skulls there is a narrow anterolateral contact with the dorsal process of the maxilla. The maxilla contact in *Ummulisani* is about the same size and position as in *Phosphatochelys*. It is narrower than in *Taphrosphys* and *Azabbaremys*.

Structures: The prefrontal in *Ummulisani* has the midline projection seen in other Taphrosphyini. It is roughly similar in size and shape to that in *Phosphatochelys*. However, there is some variation within *Ummulisani*; in AMNH 30569 and AMNH 30562 the process is larger and more ventrally directed than in AMNH 30563.

Ummulisani is unique in having a hornlike process on the anterolateral margin of each prefrontal. Contrary to the original description in Gaffney et al. (2006), these processes are not developed to exactly the same extent in all three skulls. In AMNH 30569 and AMNH 30562 the horns are more massive and protrude anterodorsally to a greater extent than in AMNH 30562. The anterior surface of the prefrontal in AMNH 30569 and AMNH 30562 faces almost directly anteriorly rather than anterodorsally as in AMNH 30563, which makes the horns more protuberant. The horn or process is cone-shaped and lies at the anterodorsal margin of the orbit. There is nothing similar in any other turtle. *Phosphatochelys* and other Taphrosphyini do not even have swellings or thickened bone in this area. The ventral surface is visible in AMNH 30563 and AMNH 30569. The prefrontal forms almost all the roof of the fossa nasalis and the major part of the sulcus olfactorius.

Frontal (figs. 1, 3, 6, 8)

Preservation: The frontal is present and nearly complete in AMNH 30569 and AMNH 30562. It is absent in AMNH 30563, but not the result of preservational damage, it was absent in life, see above. Whether this was the result of individual variation, interspecific variation, or pathology, is not known. In

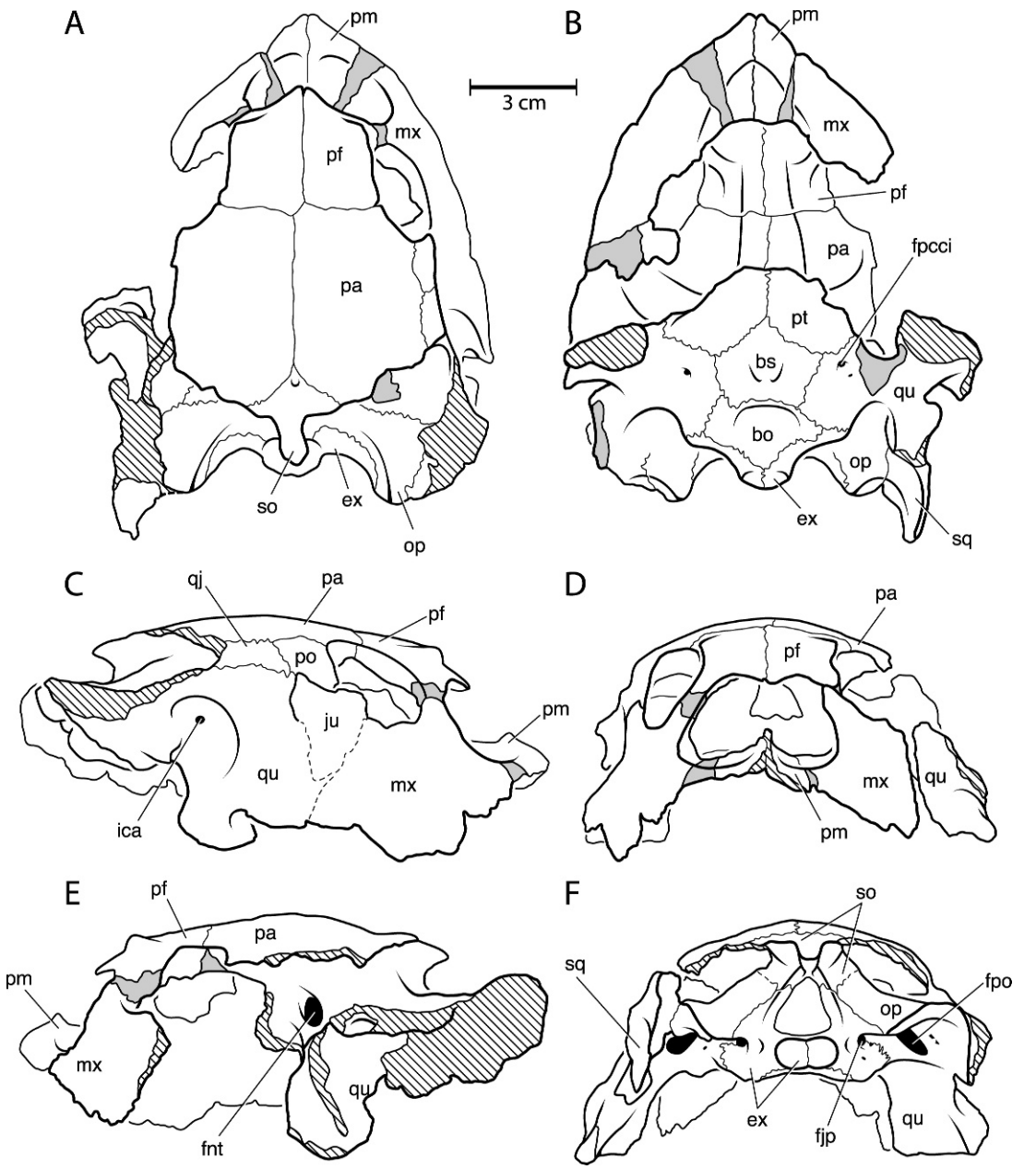

Fig. 3. *Ummulisani rutgersensis* Gaffney, Meylan, and Tong, 2006. AMNH 30563 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. (from Gaffney et al., 2006a) (C. Blik del.)

AMNH 30569 the right frontal is complete, but the left is broken laterally and its contact with the left prefrontal is indistinct. In AMNH 30562 the frontals are complete but separated along their sutures from the prefrontals and each other.

CONTACTS: The frontal contacts the prefrontal anterolaterally, the parietal posteriorly, and the other frontal medially.

STRUCTURES: The frontal has a flat dorsal surface. It does not enter the orbital margin due to the prefrontal-parietal contact. On its

