

B R E V I O R A

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NEW OR REDESCRIBED PELOMEDUSID SKULLS FROM THE TERTIARY OF AFRICA AND ASIA (TESTUDINES, PELOMEDUSIDAE)

2. A *Podocnemis* Skull from the Miocene of Moghara, Egypt.

BY ERNEST WILLIAMS

In 1952-1953 while visiting the British Museum (Natural History) as a Guggenheim Fellow I was privileged to examine an undescribed skull from the Moghara Miocene of Egypt. The skull evidently belonged to a member of the genus *Podocnemis sensu lato* or to a close relative of that genus; the critical recognition marks of this section of the Pelomedusidae — the enlarged "carotid" channel, and the contact of basioccipital and quadrate — were readily visible. Further examination left no doubt of the novelty of this fossil as compared with any previously known podocnemide¹ skull, and suggested interesting problems in regard to its proper correlation with a shell name and in regard to its phyletic position.

The British Museum Moghara skull is unfortunately imperfect in many respects. The snout is missing so that important characters and relations here cannot be checked. Major parts of the postorbitals and jugals are broken away, as are both squamosals, the quadrate of one side, parts of the parietals and the occipital condyle.

Many structural details of taxonomic and phyletic importance are therefore not ascertainable: the presence or absence of a complete temporal roof, the presence or absence of a vomer, the position of the foramina incisiva, the relations of the internal laminae of the premaxillae and maxillae to each other and to

¹I use the term "podocnemide" as a convenient and *informal* designation for a subsection of the family Pelomedusidae typified by the genus *Podocnemis*.

the choanal margin, the presence or absence of an anterior process of the palatines dividing the choanal opening, the presence or absence of a median pit in the palatal surface of the premaxillae and of a hooked process anteriorly on the premaxillae.

The following points may, however, be made out: The skull must have been rather broad, certainly very little longer than broad. The interparietal scale marked off by grooves on the skull roof is broad also, but tapers posteriorly, so that the parietal scales must have met behind it. There is no hint of a forehead groove but perhaps too little of the interorbital region is preserved. The orbits are visible in dorsal view.

There were two triturating ridges on the posterior portion of the palatal surface of the maxilla — a low, rough, median ridge and, parallel to it, a still lower, rougher, ridge at the margin of the choanae. There was no extreme development of a secondary palate.

Grooves on the postorbital bar indicate the presence of a "subocular" scute in the sense of Siebenrock (1902).

The "carotid" channel is fully enlarged in podocnemide fashion.

The ectopterygoid processes are large, blunt and almost wholly lateral in orientation. The basisphenoid is a conspicuous triangular element, the anterior apex blunted. There is a narrow basioccipital quadrate contact, more longitudinal than transverse.

The cavum tympani is large and lacks a precolumellar fossa.

These determinable characters are few indeed on which to hazard an estimate of the relationships of the Moghara form. One method of appraisal, however, is to tabulate the more diagnostic of these characters against the characters of other known podocnemide skulls. Tabulating first against the living podocnemide species (Table 1), we find that very little is learned except that the British Museum Moghara skull is not exactly like that of any modern podocnemide. If, now, we compare the British Museum Moghara skull with the previously known fossil skulls of podocnemide type (Table 2), the impressive fact is the close agreement, in cited characters, of the British Museum skull and *Dacquemys paleomorpha*. We need in fact to inquire what characters assure us that we are not dealing with *Dacquemys*.

TABLE 1

	<i>unifilis vogli leiyana</i>	<i>Podocnemis sensu stricto</i> <i>expansa</i>	<i>sertuberculata</i>	<i>Erymnochelys madagascariensis</i>	<i>Peltocephalus dumeriliana</i>
Moghara skull					
a broad skull	no	yes	yes	yes	no
parietal scales meeting behind interparietal forehead groove absent	yes	usually yes	no	yes	no
orbits visible from above	no	no	no	yes	yes
two parallel ridges on maxilla	yes	yes	yes	yes	no
extreme secondary palate absent	yes	no	no	no	no
subocular scales present	yes	yes	yes	yes	yes
narrow basioccipital- quadrate contact	yes	usually no	yes	yes or no	no
precolumellar fossa absent	yes	no	yes	yes	yes
	no	yes	yes	no	no

