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Source: American Museum Novitates, 2009(3639) : 1-26

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/608.1

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3639, 26 pp., 7 figures, 1 table March 31, 2009

Caninemys, a New Side-Necked Turtle (Pelomedusoides: Podocnemididae) from the Miocene of Brazil

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ABSTRACT

A new genus and species of podocnemidid pleurodire, *Caninemys tridentata*, is described on the basis of a skull collected by L.I. Price in 1962 from the late Miocene of Acre, Brazil. It is unique among podocnemidids (and all other turtles) in having greatly inflated maxillae, each with a ventral, toothlike process. Along with a midline process of the premaxillae, these processes form a tridentate condition in the upper triturating surface, also unique among podocnemidids but comparable to the condition in the kinosternid *Claudius*. This skull has previously been identified as the shell-based genus *Stupendemys*, but there are no associations supporting this assignment. The type specimens are separated by over 2000 km, and other large podocnemidid taxa are known from this time and region. Although relatively large with a condylobasal skull length of about 17 cm, *Caninemys* was probably about half the size of *Stupendemys*. Phylogenetic analysis of 63 skeletal characters provides evidence that this new taxon nests within the family Podocnemididae as follows: (*Bauruemys* ("*Roxochelys*" (*Podocnemis* (*Caninemys* (*Dacquemys* ((*Erymnochelys*, *Peltocephalus*) (*Neochelys* (*Shweboemys*, *Stereogenys*)))))))).

INTRODUCTION

During the last 20 years there has been important progress in our understanding of the diversity of fossil side-necked turtles (see Gaffney et al., 2006 for summary). This activity has been precipitated largely by new efforts to examine both fossil and recent pleurodires, and by the discovery of high-quality fossil skull material. Many of these

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ISSN 0003-0082

fossils are not directly related to living side-necked turtles but represent completely extinct lineages. They are essential to our realization that pleurodires have a more complex history than previously thought. Others represent extinct taxa that are closely related to the few living lineages of side-necks. Together, they reveal a previously overlooked, remarkable diversity in this clade.

Following current practice (Antunes and Broin, 1988; Broin, 1988; Meylan, 1996; Gaffney et al., 1998; Tong, 1998; Gaffney et al., 2006) the family Pelomedusidae is restricted to the living genera *Pelusios* and *Pelomedusa*, and the family Podocnemididae is outside of the Pelomedusidae. Recognition of the Podocnemididae as a family-level taxon is useful because there is clear evidence that the long accepted family Bothremydidae (Baur, 1891) is the sister group to the Podocnemididae and not to the family Pelomedusidae. For discussion of the suffix for Podocnemididae see Gaffney et al. (2006: 45). Although there are only three living genera belonging to the Podocnemididae, *Podocnemis* and *Peltocephalus* from South America, and *Erymnochelys* from Madagascar, the fossil record of this family shows that it was quite large, morphologically diverse, and geographically widespread.

In the past, the name *Podocnemis* has been applied to shell taxa that show overall similarity of the shell to that of the living members of this genus. Because of the highly conservative nature of the pelomedusoid shell (Gaffney et al., 2006), turtles in what are now recognized as separate families of the Pelomedusoides were placed in the genus *Podocnemis* (Schmidt, 1940; Zangerl, 1948). Thus, in this study we follow Gaffney (1988) and use *Podocnemis* in a restricted sense to include only the living species plus *P. bassleri* and an undescribed *Podocnemis* from Lewellyn Price's Acre 34 locality, both of which are very similar to living *P. expansa* (there are others that are valid).

Described fossil genera that belong to the Podocnemididae and are known from skull material include *Bauruemys* Kischlat, 1994; *Roxochelys* Price, 1953; *Dacquemys* Williams, 1954; *Neochelys* Bergounioux, 1954; *Shweboemys* Swinton, 1939; *Stereogenys* Andrews, 1901; *Papoulemys* Tong, 1998; and *Bairdemys* Gaffney and Wood, 2002. *Portezueloemys* de la Fuente, 2003, *Hamadachelys* Tong and Buffetaut, 1996, and *Brasilemys* Lapparent de Broin, 2000, constitute sister taxa to the family Podocnemididae and were placed in the epifamily Podocnemidinura along with the family Podocnemididae by Gaffney et al. (2006). Higher taxa below the family level within the Podocnemididae are not used here (see Lapparent de Broin, 2000); instead, we have made comparisons and discussions using genera.

This paper is part of a larger study of pelomedusoid pleurodires that has so far resulted in a revision of three of five families of the Pelomedusoides: Euraxemydidae, Araripemydidae, and Bothremydidae (Gaffney et al., 2006). Additional data have been assembled for members of the Podocnemididae, and this description is undertaken in light of our understanding of skull morphology in members of that family (Gaffney et al., 2006: 45). *Podocnemis* is included as the six living species, each of which has been scored from multiple skulls, as is the case for the two other living genera, *Peltocephalus* and *Erymnochelys*. *Dacquemys* from the early Oligocene of Egypt is included on the basis of our restudy of this taxon (Gaffney et al., 2002). *Shweboemys* from the Pliocene(?) of Burma and *Stereogenys* from the Eocene of Egypt are included on the basis of Gaffney's studies of this clade that includes the genus *Bairdemys* (Gaffney and Wood, 2002; Gaffney et al., 2008). *Neochelys* from the Eocene of southern Europe is included on the basis of study of the complete skull of the type of *N. arenarum* in the MNHN and figures and descriptions in Broin (1977). Our understanding of the somewhat problematic genus "*Roxochelys*" is based on AMNH 14444 and THUg 2160, nearly complete skulls from the Paleocene of Bolivia. *Hamadachelys* (Tong and Buffetaut, 1996) from the Cenomanian of Morocco has also been included on the basis of material listed in Gaffney et al. (2006). *Bauruemys* from the Late Cretaceous of Brazil is included on the basis of skulls and postcranial material in the AMNH, MCZ, and DNPM. The relevant outgroups are discussed in Gaffney et al. (2006).