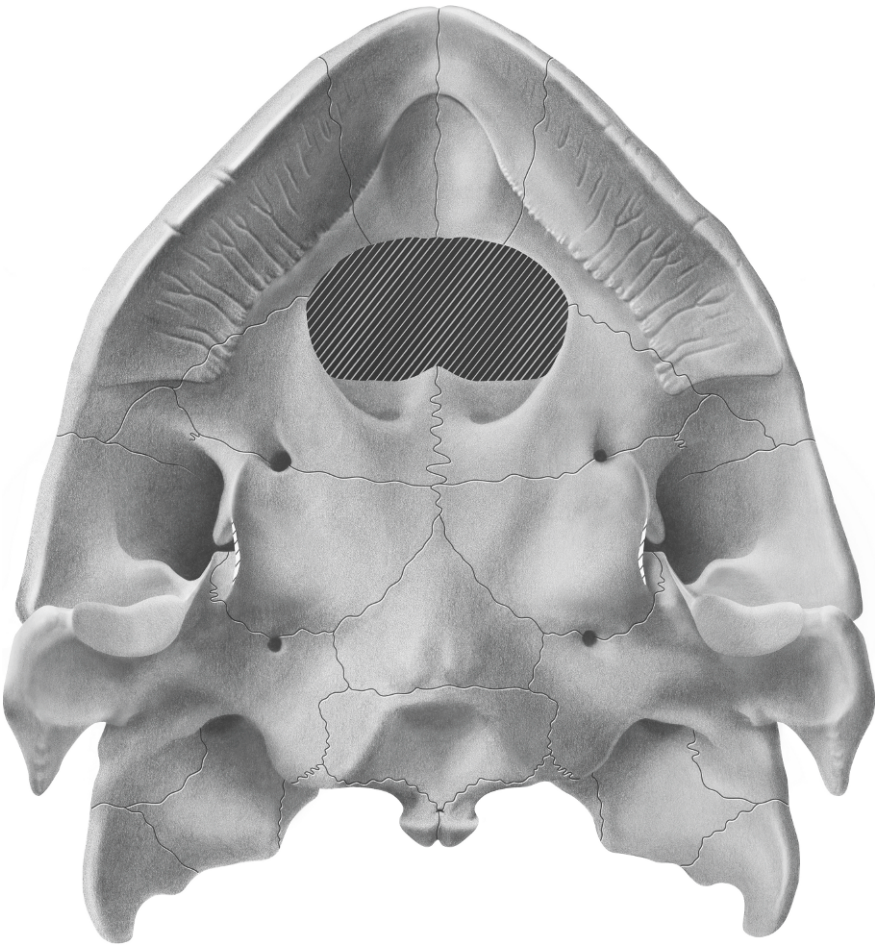

Fig. 4. *Ummulisani rutgersensis* Gaffney, Meylan, and Tong, 2006. AMNH 30569. Partially restored view of palate. (M. Vabulas del.)

ventral surface, there is a deep parasagittal ridge marking the lateral edge of the sulcus olfactorius. This ridge is formed on the prefrontal in the frontalless AMNH 30563.

PARIETAL (figs. 1, 3, 6, 8)

PRESERVATION: Both parietals are present in all three skulls. The right parietal of AMNH 30562 is broken with slight displacement of the pieces, and the left parietal of AMNH 30569 is missing some of its central area, which has been restored. In AMNH 30563 the dorsal plate of the right parietal is complete except on its posterior edge. The left one has a broken lateral and posterior margin.

In AMNH 30563 the processus inferior parietalis on both sides is present but slightly damaged by dorsoventral crushing that has obscured its ventral contacts. The anterior margin of the processus is broken on both sides. In AMNH 30569 only the right processus inferior parietalis is exposed, and in AMNH 30562 both sides are covered by matrix.

CONTACTS OF DORSAL PLATE: The large parietal of *Ummulisani* contacts the other parietal medially, the prefrontal anterolaterally and frontal anteriorly (but see Prefrontal for the frontalless AMNH 30563), the postorbital anterolaterally, the quadratojugal posterolaterally, and a small dorsal plate of the supraoccipital posteromedially.

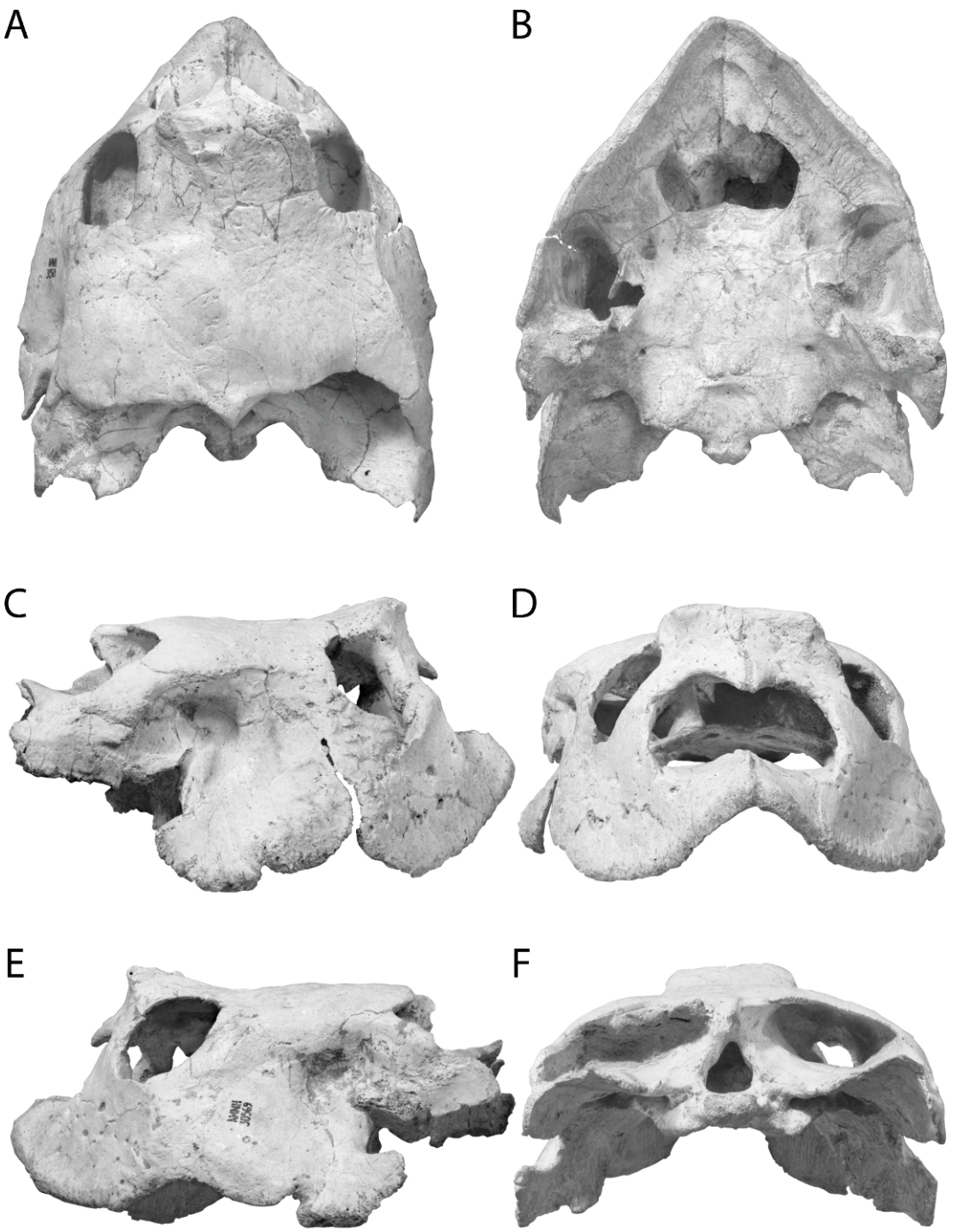

Fig. 5. *Ummulisani rutgersensis* Gaffney, Meylan, and Tong, 2006. AMNH 30569. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. (C. Facella del.)

