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Redescription of the Skull of *Dacquemys* Williams, 1954, a Podocnemidid Side-Necked Turtle from the Late Eocene of Egypt

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ABSTRACT

The known material of the side-necked turtle *Dacquemys paleomorpha* Williams, 1954, consists of the type skull and a new skull from the late Eocene of Egypt. *Dacquemys* is reaffirmed as a member of the Podocnemididae because of its well-developed cavum pterygoideus. Within the Podocnemididae *Dacquemys* uniquely possesses a fully roofed temporal region produced by a posteriorly extensive parietal and wide supraoccipital, a very wide interorbital area, and two accessory maxillary ridges meeting anteriorly to form an enclosed trough.

INTRODUCTION

The type skull of the taxon redescribed here was first described by E. Dacqué in 1912 and referred by him, doubtfully and for reasons that are unclear, to the shell-based species *Stereogenys libyca* Andrews, 1906. In 1954, Williams recognized that this attribution was inconsistent with the type skull material of *Stereogenys cromeri* Andrews, 1901, the type of the genus, and that the Dacqué skull was distinct from all other

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known Pleurodira. Williams named the form *Dacquemys paleomorpha* and provided a brief description. Since 1954 there have been no further contributions to the understanding of this genus. It is the purpose of this paper to describe the type skull, following repreparation and cleaning, and to describe a new skull discovered by the Duke University Primate Lab during ongoing fieldwork in Egypt. Despite many field seasons of paleontological work in Egypt by a number of institutions, only these two skulls of *Dacquemys* have come to light. The new skull preserves a number of areas unavailable in the type, and together they allow a complete reconstruction of the skull. This paper limits description to comparisons with the well-known forms, the living podocnemidids *Podocnemis*, *Erymnochelys*, and *Peltocephalus*.

It is worth examining the basis for Dacqué's original assignment of the type skull to *Stereogenys libyca*, primarily to see why he associated a shell with the skull. In Dacqué (1912: 337) we translate his argument as follows: ''The reasons why we assign the skull to *Stereogenys libyca* Andrews are the following: 1) because it is particularly similar to *Podocnemis* but it cannot belong to this species, 2) because [the skull] is rather convex so it was not retractable, a condition which is consistent with the epiplastral tubercles [gular projections] of *Stereogenys libyca*, 3) it is consistent with the size of the shell [of *Stereogenys libyca*], 4) [both shell and skull] are found in the same stratigraphic level''. It does not seem that any shells were associated in site with the original skull. He was probably wrong about gular projections preventing head retraction; living tortoises have projections and retract with no problem. Therefore, as Williams (1954) implied, there is no shell associated with the type skull of *Dacquemys paleomorpha*.

We use the terminology for pleurodires previously developed in Broin (1988), Antunes and Broin (1988), and more recently in Meylan (1996), Lapparent de Broin and Werner (1998), Tong et al. (1998), and Gaffney et al. (2001a, 2001b, 2001c). This usage places the families Bothremydidae, Podocnemididae, and Pelomedusidae (restricted to *Pelusios* and *Pelomedusa*) in the Pelomedusoides (which equals the Pelomedusidae in the classic sense). A useful compilation of the pelomedusoid literature is found in Broin (1988) and in Lapparent de Broin (2000). The only computer-generated cladogram of Podocnemididae available at present is Meylan (1996), which shows the relationships of these families and the included genera.

Institutional Abbreviations

AMNH	American Museum of Natural History
DPC	Duke Primate Center, Duke University, North Carolina
SMNS	Staatliches Museum für Naturkunde, Stuttgart

Anatomical Abbreviations

bo	basioccipital
bs	basisphenoid
ex	exoccipital
fr	frontal
ju	jugal
mx	maxilla
op	opisthotic
pa	parietal
pal	palatine
pf	prefrontal
pm	premaxilla
po	postorbital
pr	prootic
pt	pterygoid
qj	quadratojugal
qu	quadrate
so	supraoccipital
sq	squamosal

SYSTEMATICS

ORDER TESTUDINES LINNAEUS, 1758

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

HYPERFAMILY PELOMEDUSOIDES COPE, 1868a

FAMILY PODOCNEMIDIDAE COPE, 1868b

Dacquemys Williams, 1954

TYPE SPECIES: *Dacquemys paleomorpha* Williams, 1954.

DISTRIBUTION: Late Eocene of Egypt.

DIAGNOSIS: A genus of podocnemidid pleurodire known only from the skull; characterized by the unique possession of a fully roofed temporal region with a posteriorly ex-

tensive parietal and wide supraoccipital completely covering the otic chamber in dorsal view; broad parietal-squamosal contact not seen in other podocnemidids; prefrontal extends to anterior margin of apertura narium externa as in *Peltocephalus* but in contrast to *Podocnemis*, interorbital distance very wide with orbits facing laterally in contrast to living Podocnemididae; maxillae meet broadly behind premaxillae; premaxillae recessed and not visible laterally in contrast to all other Pelomedusoides; vomer absent; anterior part of triturating surface more extensive than in living Podocnemididae but secondary palate as seen in *Shweboemys* group absent; two accessory maxillary ridges meet anteriorly to form enclosed trough unique to this genus; antrum postoticum small as in *Podocnemis*; precolumellar fossa shallow as in *Podocnemis expansa*; pterygoid-jugal contact absent.

Dacquemys paleomorpha Williams, 1954

TYPE SPECIMEN: SMNS 12645, a nearly complete skull without lower jaws (figs. 2 and 3), lacking parts of the left side and the central basicranial region (Dacqué, 1912: pl. II, figs. 6–8; Gaffney, 1979: fig. 128; Williams, 1954: pl. 1). Measurements in table 1.

TYPE LOCALITY AND HORIZON: Dacqué (1912) gave the locality at first in reference to a shell: ''Unteroligocäne Fluviomarinestuffe nördlich der Birket Qerun; nordlich non Tamieh; ostlich vom Schweinforthplateau. Schädel: aus derselben stufe bei Dimêh. Alles Fayum'' (Dacqué, 1912: 310). Williams (1954; repeated in Gaffney, 1979) has the locality as ''Diieh'', which seems to be a misspelling of ''Dimêh''. The reference to the skull ''from the same sediment near Dimêh'' presumably means the Qasr el Sagha or Birket Qarun formations of late Eocene age.