TABLE 2

	<i>Stereogenys cromeri</i>	<i>Shueboemys pilgrimi</i>	<i>Dacquemys paleomorphia</i>
Moghara skull	yes	yes	no
a broad skull	?	?	yes
parietal scales meeting behind interparietal	yes	yes	yes
forehead groove absent	yes	yes	no
orbits visible from above	no	no	yes
two parallel ridges on maxilla	no	no	yes
extreme secondary palate absent	no	no	yes
subocular scales present	no	no	yes
narrow basioccipital- quadrate contact	?	?	yes
precolumellar fossa absent	yes	yes	yes

It is unfortunate that the unique generic character of *Dacquemys* — the long squamosal-parietal suture — cannot be verified or denied for the Moghara specimen. This region has been broken away.

There are, however, differences which may or may not imply generic distinctness. The British Museum skull is broad; that of *Dacquemys* is elongate. The orbits are visible dorsally in the Miocene specimen; they are completely concealed in Oligocene *Dacquemys*. The two triturating ridges are low and rough in the Moghara specimen, the inner parachoanal ridge especially so; the same ridges are high, smooth and sharply defined in *Dacquemys*.

The suggestive point about these differences is the fact that in each case the Moghara skull is closer in these characters to *Erymnochelys* (= *Podocnemis madagascarensis* of Boulenger) than to *Dacquemys*. The skull of *Erymnochelys madagascarensis* is relatively broad, the orbits are exposed dorsally, there is but one low ridge on the triturating surface of the maxilla. But in regard to the last character there is some roughening of the parachoanal border of the maxilla in *Erymnochelys*; the condition in that genus could be explained as a further carrying through of a trend initiated in the British Museum skull. In fact the British Museum skull might on all its characters be interpreted as an intermediate between *Dacquemys* and *Erymnochelys*, perhaps somewhat closer to *Erymnochelys*.

If we assume the reality of this intermediate phyletic station of the British Museum Moghara skull, it is then probable that this skull belongs with the common podocnemide shell of the Moghara deposit, the shell type named by Andrews *Podocnemis aegyptiaca*, which has every shell character of *Erymnochelys* and is on shell characters barely, if at all, distinguishable from *Erymnochelys madagascarensis*. I shall hereafter refer to *Podocnemis aegyptiaca* Andrews as *Erymnochelys aegyptiaca* (Andrews).

There is only one other podocnemide shell type known from Moghara — the form named by Fourtau (1920) "*Podocnemis*" *bramlyi*. This form differs from *Erymnochelys aegyptiaca* and from all *Erymnochelys* in the larger size of the intergular scale which separates the gulars as in the Recent South American

podocnemide species (*Podocnemis sensu stricto* and most specimens of *Peltocephalus*). If we could assume that *P. bramlyi* is a precursor of *Peltocephalus* then it would not be too anomalous for our Moghara skull to belong to this species, rather than to *E. aegyptiaca*. In the living species *Peltocephalus dumeriliana* (in which the gular-intergular pattern is typically very similar to that of *P. bramlyi*) the skull has definite, strong similarity to that of *Erymnochelys* or of *Dacquemys* and thus also to the Moghara skull.

I know of no grounds for decision between the two alternatives thus presented. The British Museum skull may as plausibly belong to *P. bramlyi* as to *E. aegyptiaca*. We have too little of the Moghara skull, and in addition we are probably too close to the branching off point of *Peltocephalus* and *Erymnochelys* to expect wide differences in skull structure between these two, then nascent, genera. But, though we must thus remain undecided as to the species allocation of the Moghara skull, I think that one positive statement of some importance may be made. The Moghara skull — on whichever fork of the phyletic tree it belongs — is a structural intermediate between the Recent genera, *Peltocephalus* or *Erymnochelys*, and the Oligocene *Dacquemys*.

This, indeed, is the principal suggestion that I wish to make: that there is a phyletic relationship between *Peltocephalus*, *Erymnochelys* and *Dacquemys* of the sort diagrammed below (Fig. 1).