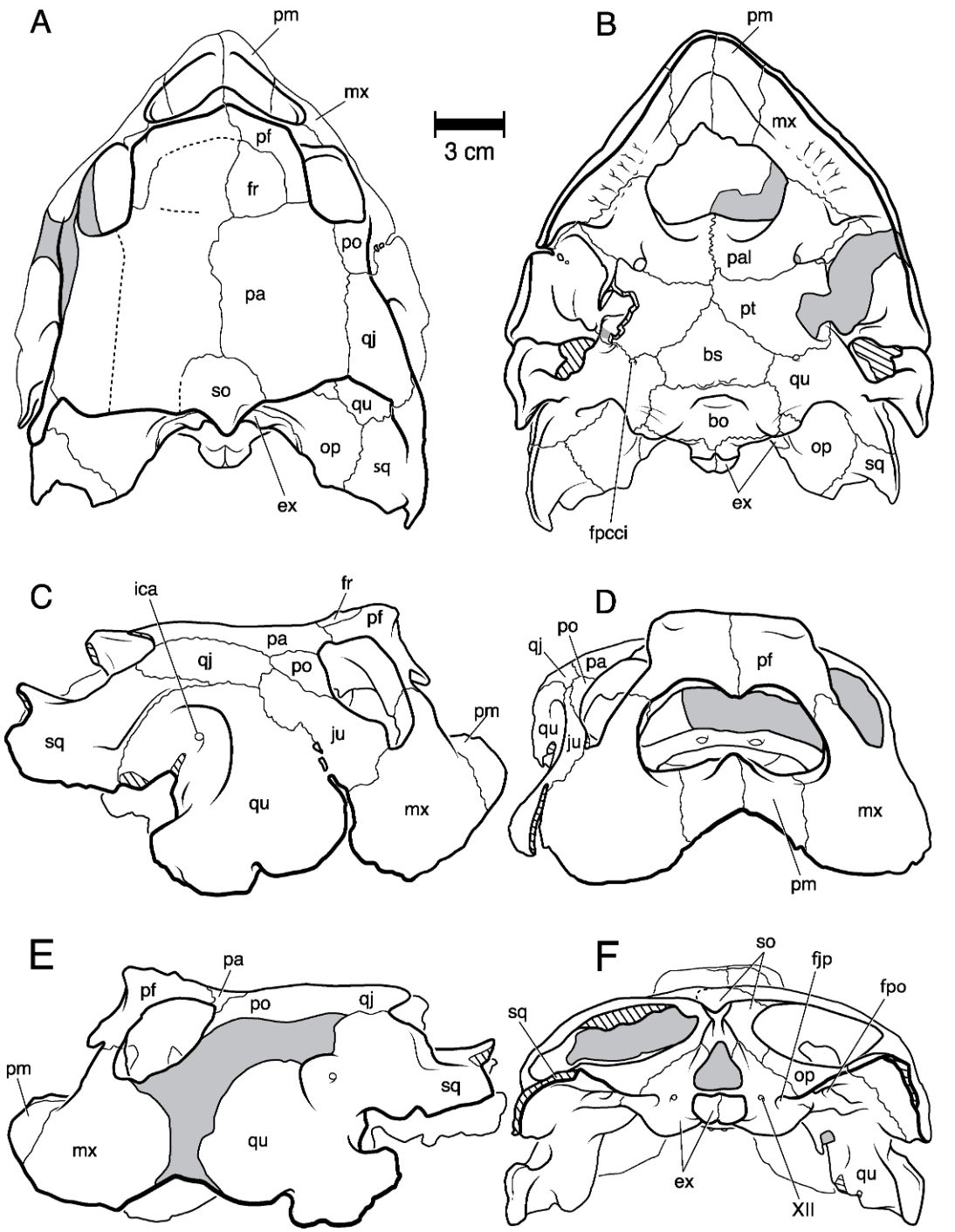

Fig. 6. *Ummulisani rutgersensis* Gaffney, Meylan, and Tong, 2006. AMNH 30569. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. (C. Facella del.)

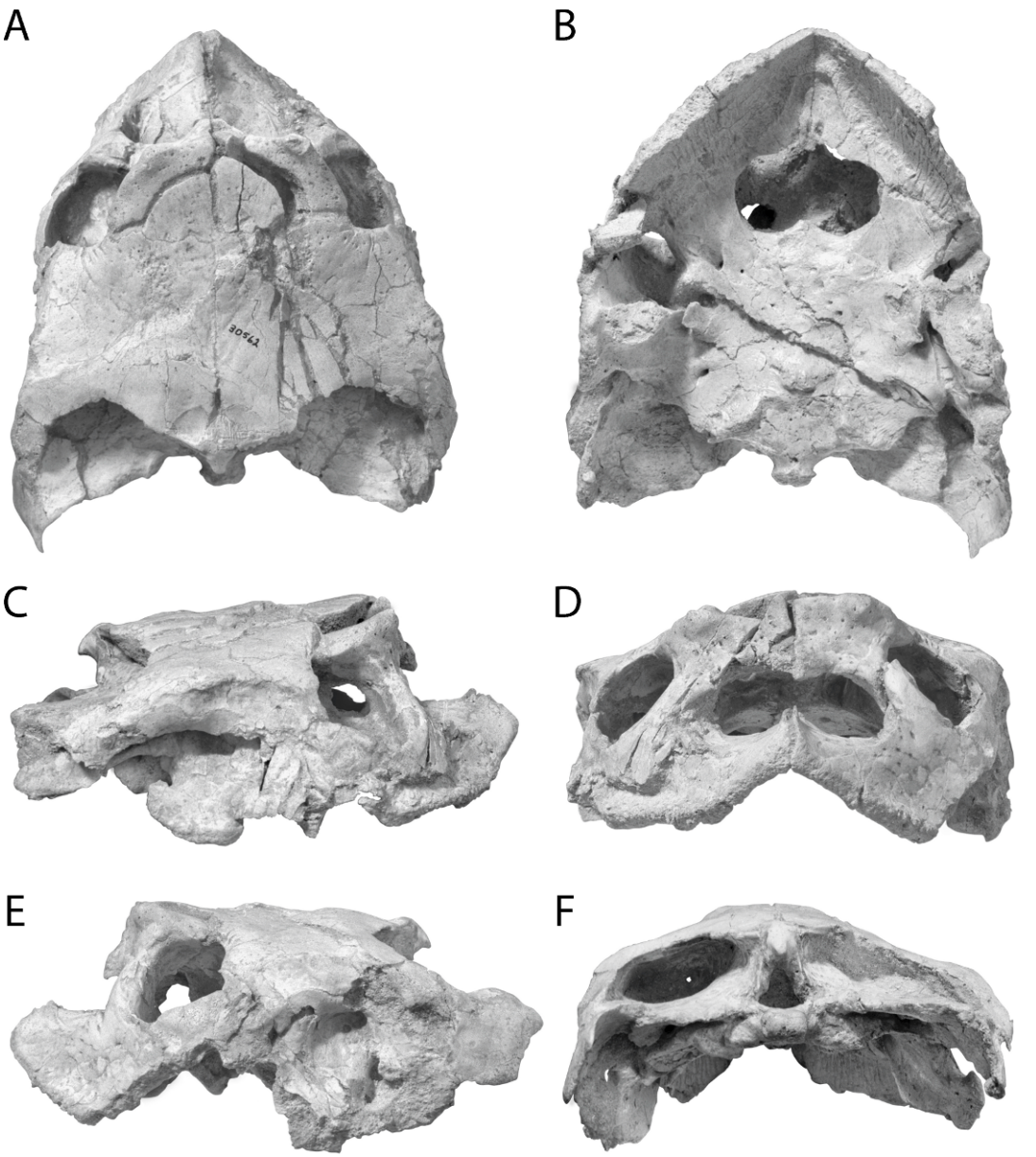

Fig. 7. *Ummulisani rutgersensis* Gaffney, Meylan, and Tong, 2006. AMNH 30562. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. (C. Facella del.)