REFERRED MATERIAL: DPC 5986, partial skull lacking anterior part of palate and some of left side (figs. 4 and 5). Field no. 86–292, collected by Alex van Nievelt. Measurements in table 1.

LOCALITY AND HORIZON: B-4 (lower Jebel Qatrani, ¼ mile southeast of A). AMNH quarry B area, Eocene (Gagnon, 1997: fig. 1; Kappelman et al., 1992).

DISCUSSION: The type specimen, housed in the Staatliches Musuem für Naturkunde, Stuttgart, was presumably part of a collection obtained from German geologist and private collector Richard Markgraf who lived in Egypt and made extensive collections in the Fayum region during the early 20th century. During this early period of collecting in the Fayum, locality information was typically vague and lacked attention to precise stratigraphic level (Simons, 1968; Simons and Rasmussen, 1990). The locality given in Dacqué (1912) first in reference to the shell and then the skull is ''Unteroligocäne Fluviomarinestuffe nördlich der Birket Qarun; nördlich non Tamieh; ostlich vom Schweinforthplateau. Schädal: aus derselben stufe bei Dimêh. Alles Fayum'' (Dacqué 1912: 310), which we translate as ''Early Oligocene fluviomarine sediment north of Birket Qarun; north of Tamieh; east of the Schweinfurth Plateau. Skull from the same level near Dimêh. All specimens being from the Fayum area''. The beginning of this entry is similar to that typically given for fossils found in the Jebel Qatrani Formation during this period, which are ''north of Birket Qarun'' or ''fluviomarine series north of Birket Qarun'' (Simons, 1968). Birket Qarun is the name of the large lake in the north of the Fayum depression. The reference to early Oligocene is also consistent with the Jebel Qatrani Formation, which was thought to be late Eocene by the earliest workers (i.e., Beadnell, 1905; Andrews, 1906) but by the time of Dacqué's study was interpreted to be early Oligocene (Stromer, 1907; Osborn, 1908), with the underlying Qasr el Sagha Formation considered to be late Eocene. The reference to the skull ''from the same sediments near Dimêh'' is more difficult to interpret. Dimêh refers to the ruins of a Greco-Roman temple and settlement located on the north shore of Birket Qarun. It is possible that this reference indicates information given by the collector to more accurately place the locality of this specimen, or it may be a general reference to the region north of Birket Qarun. The sediments surrounding Dimêh include those of the Umm Rigl Member of the Qasr el Sagha Formation (Gingerich, 1992) and of the underlying Birket Qarun Formation, both covered in part by Pleistocene and Holocene lake deposits from the once more extensive

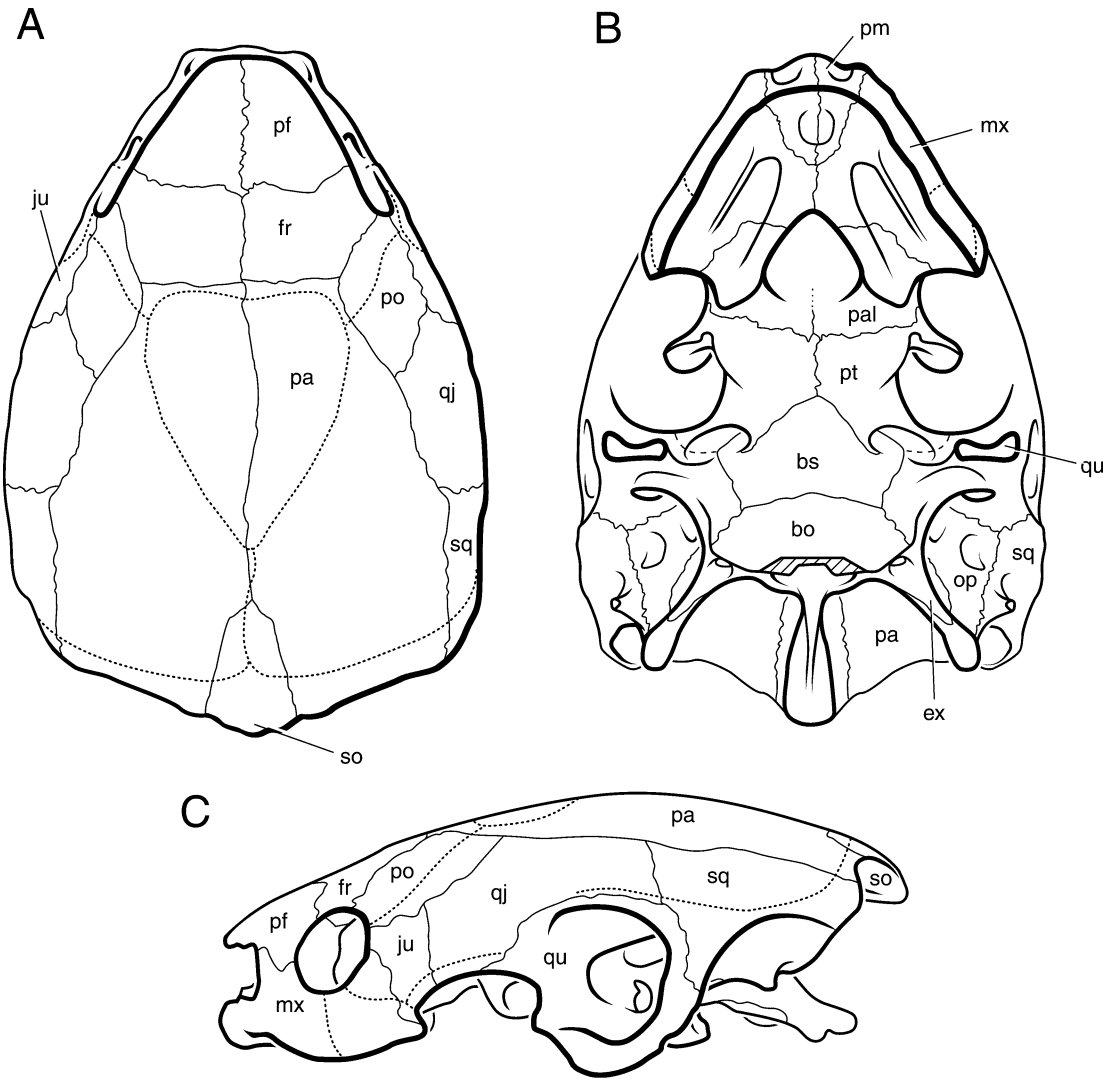

Fig. 1. *Dacquemys paleomorpha*, late Eocene, Fayum, Egypt, restorations based on SMNS 12645 and DPC 5986. **A,** Dorsal; **B,** ventral; **C,** lateral. Dotted lines indicate scale margins.