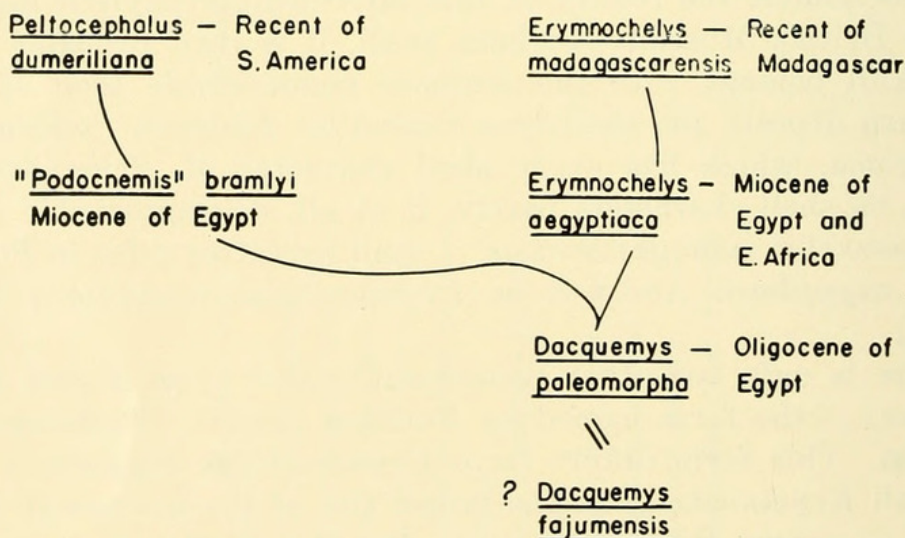


Fig. 1 Presumed phyletic position of the Egyptian Miocene podocnemides

It cannot be denied that this suggested phylogeny rests upon a rather elaborate structure of inferences, any or all of which may be wrong; nothing else, however, is possible in the current state of the evidence.

It may be useful, here, to compare this suggestion with the previous phyletic scheme for "*Podocnemis*" which was set up by Dacqué and has been accepted by Zangerl. The points of agreement will be found to be more numerous than at first seems the case. We are agreed that there are two lines within the pelomedusid species grouped as *Podocnemis* by Boulenger, Andrews and others — an African and a South American line. I differ with Dacqué, Zangerl and others in that I separate from the South American group the species *dumeriliana* (type of *Peltocephalus*) and regard the few resemblances of the latter species to the other South American forms — similarity in gular pattern and in cervical articulations — as convergent only. I further postulate a considerable evolution in skull structure within the line which we may still, for convenience, call African — an evolution involving so much morphological divergence that I recognize three genera within this lineage.

Of these two respects in which I differ with the Dacqué-Zangerl phylogeny, the recognition of African affinities in *Peltocephalus dumeriliana* is the more solidly founded. I shall argue this point at length in a future discussion of the rank, characters and variation of the living species placed by Boulenger in *Podocnemis*. The second conception — that of the *Dacquemys-Erymnochelys-Peltocephalus* series — is as yet hypothesis only, and the grounds for this view have been stated here.

It needs to be mentioned that Dacqué (1912) described another skull from Moghara which he named *Sternothaerus blanckenhorni*. The description is very brief and the only figure is a dorsal view. The skull was also quite imperfect, lacking the temporal and occipital regions.

If it belongs to *Sternothaerus* (= *Pelusios*) — an assignment neither contradicted nor specially supported by the figure — it has, of course, nothing to do with the skull which has here been described. However, in dorsal view there would be few differences in such imperfect fragments as these two skulls from Moghara; I think, nevertheless, that the interorbital width is greater in the skull which has been here discussed than in the

type of *blanckenhorni*. Beyond this, we must rely on Dacqué's description of differences, and his most significant remark appears to be his observation: "Bemerkenswert erscheint, dass die Maxillaria die Choane auf der Schädelunterseite offenbar ganz überdecken." This remark would appear to imply a strongly developed secondary palate, a striking difference from the skull here noticed; maxillary ridges are also unmentioned. It must be commented that a strong secondary palate would be remarkable also in the genus *Pelusios* and resembles more closely conditions in the *Stereogenys-Shweboemys* series (which will be discussed in the concluding paper of this series), but in any event "*Sternotherus*" *blanckenhorni* would appear to have no bearing on the problems raised by the skull in the British Museum.

I am indebted to Dr. W. E. Swinton for the privilege of examining and describing the British Museum skull from Moghara. The photographs of this specimen are published with the permission of the Trustees of the British Museum; they were made by Peter Green of the British Museum staff.

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