Except for the absence of a frontal contact in the type specimen, AMNH 30563, these contacts are similar to those found in *Phosphatochelys*.

STRUCTURES OF DORSAL PLATE: The posterior temporal emargination in *Ummulisani* is about the same as in *Phosphatochelys*.

On the ventral surface of the dorsal plate, AMNH 30563 lacks a complete septum orbitotemporale and has a transverse ridge instead, marking the posterior limits of the fossa orbitalis and the dorsal position of the septum. In AMNH 30569 and AMNH 30562 the septum orbitotemporale is present but in

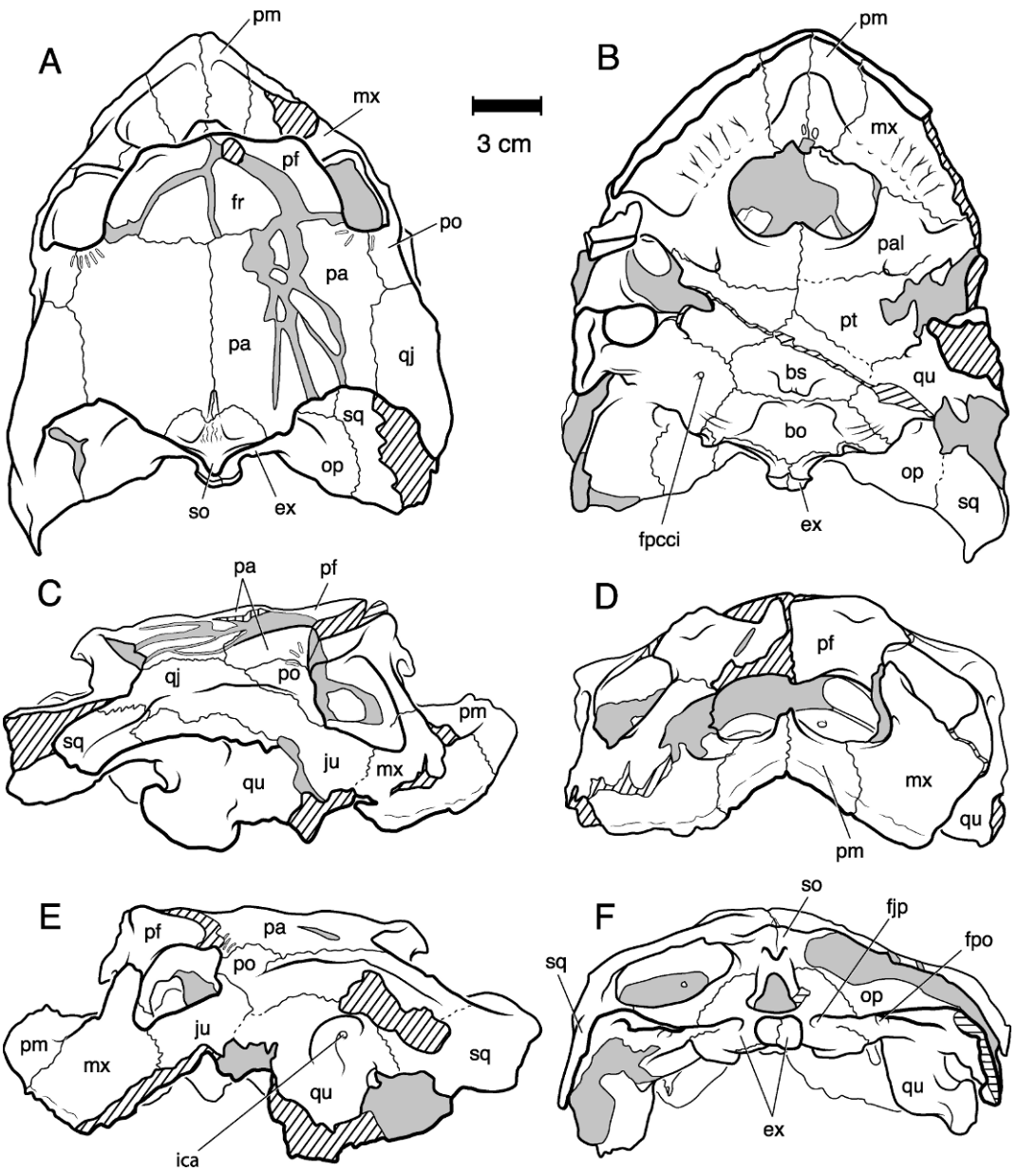

Fig. 8. *Ummulisani rutgersensis* Gaffney, Meylan, and Tong, 2006. AMNH 30562. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. (C. Facella del.)

contrast to most bothremydids, there is a large fenestra or space between the barlike septum and the side wall of the cheek. Medial to the columnar septum orbitotemporale is the sulcus palatinopterygoideus, as in other pleurodires. The parietal makes up the dorsal third of the septum while the palatine forms the ventral two-thirds.

CONTACTS OF PROCESSUS INFERIOR PARIETALIS: The anterior margin of the processus inferior parietalis contacts the palatine, as in *Phosphatochelys*. The pterygoid con-

TABLE 1
Cranial Measurements of *Ummulisani* skulls in millimeters (see Gaffney et al., 2006a: fig. 315)

	AMNH 30563	AMNH 30569	AMNH 30562
A. Midline length as preserved	124.0	197.0	201.0
B. Maximum width	114.0[1]	186.0	181.0
C. Width between orbits	37.0	75.0	98.0[1]
D1. Width of left orbit	—	46.0	35.0
D2. Width of right orbit	25.2	36.0	39.0
E. Width of external nares	39.5	71.0	69.0
F. Width of internal nares	—	63.5	61.5
G. Maximum height at quadrate	58.0	102.0	94.0
H. Width of skull at middle of orbits	66.5	123.0	151.0
I. Length from anterior margin of prefrontals to posterior margin of supraoccipital	97.0	151.0	188.0
J1. Height of left orbit	24.0	48.0	44.0
J2. Height of right orbit	—	50.0	37.0
K. Skull height at occipital condyle	44.0	51.0	47.0
L. Anterior width of triturating surface	19.0	37.0	38.0
M. Posterior width of triturating surface	—	32.0	28.0
N. Width of palate across foramina palatinum posterius	—	103.0	109.0
O. Length from front of skull to posterior edge of condylus articularis	87.0	143.0	153.0

[1]damaged

tact is much wider in *Ummulisani* than in *Phosphatochelys*. The prootic contact above the foramen nervi trigemini is unclear posteriorly.

STRUCTURES OF PROCESSUS INFERIOR PARIETALIS: The processus inferior parietalis in *Ummulisani* is much wider than it is in *Phosphatochelys*. In *Phosphatochelys* the parietal has a ventral process that meets the pterygoid lateral to the sulcus palatinopterygoideus. In *Ummulisani*, the pterygoid area defining the sulcus is gone, but a small parietal process is present, although it does not seem to have been long enough to reach the pterygoid when the pterygoid was there.