Birket Qarun (Bown and Kraus, 1988). The age and nature of the contact between these formations in the area around Dimêh are presently being investigated, but both marine and continental vertebrate remains are found in these sediments. This, along with the faunal continuity that is a general feature of the Fayum sequence (Rasmussen et al., 1992), makes it entirely possible that the type specimen of *Dacquemys* was collected from either the Qasr el Sagha or Birket Qarun formations. It is possible that the reference to ''east of Schweinfurth Plateau'' may indicate these lower sediments. We are not aware of the location of this plateau but the Qasr el Sagha temple was known as Schweinfurth's Temple, so it may be that his ''plateau'' is located near the temple. Schweinfurth is known to have worked primarily in the area around Birket Qarun. At present, the Qasr el Sagha Formation is generally thought to be late Eocene (Priabonian) in age (Bown and Kraus, 1988; Gingerich, 1992) with the possibility that the lower part of the Qasr el Sag-

TABLE 1
Measurements of *Dacquemys* Skulls

	SMNS 12645	DPC 5986
A. Midline length as preserved	73.2[a]	79.4[a]
B. Maximum width	67.3	76.8[a]
C. Width between orbits	28.8	34.0
D1. Width of left orbit	14.2	—
D2. Width of right orbit	14.2[b]	16.0
E. Width of external nares	19.0	—
F. Width of internal nares	13.7	—
G. Maximum height at quadrate	38.2	—
H. Maximum width of skull taken at middle of orbits	33.7	34.0[b]
I. Length, anterior margin of prefrontals to posterior margin of parietals	98.8	100.1
J1. Height of left orbit	13.5	—
J2. Height of right orbit	12.3	—
K. Skull height at occipital condyle	33.5	27.3[b]
L. Anterior width of triturating surface	15.2	—
M. Posterior width of triturating surface	14.9	—
N. Width of palate across foramina palatinum posterius	23.9[b]	29.9
O. Length, front of skull to posterior edge of condylus articularis	53.6	—

[a]Estimated.
[b]Damaged.

ha along with the Birket Qarun Formation are close to the middle Eocenelate Eocene (Bartonian-Priabonian) boundary (Holroyd et al., 1996). Because the only other known specimen of *Dacquemys* was collected from the lower sequence of the Jebel Qatrani Formation, and it is difficult to know how much credence should be given to the reference to Dimêh, the assignment of this specimen to one of these earlier formations must remain tentative until further specimens are recovered.

The second specimen of *Dacquemys* (DPC 5986) was collected by a Duke University expedition from AMNH Quarry B (B-4). Quarry B is located in the middle gravelly sandstone unit of the lower sequence of the Jebel Qatrani Formation (the lower fossil wood zone of early authors) from which many of the specimens collected by the American Museum of Natural History, with the help of Richard Markgraf, were obtained (Bown and Kraus, 1988). These sediments represent the second of four faunal zones that are recognized in the Jebel Qatrani Formation (Rasmussen and Simons, 1991; Gagnon, 1997). Quarry B is thought to lie just below the EoceneOligocene boundary (Kappleman et al., 1992; Rasmussen et al., 1992; Simons and Chatrath, 1998), although the lack of substantial faunal turnover across this boundary in the Fayum region led to some debate as to the exact placement of this boundary (Gingerich, 1992; Van Couvering and Harris, 1991).

DESCRIPTION

PREFRONTAL

Both prefrontals are preserved on both sides of SMNS 12645 and DPC 5986, although its ventral process is complete only on the left side of SMNS 12645. The prefrontal of *Dacquemys* is similar to that in *Podocnemis* except for its much larger size, being longer and wider. *Erymnochelys* and *Peltocephalus* have wider prefrontals than does *Podocnemis*, but not as wide as in *Dacquemys*. The anterior projection of the prefrontal extends to the anterior margin of the apertura narium externa, not posterior to it as in *Podocnemis*.

FRONTAL

Both frontals are preserved in SMNS 12645 and DPC 5986. Their ventral surface is visible in DPC 5986. The frontal in *Dacquemys* has the same contacts as in the living podocnemidids, but it differs in its greater width. The orbits are visible in dorsal view in *Podocnemis*, *Erymnochelys*, and *Peltocephalus* but not in *Dacquemys*. In ventral view, *Dacquemys* has a much more extensive roof to the fossa orbitalis than in the living genera. The sulcus olfactorius and fossa nasalis are about the same size in the living genera and *Dacquemys*, but the roof of the fossa orbitalis is more extensive in *Dacquemys*, due mostly to the lateral extension of the frontal, although both the prefrontal and postorbital contribute to this.