JUGAL (figs. 1, 3, 6, 8)

PRESERVATION: Despite the fact that all three skulls have cheeks preserved, this area is still poorly known due to the very thin nature of the bone making up the cheek area. Only part of the right jugal is probably present in AMNH 30563, and that seems to have been displaced during an earlier bout of preparation. A bone below the orbit has a broken medial process that seems to be identifiable as a jugal, but it overlaps part of the quadrate behind it. The orbital margin and possible sutures, however, suggest that the bone may be the jugal and may only be displaced from its original position. In AMNH 30569 the jugal is present on both sides, but is complete only on the right. In AMNH 30562 both jugals are present, but both are damaged, the left one lacking only its ventral margin.

CONTACTS OF LATERAL PLATE: AMNH 30569 has the best cheek and shows what seems to be a complete set of contacts for the jugal in *Ummulisani*. The jugal contacts the postorbital dorsally, the quadratojugal posterodorsally, the quadrate posteroventrally, and the maxilla anteroventrally. These contacts are all consistent with the preserved morphology in the other two *Ummulisani* skulls, although their interpretation is more ambiguous. The Gaffney et al. (2006a: fig. 204) restoration of the cheek showing no jugal-quadratojugal contact is probably wrong.

STRUCTURES OF LATERAL PLATE: The jugal widely enters the orbital margin, but does not enter the ventral margin of the cheek.

CONTACTS OF MEDIAL PROCESS: The medial process of the jugal is clearly seen on the left side of AMNH 30569. The jugal contacts the maxilla in a short suture anteriorly and the

palatine in a long suture laterally back to the base of the septum orbitotemporale.

STRUCTURES OF MEDIAL PROCESS: The medial process forms much of the floor of the orbit, but does not extend dorsally into the septum orbitotemporale. It is exposed in the anterior face of the fossa temporalis inferior.

QUADRATOJUGAL (figs. 1, 3, 6, 8)

PRESERVATION: AMNH 30569 has a nearly complete right quadratojugal, while its left is restored, although some original bone is present. AMNH 30562 has both quadratojugals present but damaged, although the right one is relatively complete. Only a fragment is retained in AMNH 30653.

CONTACTS: The quadratojugal in *Ummulisani* contacts the parietal medially for most of its length, the postorbital anterodorsally, the jugal anteroventrally, the squamosal posteroventrally, and the quadrate ventrolaterally.

STRUCTURES: The quadratojugal in *Ummulisani* is a small element placed well dorsal to the cheek margin. It is rectangular and not C-shaped. In these features it agrees with the quadratojugal in *Phosphatochelys* and *Azabbaremys*.

SQUAMOSAL (figs. 1, 3, 6, 8)

PRESERVATION: The vicissitudes of death have dealt harshly with the squamosals of AMNH 30563: both are badly broken. However, AMNH 30562 and AMNH 30569 have much better preserved squamosals. AMNH 30562 has a good left squamosal that retains the posterior margin but is broken anteriorly. Its right squamosal is missing most of its edges but retains the anterior contacts. AMNH 30569 has a well-preserved right squamosal lacking only some of the posterior margin. The left one is broken on most of its margins.

CONTACTS: The squamosal in *Ummulisani* contacts the quadrate anteriorly and anteromedially, the quadratojugal anterodorsally, and the opisthotic medially.

STRUCTURES: The antrum postoticum is absent in *Ummulisani*, and the squamosal has no sign of a remnant canal or space. The ventral squamosal flange in *Ummulisani* is large and similar to that structure in *Taphrosphys*, *Rhothonemys*, *Phosphatochelys*, and *Labrostochelys*. There is no indication of a lateral tubercle in any of the three skulls.

POSTORBITAL (figs. 1, 3, 6, 8)

PRESERVATION: Only the right postorbital is present in a damaged area of AMNH 30563. In AMNH 30562 the postorbital is present on both sides; both bones are cracked but relatively well preserved and complete. In AMNH 30569 the right postorbital is nearly complete, but the area of the left one is largely restored and the element is apparently missing. The internal surface of the postorbital is visible and preserved at least to some extent in all three skulls.

CONTACTS OF LATERAL PLATE: The postorbital in *Ummulisani* contacts the parietal dorsomedially, the quadratojugal posteriorly, and the jugal ventrally. The quadrate contact reported by Gaffney et al. (2006a) in AMNH 30563 is in a damaged area and we now discount this interpretation.

STRUCTURES OF LATERAL PLATE: The postorbital in *Ummulisani* forms the posterodorsal margin of the orbit and does not enter the temporal margin due to its relatively small size, in comparison to a form like *Azabbaremys*.

CONTACTS OF MEDIAL PROCESS: In AMNH 30563 the medial process contacts the parietal only medially, as the septum orbitotemporale is either absent, as in AMNH 30563, or the septum orbitotemporale has a large opening in the middle of it, as in AMNH 30562 and AMNH 30569.

STRUCTURES OF MEDIAL PROCESS: In AMNH 30563 the orbit is open posteriorly and the septum orbitotemporale is nearly absent. The postorbital and parietal form a transverse ridge on the ventral surface of the skull roof. This ridge is the remnant of the septum orbitotemporale and forms the posterior margin of the fossa orbitalis. In AMNH 30562 and AMNH 30569 the septum orbitotemporale has a large opening in it, but it is present. However, the portion usually formed by the postorbital is the area that is reduced in *Ummulisani*, so the ventral form of the postorbital is the same in all three

skulls. The postorbital forms part of the ridge above the large fenestra or opening resulting from the incomplete formation of the septum orbitotemporale.

Premaxilla (figs. 1, 3, 4, 6, 8)

Preservation: Both premaxillae are present in all three *Ummulisani* skulls.

Contacts: The premaxilla in *Ummulisani* contacts the other premaxilla medially and the maxilla posterolaterally. The vomer and the vomer contact, if present, are not preserved in any of the three skulls.

Structures on Dorsal Surface: The premaxilla forms the floor of the fossa nasalis, which in *Ummulisani* is relatively large. The apertura narium externa is separated from the anterior skull surface only by a low ridge and a slight change in slope in *Ummulisani*, rather than by a sharp change in slope, as in *Phosphatochelys* and other Taphrosphyini. There is a midline ridge or carina that runs from the anterior margin of the premaxilla, the labial ridge, posteriorly through the apertura narium externa and into the fossa nasalis. In *Phosphatochelys*, the ridge is only within the fossa nasalis. In *Ummulisani*, the premaxilla is protuberant on the midline, forming an acute point, rather than the curved snout margin seen in *Phosphatochelys*, *Taphrosphys*, and *Nigeremys*. *Rhothonemys* has a slight protuberance, but not to the extent seen in *Ummulisani*. *Labrostochelys* has an extensive premaxillary process, but it ends in a blunt edge different from that in *Ummulisani*.

The floor of the fossa nasalis is a broad, curved trough separated by the midline carina. There is a groove along the inner margin of the apertura narium externa, like that seen in *Phosphatochelys*. The midline carina has a dorsal process where it intersects the apertura narium externa.