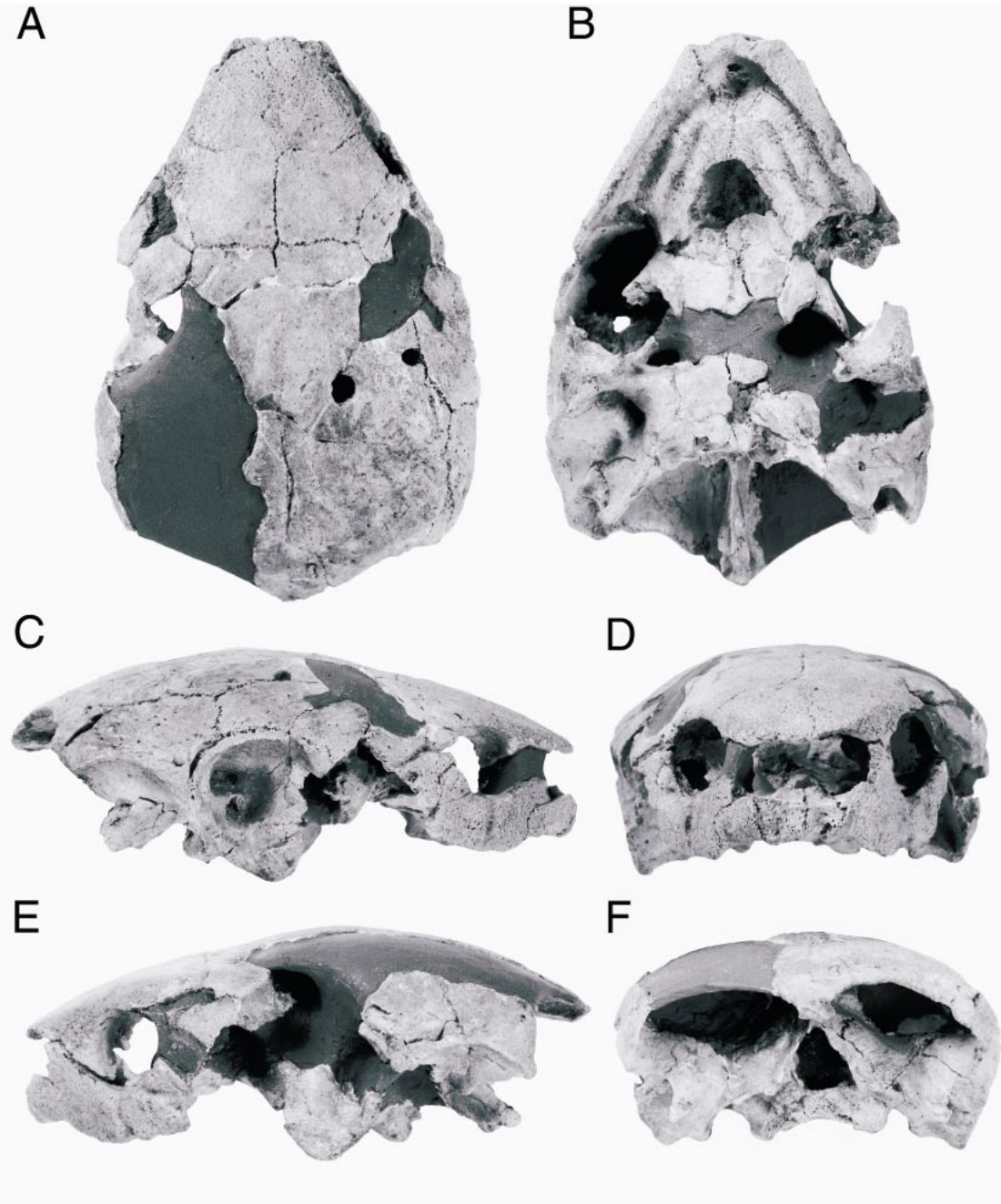

Fig. 2. *Dacquemys paleomorpha*, SMNS 12645, holotype, probably Jebel Qatrani Formation, Fayum, Egypt. **A,** Dorsal; **B,** ventral; **C,** right lateral; **D,** anterior; **E,** left lateral; **F,** posterior. See figure 3 for key.

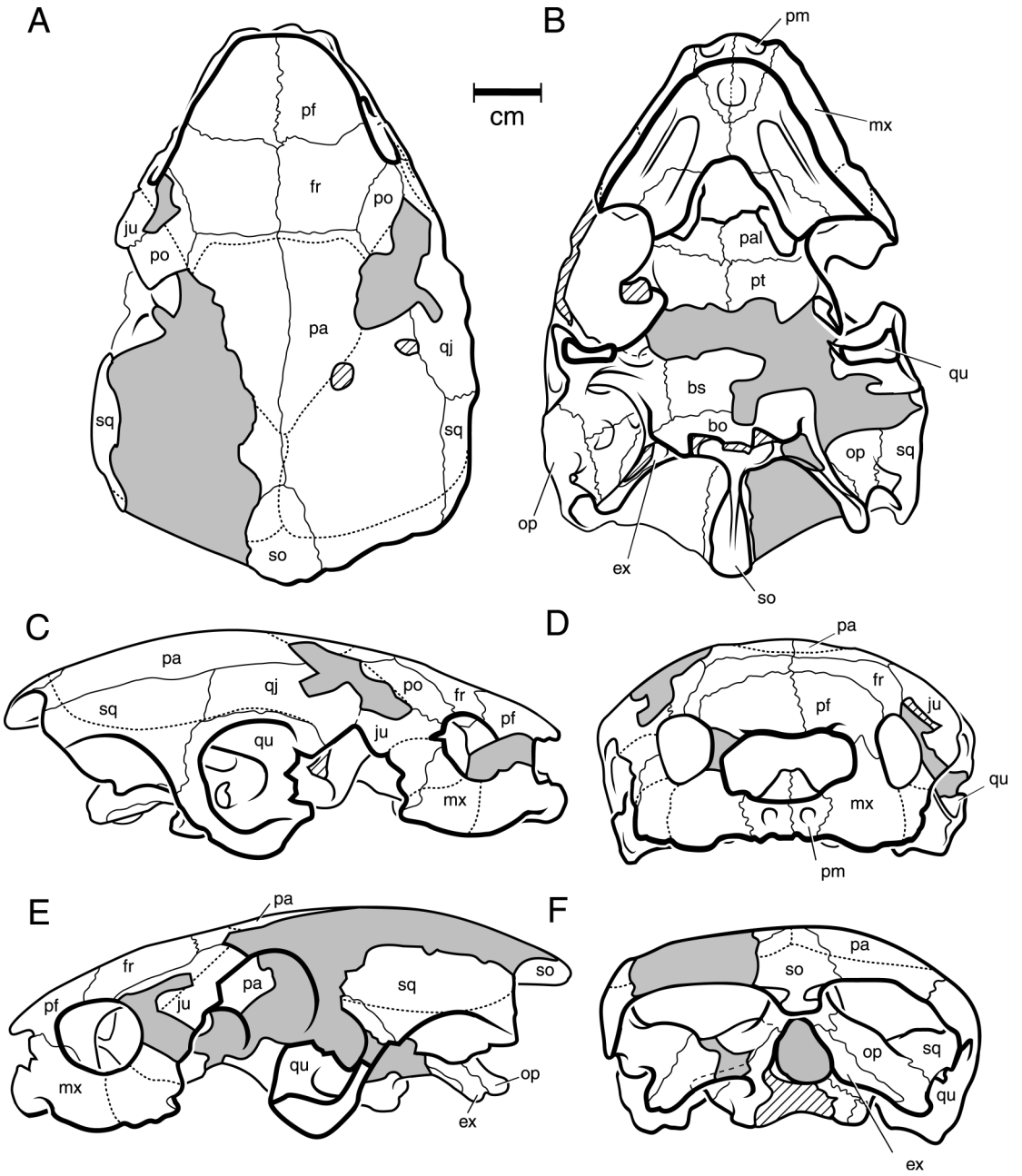

Fig. 3. *Dacquemys paleomorpha*, SMNS 12645. Key to figure 2. Dotted lines indicate scale margins, shaded areas are plaster, and hatched areas are broken edges.