Structures on Ventral Surface: The labial ridge is inclined in *Ummulisani*, different from the vertical ridge in *Phosphatochelys*. The edge of the ridge is sharp and the bone is much thinner than in *Phosphatochelys*, and the more horizontal triturating surface produces a wider flat area behind the labial ridge. The midline embayment in *Ummulisani* is wide as in *Phosphatochelys*, but much shallower. As on the dorsal surface, the labial ridge forms a pointed anterior protuberance in *Ummulisani* not seen in *Phosphatochelys*.

The premaxillae of the three *Ummulisani* skulls differ among themselves only in that the smallest skull, AMNH 30563, has a thinner and less robust labial ridge than do the other two larger skulls.

Maxilla (figs. 1, 3, 4, 6, 8)

Preservation: Most of the right maxilla is present in AMNH 30563, but the ventral margin is missing some of its edges; and its medial margin is missing posteriorly. There seems to be a natural edge just behind the premaxilla. The left maxilla only consists of the anterior half of the bone. Its ventral margin is a broken edge. Its medial edge seems to be natural anteriorly, as on the right side. Both maxillae have a posterior broken edge. AMNH 30562 has both maxillae preserved, but they are broken, the left lacking its posterior half and the right being crushed dorsoventrally. AMNH 30569 has a nearly complete right maxilla, although its posterior margin is a free edge, and its left maxilla is similarly complete, but its posterior edge is embedded in a restored cheek area so its actual limits are ambiguous.

Contacts of Vertical Plate: The maxilla contacts the premaxilla anteriorly, the prefrontal anterodorsally, the jugal posterodorsally, and the quadrate posteroventrally. The quadrate "contact" is not actually present, but a narrow space separates them, which is well preserved on the right side of AMNH 30569. During preparation of that skull (by H.T.), the gap was present between the maxilla and the quadrate. The posterior edge of the maxilla, as well as the anterior edge of the quadrate are undamaged, smooth edges. The fake matrix/glue mixture added by a local collector to fill the gap was removed. However, the maxilla/quadrate contact is present only on the left side of AMNH 30563 and the right side of AMNH 30569. In the latter: "the quadrate suture is in a broken area, its position is unclear" (Gaffney et al., 2006a: 451). So it seems that a gap is present in AMNH 30569 but probably absent in AMNH 30563.

STRUCTURES OF VERTICAL PLATE: The maxilla forms the ventral part of the orbital margin. There is a sharp rim with a concave pocket below the internal surface, as in *Phosphatochelys* and *Rhothonemys*. Anteriorly the maxilla forms the lateral wall and lateral part of the floor of the fossa nasalis. The orbitonasal bar in *Ummulisani* is narrow, as in *Phosphatochelys*, not wide, as in *Taphrosphys* and other Taphrosphyini.

The maxilla in *Ummulisani* is unusually deep, deeper than other Taphrosphyini except *Phosphatochelys*. Due to the greater snout foreshortening in *Phosphatochelys*, *Ummulisani* has a longer anterior part of the maxilla, as in the other Taphrosphyini. The narrow cheek emargination seen in *Phosphatochelys* is present but poorly preserved in the type skull of *Ummulisani*, but it is clearly present in the other two skulls of *Ummulisani*.

CONTACTS OF HORIZONTAL PLATE: The maxilla contacts the premaxilla anteromedially, the palatine posteromedially, and the jugal posterolaterally. There is no midline maxilla contact. It cannot be determined (at least not by my feeble brain) whether the absence of a vomer is pre- or postmortem. But if one were present it could have contacted the maxilla.

STRUCTURES OF HORIZONTAL PLATE: On the ventral surface, the triturating surface in *Ummulisani* is relatively narrow, as in other Taphrosphyini and in contrast to the wide surface of the Bothremydini. The labial ridge in *Ummulisani* is deep, as in *Phosphatochelys*, but it is very thin and curved, in contrast to the thicker wedge shape in *Phosphatochelys*. The entire triturating surface is curved, as in *Labrostochelys*; it is not a distinct labial ridge meeting a horizontal triturating surface at right angles.

On the dorsal surface, the maxilla forms the anterolateral edge of the apertura narium interna. This is similar to the apertura in *Phosphatochelys* and *Taphrosphys*. The maxilla forms most of the floor of the fossa orbitalis. There is a high, sharp rim to the orbital margin and a ventral pocket formed by the maxilla, as in *Rhothonemys* and *Phosphatochelys*.

The only difference among the maxillae of the three *Ummulisani* skulls is that the larger AMNH 30562 and AMNH 30569 have thicker, more robust, labial ridges than the smaller AMNH 30563.

VOMER

PRESERVATION: Not preserved in any of the three skulls. The anterior margins of the palatines on the midlines in AMNH 30562 and AMNH 30569 show what seem to be natural edges, not sutural surfaces, suggesting that vomers were never present. However, small, narrow vomers may not have distinct sutural contact areas so the question remains open.

PALATINE (figs. 3, 4, 6, 8)

PRESERVATION: The palatine is not preserved in AMNH 30563, but both palatines are preserved almost completely in AMNH 30562 and AMNH 30569.

CONTACTS: The palatine in *Ummulisani* contacts the maxilla anterolaterally, the pterygoid posteriorly, the jugal laterally, and the other palatine medially. On the dorsal surface the palatine sends what is essentially a column dorsally to contact the parietal. This column is the remnants of the reduced septum orbitotemporale. This structure and contact are in AMNH 30562 and AMNH 30569. In AMNH 30563 the palatine is missing and the dorsal part of the septum seems to lack any ventral extension.

STRUCTURES ON DORSAL SURFACE: The palatine has a dorsal process as discussed above, with the sulcus palatinopterygoideus medially positioned and floored by the palatine. The process is clearly the remnant of the septum orbitotemporale. It is intact and visible on both anterior and posterior surfaces of the right side of AMNH 30569, visible on the anterior surface on the left side of AMNH 30562.

STRUCTURES ON VENTRAL SURFACE: The palatine in AMNH 30562 and AMNH 30569 is relatively flat, with a step anteriorly where the palatine surface lies more dorsally and forms the posterior margin of the apertura narium interna. There is no choanal arch or grooves as in some other bothremydids. At the posterior edge of the apertura step is a prominent foramen, on both palatines, that

penetrates to the dorsal surface of the palatine, presumably containing some sort of vascular tissue. The palatine forms most of the foramen palatinum posterius, at the junction with the pterygoid. There is a slight extension of the vascularized surface of the triturating surface onto the palatine at its anterolateral edge, but the palatine does not form a significant part of the triturating surface in *Ummulisani*.

Quadrate (figs. 1, 3, 4, 6, 8)

Preservation: Both quadrates are present in AMNH 30563; the right one is nearly complete except for damage along its anterior margin, and the left is missing its dorsal portions. In AMNH 30562 both quadrates are present but damaged. However, the left one preserves the cavum tympani and anterior sutures, the right one is more crushed but preserves the ventral margin. AMNH 30569 has the best-preserved quadrate of the three skulls on its right side, but the left quadrate is damaged anteriorly and dorsally by restoration.

Contacts on Lateral Surface: The quadrate in *Ummulisani* contacts the quadratojugal dorsomedially, the jugal anterodorsally, and the maxilla anteriorly, as in *Phosphatochelys*. The quadrate contacts the squamosal posterodorsally. The postorbital contact interpreted by Gaffney et al. (2006a) was based on a damaged area and was probably in error.

Structures: The quadrate does not enter the temporal emargination in *Ummulisani*. The degree of emargination is similar in *Ummulisani* and *Phosphatochelys*, and *Phosphatochelys* also has no quadrate exposure along the margin. The lateral surface of the quadrate in *Ummulisani* is expanded anteriorly as in *Phosphatochelys*, compared with other bothremydids, forming much of the cheek. Although the cavum tympani is clearly defined, there is a wider shallow depression paralleling the anterior curved edge of the cavum. This depression extends well onto the cheek.

The cavum tympani in *Ummulisani* is similar to that in *Phosphatochelys*. The incisura columellae auris is the usual bothremydid canal, with the deepest part of the cavum dorsal and anterior to it. The ventral shelf seen in many bothremydids is present, but not as deep or as well defined as in other taxa, such as *Bothremys*. The antrum postoticum is closed, although the area is a deep concavity posterodorsal to the incisura columellae auris. The sulcus eustachii is a V-shaped notch, widely separated from the incisura columellae auris, forming a shallow groove extending toward the incisura columellae auris. There is a ventrally directed process on the dorsal edge of the sulcus, as in *Phosphatochelys* and *Labrostochelys*. There is also a dorsally directed process on the lower margin of the sulcus eustachii.

Contacts on Dorsal and Anterior Surface: On the dorsal surface of the otic chamber, the quadrate contacts the prootic anteromedially, the opisthotic posteromedially, and the squamosal posteriorly. There is no supraoccipital contact, agreeing with the other Taphrosphyini.

Structures on Dorsal and Anterior Surface: The foramen stapedio-temporale is only separated from the foramen nervi trigemini by a thin bar. Only a small part of quadrate seems to reach the margin of the foramen stapedio-temporale due to this very medial position. These relations are similar in both *Ummulisani* and *Phosphatochelys*.

Contacts on Ventral Surface: The quadrate in *Ummulisani* contacts the pterygoid anteromedially, the basisphenoid medially, the basioccipital posteromedially, and the exoccipital posteromedially as well. The basisphenoid contact is wide in *Ummulisani*, as in *Taphrosphys* and in contrast to the narrow contact of other Taphrosphyini. The basisphenoid-quadrate contact is wider in AMNH 30563 than it is in AMNH 30569 and AMNH 30562.

Structures on Ventral Surface: There is no fossa pterygoidea in *Ummulisani*, although there is a slight concavity here. The condylus mandibularis is well anterior to the condylus occipitalis and the basisphenoid-basioccipital suture. The posterior surface of the condylus mandibularis has a shallow depression for the depressor mandibulae as in *Phosphatochelys*, not a deep depression as in *Labrostochelys*. The foramen posterius

canalis carotici interni is formed completely by the quadrate in AMNH 30563 and AMNH 30562, but in AMNH 30569 the foramen lies very close to the pterygoid contact and a small part of pterygoid enters the anterior margin of the foramen. *Ummulisani* and *Labrostochelys* are the only pleurodires with the foramen posterius canalis carotici interni entirely formed by the quadrate.

CONTACTS ON POSTERIOR SURFACE: The quadrate in *Ummulisani* contacts the squamosal dorsolaterally, the opisthotic dorsomedially, the exoccipital medially, and the basioccipital ventromedially.

STRUCTURES ON POSTERIOR SURFACE: The fenestra postotica in *Ummulisani* is fully enclosed by bone, and widely separated from the foramen jugulare posterius. The fenestra postotica is oval, roughly horizontal, with no sign of divisions.

PTERYGOID (figs. 1, 3, 4, 6, 8)

PRESERVATION: Both pterygoids are present in AMNH 30563, but they lack the processus trochlearis pterygoidei and anterior edges. The left one is missing its lateral edge, which is present on the right. The pterygoids are more complete in AMNH 30562 and AMNH 30569, but in neither is the dorsal surface visible. In both, some of the processus trochlearis pterygoidei lacks its edges, but when taken together nearly all of the processus and its associated flange seem to be preserved.

CONTACTS ON VENTRAL SURFACE: The pterygoid in *Ummulisani* contacts the quadrate posterolaterally, the basisphenoid posteromedially, the palatine anteriorly, and the other pterygoid medially.

STRUCTURES ON VENTRAL SURFACE: There is no deep fossa pterygoidea, only a very shallow, ill-defined depression in the area. The quadrate ramus is slightly more extensive than in *Phosphatochelys*. The foramen palatinum posterius is largely formed by the palatine with a small contribution from the pterygoid. The foramen posterius canalis carotici interni has some contribution from the pterygoid in AMNH 30569, but not in the two other specimens.

CONTACTS ON DORSAL SURFACE: The crista pterygoidea of the pterygoid contacts the parietal dorsally and the quadrate posteroventrally below the foramen nervi trigemini. The sutures around the foramen nervi trigemini (visible only in AMNH 30563) are not clear, but there seems to be no prootic contact; the parietal enters the margin of the foramen between the pterygoid and prootic.

STRUCTURES ON DORSAL SURFACE: The crista pterygoidea rises posteriorly to just anterior to the foramen nervi trigemini where it drops ventrally, and only a small part enters the foramen margin. The pterygoid bears a prominent, rounded ridge that is oriented anterodorsally-posteroventrally. It extends from a position anterior to the foramen nervi trigemini ventrally along the quadrate ramus paralleling the quadrate-pterygoid suture. As in *Phosphatochelys* this ridge is large and acute, defining a tubular space anterior to the ridge (see Gaffney et al., 2006: 431).

SUPRAOCCIPITAL (figs. 1, 3, 4, 6, 8)

PRESERVATION: The supraoccipital is present and nearly complete in AMNH 30563, AMNH 30562, and AMNH 30569.

CONTACTS: The supraoccipital in *Ummulisani* contacts the parietals anteriorly, the exoccipitals posteroventrally, the prootic anterolaterally, and the opisthotic posterolaterally. There is no quadrate contact, agreeing with other Taphrosphyini.

STRUCTURES: The crista supraoccipitalis in *Ummulisani* is a very short, blunt process, with little similarity to the usual flat, vertical plate seen in other turtles. *Phosphatochelys* also has a short crista, but it has a clear vertical plate. *Ummulisani* has a low crista with a blunt posterior end that is only slightly raised above the foramen magnum. The supraoccipital in *Ummulisani* has a horizontal contribution to the skull roof that extends anteriorly and laterally more than in other bothremydids. *Taphrosphys* has a wide plate, but not as deep as in *Ummulisani*.

EXOCCIPITAL (figs. 1, 3, 6, 8)

PRESERVATION: Both exoccipitals are present and nearly complete in AMNH 30563, AMNH 30562, and AMNH 30569.

CONTACTS: The exoccipital in *Ummulisani* contacts the supraoccipital dorsally, the

opisthotic laterally, the quadrate ventrolaterally, and the basioccipital ventrally.

STRUCTURES: The foramen magnum in *Ummulisani* is about the same as in other Taphrosphyini. The condylus occipitalis is formed entirely by the exoccipitals. There is very little constriction to form a neck for the condyle, particularly in AMNH 30563. The foramen nervi hypoglossi consist of a larger, more medial foramen and a much smaller, more lateral one, as in other Taphrosphyini. As in *Phosphatochelys*, the more lateral one is very close to the foramen jugulare posterius, although in *Ummulisani* it is not actually within the margin of the foramen jugulare posterius as it is in *Phosphatochelys*. The foramen jugulare posterius is completely closed laterally by the opisthotic-exoccipital contact. The foramen is recessed, with a blunt shelf below, so that it faces more laterally than the foramen does in *Phosphatochelys*.