PARIETAL

Most of the right parietal is preserved in SMNS 12645, and all of the right and most of the left are present in DPC 5986. As in the living genera, the parietal in *Dacquemys* contacts the frontal anteriorly, the postorbital anterolaterally, and the quadratojugal laterally. In *Podocnemis* there is a jugal-parietal contact that is absent in *Peltocephalus* and *Erymnochelys*, as well as in *Dacquemys*. In

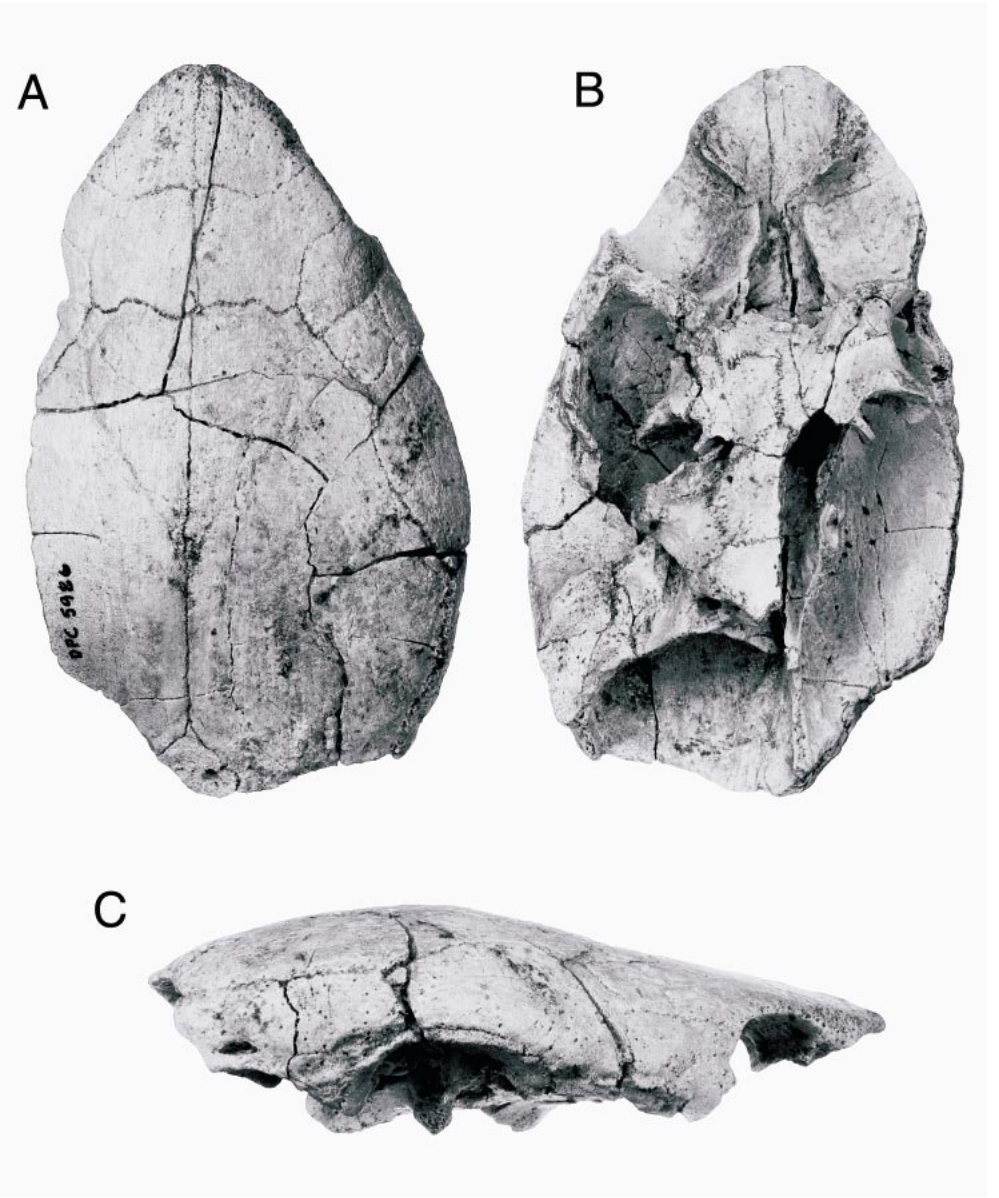

Fig. 4. *Dacquemys paleomorpha*, DPC 5986, Jebel Qatrani Formation, Fayum, Egypt. **A,** Dorsal; **B,** ventral; **C,** right lateral. See figure 5 for key.

Dacquemys, however, there is a broad parietal-squamosal contact not seen in other podocnemidids. The parietal extends posteriorly to a greater extent than in any other described podocnemidid, completely covering the otic chamber. Posteromedially the parietal contacts an expanded supraoccipital when compared with *Erymnochelys* and *Peltocephalus*, which are more roofed than is *Podocnemis*. *Dacquemys* has a posterolaterally expanded parietal which results in contact to the squamosal.

The processus inferior parietalis is not well preserved in either *Dacquemys* specimen, but it is best seen on the right side of DPC 5986. The processus contacts the supraoccipital pos-

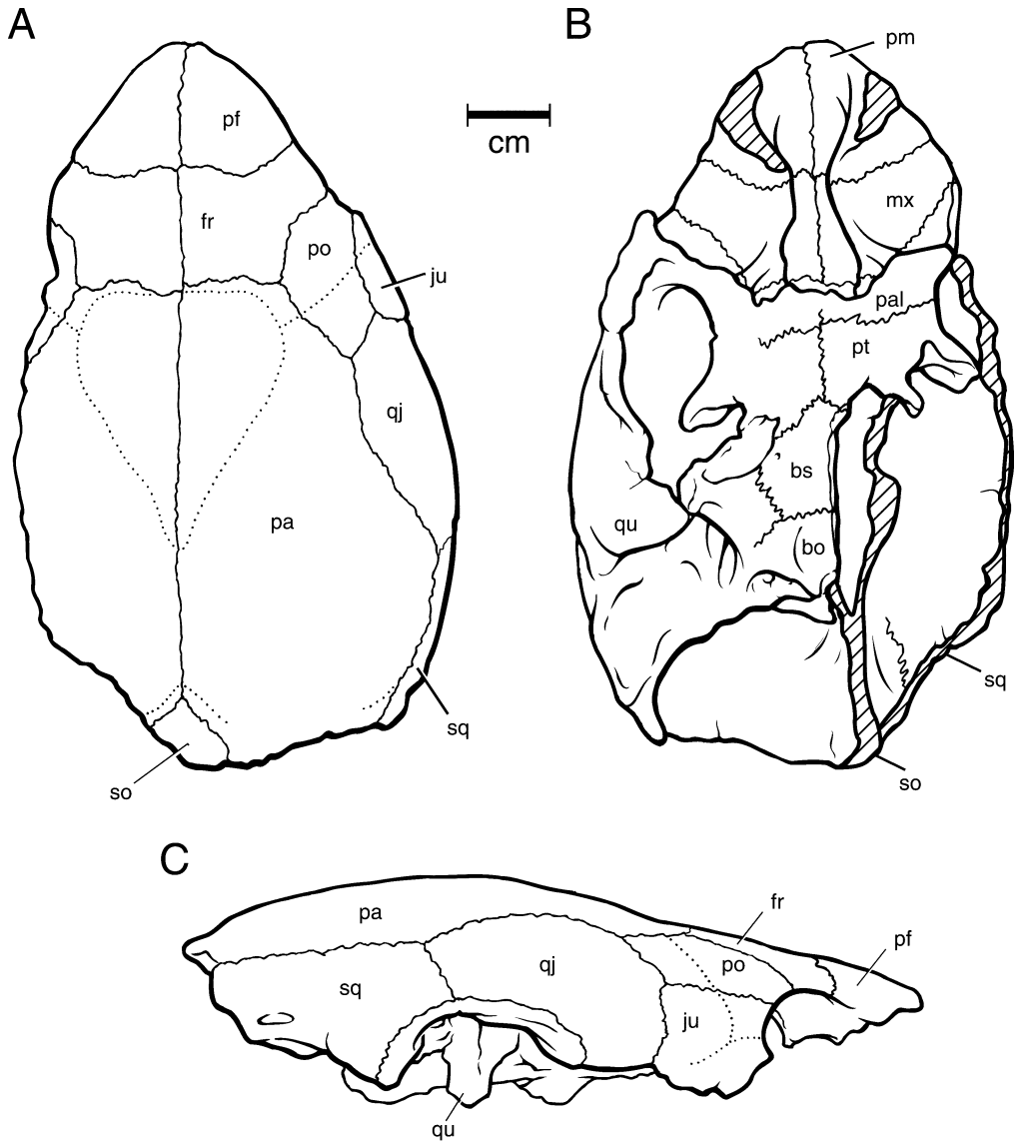

Fig. 5. *Dacquemys paleomorpha*, DPC 5986. Key to figure 4. Dotted lines indicate scale margins, hatched areas are broken edges.

teriorly and the prootic posteroventrally, and probably the pterygoid ventrally, all as in the recent podocnemidids. The more anterior contacts and the formation of the foramen nervi trigemini are not preserved.

JUGAL

The jugal is preserved in part in both skulls, but neither shows the internal relations of the bone clearly. The lateral plate of the jugal enters the orbit anteriorly, contacts the maxilla anteroventrally, the postorbital anterodorsally, and the quadratojugal posteriorly. Ventrally the jugal forms the anterior part of the shallow cheek emargination. The degree of cheek emargination in *Dacquemys* is far greater than in *Erymnochelys* and *Peltocephalus*, but less than in *Podocnemis* and *Hamadachelys*. It is most comparable to *Neochelys* and *Bauruemys*.

The jugal in *Dacquemys* is small in comparison to the much larger jugal of *Erymnochelys* and *Peltocephalus*, in which the jugal extends posteriorly to meet the quadrate, and the cheek emargination is quite reduced. The medial process of the jugal is present in SMNS 12645, but its contacts are not clearly visible. As in the living podocnemidids, the jugal does not appear to form any of the triturating surfaces.

Quadratojugal

A nearly complete right quadratojugal is preserved in DPC 5986 and a partial one is present on the right side of SMNS 12645. In *Dacquemys*, the quadratojugal contacts the parietal medially, the squamosal posteriorly, the quadrate laterally, the postorbital anterodorsally, and the jugal anteroventrally. The quadratojugal forms the dorsalmost part of the margin of the cheek emargination.

Squamosal

The right squamosal is nearly complete in DPC 5986, and in SMNS 12645 the bone is complete on the right side and partial on the left. In *Dacquemys* the squamosal has a long medial contact with the parietal that is absent in all other described podocnemidids, and an anterior contact with the quadratojugal that is comparable in size to the contact seen in *Peltocephalus* and wider than in *Podocnemis*. Medially the squamosal contacts the opisthotic and anteromedially the quadrate, as in other podocnemidids. The squamosal forms part of the antrum postoticum (see Quadrate). The posterior margin of the squamosal in podocnemidids is a flange oriented dorsolaterally to ventromedially and reaching the opisthotic. In most podocnemidids this flange is a continuous sheet, but in SMNS 12645 (it is absent in DPC 5986) the sheet, as seen on the right side, curves anteriorly before reaching the opisthotic.

Postorbital

The postorbital is present but incomplete on both sides of SMNS 12645, and is complete on the right side of DPC 5986. The postorbital of *Dacquemys* is not reduced as in *Podocnemis* and has the shape and contacts seen in most other podocnemidids, such as *Neochelys*. The postorbital enters the posterodorsal margin of the orbit as in the other podocnemidids. The medial process of the postorbital is visible in DPC 5986 and contacts the frontal dorsomedially, the jugal ventrolaterally, and the palatine ventromedially.

Premaxilla

Both premaxillae are preserved in SMNS 12645, but neither is present in DPC 5986.