BASIOCCIPITAL (figs. 1, 3, 4, 6, 8)

PRESERVATION: The basioccipital in AMNH 30563, AMNH 30562, and AMNH 30569 is nearly complete.

CONTACTS: The basioccipital in *Ummulisani* contacts the basisphenoid anteriorly, the quadrate in a wide suture laterally, and the exoccipital posterolaterally.

STRUCTURES: *Ummulisani* has a blunt, low tuberculum basioccipitale formed by the basioccipital and exoccipital that is similar in size and extent to that in *Labrostochelys* and is lower than that in *Phosphatochelys*. There is a shallow concavity on the midline, much the same as in other Taphrosphyini.

PROOTIC (figs. 1, 3, 6, 8)

PRESERVATION: Both prootics in AMNH 30563 are present and nearly complete, but some of the sutures are dim. Among the two new specimens, only on the right side of AMNH 30569 can the prootic be seen in its entirety. It is presumably present on the left side of AMNH 30569 and in AMNH 30562, but it is covered by matrix.

CONTACTS: The prootic in *Ummulisani* contacts the parietal dorsomedially, the quadrate laterally, the supraoccipital posterodorsally, and the opisthotic posteriorly.

STRUCTURES: The prootic forms a thin bar separating the foramen nervi trigemini from the foramen stapedio-temporale. In *Ummulisani* the two foramina are not sunk into a common recess, as in *Taphrosphys*, but are still very close, as in *Phosphatochelys*. The prootic forms most of the foramen stapedio-temporale. The foramen stapedio-temporale faces mostly anteriorly and the foramen nervi trigemini faces mostly laterally.

OPISTHOTIC (figs. 1, 3, 4, 6, 8)

PRESERVATION: Both opisthotics are present in AMNH 30563. The left one is damaged along its posterolateral margin; the right one is also damaged posterolaterally and medially as well, so that some of the sutures are obscured. Both opisthotics are present and nearly complete in AMNH 30569 and AMNH 30562.

CONTACTS: The opisthotic in *Ummulisani* contacts the supraoccipital anteromedially, the prootic anteriorly, the quadrate anterolaterally, the exoccipital posteromedially, and the squamosal posterolaterally.

STRUCTURES: The opisthotic enters into the fenestra postotica (see Quadrate) and the foramen jugulare posterius. The opisthotic is part of a posterior flange that, along with the squamosal, forms a ventrally open trough similar to that seen in *Labrostochelys* and *Taphrosphys*, and, to a lesser extent, in *Phosphatochelys*.

BASISPHENOID (figs. 1, 3, 4, 6, 8)

PRESERVATION: The basisphenoid is present and nearly complete in AMNH 30563, AMNH 30569, and AMNH 30562. Its dorsal surface is partially visible only in AMNH 30563.

CONTACTS ON VENTRAL SURFACE: The basisphenoid in *Ummulisani* contacts the pterygoids anterolaterally, the basioccipital posteriorly, and the quadrate in a wide suture laterally. The basisphenoid-quadrate contact is wider in AMNH 30563 than it is in AMNH 30569 and AMNH 30562.

STRUCTURES ON VENTRAL SURFACE: The basisphenoid in *Ummulisani* is pentagonal and similar in shape to that in *Taphrosphys*.

TABLE 2
Comparison of *Ummulisani* skulls

	AMNH 30563	AMNH 30569	AMNH 30562
Frontal	absent	present	present
Prefrontal horns	smaller	larger	larger
Labial ridge	thinner	thicker	thicker
Septum orbitotemporale	absent	present but small	present but small
Foramen posterius canalis carotici interni	quadrate	quadrate and pterygoid	quadrate
Relative size	100%	158%	162%

However, its anterior margin does have a point on the midline, similar to that in *Phosphatochelys*.

CONTACTS ON DORSAL SURFACE: Not determinable.

STRUCTURES ON DORSAL SURFACE: The rostrum basisphenoidale is fused into a single rod anterior to the sella turcica. The sella seems to be wide, not narrow as in *Taphrosphys congolensis*. The dorsum sellae seems to be damaged, but was probably higher than in *T. sulcatus*.

CONCLUSIONS

The three skulls described here are an addendum to the descriptions and analyses presented in Gaffney et al. (2006a). The present paper is essentially a replacement for the *Ummulisani* cranial morphology text in that paper (Gaffney et al., 2006a: 447–457). The original description was based primarily on one skull, AMNH 30563, the type of *Ummulisani rutgersensis*. Because they are more complete, the new information obtained from the two previously undescribed skulls, AMNH 30569 and AMNH 30562, significantly adds to our understanding of this taxon. However, it does not alter the results of the phylogenetic analysis by Gaffney et al. (2006a).

The original skull, AMNH 30563, lacked much of the palate and had poorly preserved cheek regions. The two new skulls have these areas nearly complete, and one of them, AMNH 30569, is particularly well preserved, allowing a full tonal drawing of the palate (fig. 4). The (now available) palatines and pterygoids are seen to be similar in morphology to those in *Phosphatochelys*, the sister taxon of *Ummulisani* in the Gaffney et al. (2006a) analysis. The cheek region is also now determined to be similar to that in *Phosphatochelys*.

One question that the new skulls suggest is the presence of more than one taxon. A case could be made for a new taxon, based on AMNH 30569 and AMNH 30562, characterized by:

1. The presence of frontal bones
2. A more complete septum orbitotemporale
3. Larger prefrontal horns
4. Thicker labial ridges
5. 40% greater size

The three known skulls do show differences that may be of systematic significance (table 2). AMNH 30569 and AMNH 30562, the larger skulls, do have a series of characters in common lacking in the smaller skull, AMNH 30563. AMNH 30563 is about 60% smaller than the other skulls, which are close to each other in size. AMNH 30563 is also extremely unusual in lacking frontal bones. This feature, however, is very difficult to interpret and is more likely to be an individual pathology than an interspecific distinction. There is no other instance of frontals absent in a turtle, whether as an anomaly or a consistent variation. The larger, thicker prefrontal horns in AMNH 30569 and AMNH 30562 could be size or gender related as could the thicker labial ridge. Neither of these features is particularly distinctive and could easily be due to individual variation. The complete absence of the septum orbitotemporale in AMNH 30563, however, is a character not apparently related to size or growth, but it may be related to the absence of the frontals, as this bone is involved in the septum orbitotemporale of pleurodires.

The three specimens come from the same horizon, and there is the possibility that there are different genders represented. For example, AMNH 30563 might be a female and AMNH 30562 and AMNH 30569 might be males, as the latter have larger prefrontal horns and in some living turtles, the male is larger than the female, although the reverse also holds true.

The position of the foramen posterius canalis carotici interni runs contrary to the association of AMNH 30563 as one taxon and AMNH 30569 and AMNH 30562 as another taxon. AMNH 30569 has a pterygoid contribution to the foramen while AMNH 30563 and AMNH 30562 have only the quadrate making up the foramen. At the present time and in the absence of another specimen with the features of AMNH 30563, it seems best to refer all three specimens to the same species, *Ummulisani rutgersensis*.

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