The premaxilla of *Dacquemys* contacts the maxilla laterally and the other premaxilla medially. There is no vomer contact, as that bone is absent and the maxillae meet on the midline behind the premaxillae as in *Podocnemis*. *Dacquemys* is unique among Pelomedusoides because the premaxillae are recessed and not visible laterally. There is a shallow, anteroventral trough on the anterior surface of each premaxilla, another feature found only in *Dacquemys*. As far as can be determined, the foramen praepalatinum is absent. The midline concavity on the triturating surface in *Dacquemys* is very deep, deeper than in *Peltocephalus*, and much deeper than in *Podocnemis* and *Erymnochelys*.

Maxilla

Both maxillae are preserved in SMNS 12645, and both are absent in DPC 5986.

The vertical plate of the maxilla in *Dacquemys* is shallower than in *Podocnemis* and *Bauruemys* and is comparable to *Peltocephalus* and *Erymnochelys*. The contacts are as in the living podocnemidids. The horizontal plate of the maxilla in *Dacquemys* has the same contacts as in *Podocnemis expansa*: premaxilla anteromedially, other maxilla on midline, palatine posteromedially, and jugal posterolaterally. The midline maxilla contact is more extensive than in *Podocnemis expansa* and *Podocnemis unifilis*, the only other Pelomedusoides that have this character.

The triturating surface of *Dacquemys* is characterized by two well-developed accessory ridges parallel to the lingual and labial ridges. Similar accessory ridges occur in some species of *Podocnemis* (*expansa*, *unifilis*, *lewyana*, *vogli*), but only in *Dacquemys* are they curved anteriorly to join each other close to the premaxilla-maxilla border.

VOMER

Although the anterior edges of the palatines are broken in both *Dacquemys* specimens, enough of their morphology is preserved, along with the posterior edge of the maxillae, to show that a vomer is absent.

PALATINE

Most of both palatines are preserved in SMNS 12645, but in DPC 5986 only the posterior portions of the palatines are present.

The contacts of the palatine in *Dacquemys* are as in *Podocnemis* except for *P. vogli*, which has a ''vomer'', interpreted here as a neomorphic ossification, probably part of the palatine. As the anterior margins of both palatines in *Dacquemys* are broken edges, the presence of an anterior process as seen in *Podocnemis* cannot be determined. The area of the foramen palatinum posterius is damaged on both sides, but enough can be seen to show that one was present. As in the living podocnemidids, the palatine contributes to the triturating surface, but not to the extent seen in the *Shweboemys* group.

QUADRATE

Nearly all of the right quadrate is preserved and visible in SMNS 12645, which also has part of the left one. Only the dorsal portion of the right quadrate is present in DPC 5986.

The quadrate in *Dacquemys* is similar in size, shape, and contacts to that in *Podocnemis*. The antrum postoticum, which varies in the Podocnemididae, is about the same size in *Dacquemys* and *Podocnemis expansa*, smaller than in *Peltocephalus*. The precolumellar fossa, a distinct concavity in such forms as *Podocnemis unifilis*, is only a shallow dimple in *Dacquemys*, but not absent as in *Stereogenys*. The incisura columellae auris of *Dacquemys* is preserved on the right side of SMNS 12645. Although a small part of the edge is eroded anteroventrally, the opening is oval rather than slightly L-shaped as in *Podocnemis*.

The medial contacts of the quadrate in *Dacquemys* are as in *Podocnemis*. The right side of SMNS 12645 shows these features, and the right side of DPC 5986 has the upper portions of the incisura columellae auris and fenestra postotica visible. The quadrate forms the dorsal portion of the cavum pterygoideus in *Dacquemys*, as in all other Podocnemididae.

PTERYGOID

The pterygoid is present but incomplete in both *Dacquemys* specimens, but all of its ventral morphology can be determined.

In ventral view the contacts are with the palatine anteriorly, the other pterygoid medially, the basisphenoid posteromedially, and the quadrate posterolaterally, all as in the living podocnemidids. Due to the postorbital-palatine contact in the postorbital wall, there is no pterygoid-jugal contact as found in the living podocnemidids. The processus trochlearis pterygoidei is preserved on both sides of both specimens, but the left processus of DPC 5986 is best preserved. Its size is about the same as in the living podocnemidids. It is oriented slightly more posteriorly than in *Podocnemis expansa* and slightly more anteriorly than in *Peltocephalus*. The quadrate ramus is not well preserved in either specimen, but from the right side of SMNS 12645, it looks very similar to *Podocnemis expansa*. The cavum pterygoidei (enlarged ''carotid'' chamber) is also not well preserved in either skull; although its presence can be seen in both, its internal morphology is obscured by breakage. Its posterior part, seen on the right side of DPC 5986, seems to be about the same size as in the living podocnemidids, but its anterior size and limits are not preserved. The foramina and sutures within the anterior end of the cavum pterygoidei are also not determinable. Although the pterygoid flange itself is not preserved in either specimen, its base is visible in DPC 5986 on the right side. The foramen posterius canalis carotici interni is not preserved in either skull.

The dorsal surface of the pterygoid is mostly missing or obscured by breakage in both specimens. The anterolateral contact with the postorbital and dorsal contact with the parietal are visible on the left side of DPC 5986, but prootic contact is not visible.

The crista pterygoidea is collapsed and telescoped in DPC 5986, making the sulcus palatinopterygoideus only partially pre-

served. In SMNS 12645 the sulcus is completely obscured by plaster and matrix.

Supraoccipital

The supraoccipital is preserved in both specimens. It is nearly complete in DPC 5986, but broken on the right; its internal surfaces are completely visible. The crista supraoccipitalis is broken ventrally. In SMNS 12645 the supraoccipital seems to be complete.

In *Dacquemys*, the supraoccipital has a dorsal plate that is wider than in other podocnemidids. It partially separates the parietals along the midline posteriorly. Its other contacts are as in *Podocnemis*. The crista supraoccipitalis of *Dacquemys* extends posteriorly from the foramen magnum about as far as in *Podocnemis*. But the crista in *Dacquemys* is not visible in dorsal view because the parietals extend posteriorly to cover the temporal region.

Exoccipital

The dorsal parts of the exoccipitals are preserved in SMNS 12645. DPC 5986 preserves most of the right exoccipital, but the condylus occipitalis is missing in both specimens.

The exoccipital as preserved in *Dacquemys* is very similar to that bone in *Podocnemis*. It forms the lateral part of the foramen magnum, lying against the supraoccipital and opisthotic. The exoccipitals do not meet on the midline above the foramen. Ventrally, as seen in DPC 5986, the exoccipital forms two foramina nervi hypoglossi and the dorsal part of the closed foramen jugulare posterius. The ventral part of the exoccipital contacts the basioccipital in a broad suture as in the living podocnemidids.

Although the condylus occipitalis is broken off in both *Dacquemys* specimens, in DPC 5986 the basioccipital and exoccipital are preserved at the base of the condyle. Based on the large amount of basioccipital entering the condyle at this point, it is likely that the basioccipital is present posteriorly and the condyle is not made up solely of exoccipital, as in *Erymnochelys*.

Basioccipital

Portions of the basioccipital are preserved in both skulls, but both lack the condylus occipitalis.

In *Dacquemys* the basioccipital contacts the basisphenoid anteriorly, the quadrate anterolaterally, the exoccipitals dorsally, and the opisthotic posterodorsally, all as in *Podocnemis*. The strong opisthotic-quadrate contact forms a bar separating the basioccipital and foramen jugulare posterius from the fenestra postotica. This is the condition in *Erymnochelys*, *Peltocephalus*, and most *Podocnemis* we have seen, although in some *Podocnemis expansa* the basioccipital barely enters the fenestra postotica.

The basisphenoid has paired tubercula basioccipitale that in *Dacquemys* are distinct but relatively short as in *Erymnochelys* and *Peltocephalus*, not elongate as in *Podocnemis*. This elongation is associated with a horizontal shelf below the foramina hypoglossi in *Podocnemis* that is absent in *Dacquemys* and the other living podocnemidids.

Prootic

A portion of the right prootic is preserved in SMNS 12645, and most of the right prootic is present in DPC 5986, but its medial margins are damaged.

As in the living podocnemidids, the prootic of *Dacquemys* does not contain the foramen posterius canalis carotici interni and is exposed ventrally only in the roof of the cavum pterygoideus. The prootic of *Dacquemys* contacts the parietal medially, the quadrate laterally, the supraoccipital posterodorsally, and the pterygoid ventrally. The foramen nervi trigemini is not preserved in either skull, but the foramen stapedio-temporale can be seen on the right side of DPC 5986. The internal features of the prootic are not visible.

Opisthotic

The opisthotic is preserved on the right side of DPC 5986 and in part on both sides of SMNS 12645.

The opisthotic in *Dacquemys* has the same contacts as in *Podocnemis*. There is a distinct groove on the ventral surface of the opis-

TABLE 2
***Dacquemys* Compared with Other Podocnemididae**

	Dacquemys	*Podocnemis*	*Erymnochelys*	*Peltocephalus*	*Bauruemys*	*Neochelys*
Anterior overhang of prefrontal onto apertura narium externa	reaches anterior margin	well posterior to anterior margin	reaches anterior margin	reaches anterior margin	well posterior to anterior margin	reaches anterior margin
Prefrontal width	wide	very narrow	narrow	narrow	very narrow	narrow
Interorbital distance	very wide	narrow	wide	wide	narrow	wide
Temporal emargination	otic chamber covered	otic chamber exposed	otic chamber exposed	otic chamber exposed	otic chamber exposed	otic chamber exposed
Parietal extended posterolaterally to reach or nearly reach squamosal	yes	no	yes	yes	no	yes
Broad parietal-squamosal contact	yes	no	no	no	no	no
Premaxilla recessed with anteroventral trough	yes	no	no	no	no	no
Foramen praepalatinum	absent	present	present	absent	present	present
Midline concavity formed by premaxillae	deep	shallow	shallow	deep	shallow	shallow
Maxillae meet broadly behind premaxillae	yes	yes and no	no	no	no	no
Two accessory maxillary ridges	yes	yes	no	no	no	no
Vomer	absent	absent	absent	absent	present	absent
Precolumellar fossa	shallow	deep to shallow	deep	deep	absent	shallow
Pterygoid-jugal contact	no	yes	yes	yes	?	?
Supraoccipital skull roof exposure	large	small	small	small	small	small
Tuberculum basioccipitale	short	long	intermediate	intermediate	short	short
Foramen anterius canalis carotici interni	small	large	small	small	small	small
Foramen nervi abducentis	small	large	small	small	small	indeterminate
Jugal-quadrate contact	absent	absent	present	present	absent	absent

thotic leading into the fenestra postotica that is presumably for the stapedial artery as it seems to be trending toward the poorly preserved aditus canalis stapedio-temporalis. The posterolateral process of the opisthotic is about as extensive in *Dacquemys* as it is in *Podocnemis*.

Basisphenoid

The basisphenoid is preserved in part in both skulls of *Dacquemys*. Some of its dorsal surface can be seen in DPC 5986.

The basisphenoid in *Dacquemys* has the same contacts as in *Podocnemis*. As in the living podocnemidids, it forms the lateral margin of the cavum pterygoidei. Internally the formation of the cavum is obscured in both specimens, but the posterior part of the cavum pterygoidei is as extensive in *Dacquemys* as it is in *Podocnemis*. The dorsal surface of the basisphenoid is preserved in DPC 5986 and it shows the sella turcica, dorsum sellae, processus clinoideus, and foramen anterius canalis carotici interni. The latter foramen is relatively small as in *Erymnochelys*, not large as in *Podocnemis*. Although the foramen nervi abducentis cannot be seen, it is not possible that it was large as in *Podocnemis* because the area in which it occurs is preserved in DPC 5986.

SUMMARY

This paper redescribes the type skull and describes a new skull of *Dacquemys paleomorpha* and compares this genus with the living podocnemidids (table 2). Phylogenetic analyses are intended for a later paper. As concluded by both Dacqué (1912) and Williams (1954), *Dacquemys* is a podocnemidid because it has a well-developed cavum pterygoideus. A broad parietal expansion meeting a wide supraoccipital completely covers the skull roof in contrast to all other podocnemidids. The vomer is absent, as in *Podocnemis* (the ''vomer'' appearing in some recent species of *Podocnemis* is interpreted as a neomorph), *Erymnochelys*, *Peltocephalus*, and *Neochelys*, but in contrast to *Bauruemys*. *Dacquemys* lacks the jugal- quadrate contact found only in *Erymnochelys* and *Peltocephalus*. It also lacks the secondary palate seen in *Shweboemys* and *Stereogenys*, but it does have two accessory ridges on the trituratingsurface as in *Podocnemis*. A unique feature of *Dacquemys* is that the ridges join anteriorly to form an enclosed trough.

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