Among the many fossils of the Podocnemididae is a large skull, DNPM-MCT 1496-R, from the late Tertiary of western Brazil that was mentioned by Lapparent de Broin et al. (1993) and Gaffney et al. (1998). Because there is no corroboration for an assignment to any shell-based taxon at this time, we describe this skull as new. Lapparent de Broin et al. (1993) included a description of three isolated elements (a costal bone, a peripheral bone, and a humerus) representing one or more large podocnemidids from the late Miocene–early Pliocene of southwestern Amazonia. DNPM-MCT 1496-R is mentioned under the description of a first left peripheral (UFAC 1294). Lapparent de Broin et al. (1993) interpreted the morphology of this peripheral as indicating the presence of a large, deep midline notch in the nuchal bone, as is known in the type of *Stupendemys geographicus* Wood, 1976, and they used this morphology to assign the isolated peripheral to *Stupendemys* sp. In their discussion of this peripheral element, they observed that the nearly fully roofed condition in DNPM-MCT 1496-R would be consistent with the deeply notched shell of *Stupendemys*, but they proceeded to say that other well-roofed genera in the Podocnemididae, such as *Podocnemis* itself, lack an anterior notch in the shell. They concluded that (Lapparent de Broin et al., 1993:664):

> it is impossible to link the two characters [large nuchal notch and complete skull roof] in every case and to refer the DNPM skull to *Stupendemys*. It might represent a new form, more similar to *Podocnemis* by its shell.

Indeed, the isolated skulls of *Podocnemis bassleri* Williams (1956) from Amazonian Peru and a large and undescribed *Podocnemis* skull from Lewellyn Price's Acre 34 locality (in the Acre region), all of which are comparable in size to living *P. expansa*, suggest that other large podocnemidids were present in the late Miocene/early Pliocene of greater Amazonia. Lapparent de Broin (2000: 72) discussed the phylogenetic position of *Stupendemys* but apparently did this on the basis of two isolated cervical vertebrae described by Bocquentin and Negri (1993) that are considered to represent this taxon. There is no mention of DNPM-MCT 1496-R in Lapparent de Broin's (2000) assignment of *Stupendemys* to the subfamily Podocnemidinae.

Bocquentin and Melo (2006) included the three isolated elements described by Lapparent de Broin et al. (1993), the two isolated vertebrae described by Bocquentin and Negri (1993), and six other isolated elements in their hypodigm of a new species, *Stupendemys souzai*. They did not mention DNPM-MCT 1496-R. There was no attempt by these authors to justify their assumption that these 11 solitary elements represent a single taxon, and some of them may not even belong to *Stupendemys*. For maps and localities of isolated skeletal elements referred to cf. *Stupendemys*, *Stupendemys* sp., and *Stupendemys souzai* from the southwestern Amazonian region (i.e., Alto Rio Acre, Rio Alto Purus, Rio Alto Jurua), see Lapparent de Broin et al. (1993), Bocquentin and Negri (1993), Gaffney et al. (1998), and Bocquentin and Melo (2006).

We are in agreement with Lapparent de Broin et al. (1993) that there is probably more than one very large podocnemidid in the late Miocene of Amazonia. As most of this material is shell-based, fragmentary, and not even overlapping morphologically, we describe DNPM-MCT 1496-R as a new skull-based taxon in order to provide a name that can be used in a phylogenetic framework of other Pelomedusoides. Associating the *Stupendemys* shell with DNPM-MCT 1496-R could be adding a chimera to a phylogenetic analysis. On the other hand, we do think that there is a higher probability that the lower jaw, LACM 141498, does belong to *Caninemys* (see "Discussion"). We realize that naming this new skull-based species will make it impossible to identify postcranial fragments of large podocnemidids from the Amazonian Tertiary to genus, but this is a more realistic reflection of the present situation.

ABBREVIATIONS

Institutional Abbreviations

AMNH	American Museum of Natural History
DNPM-MCT	Departmento Nacional de Produção Mineral, Divisão de Geologia e Mineralogia, Museu de Paleontologia, Rio de Janeiro, Brazil
LACM	Natural History Museum of Los Angeles County, Los Angeles
MCZ	Museum of Comparative Zoology–Harvard University, Cambridge, Mass.
MNHN	Museum National d'Histoire Naturelle, Paris
THUg	Teikyo Heisei University, Chiba, Japan
UFAC	Vertebrate Paleontology Collection, Universidade Federal do Acre, Rio Branco, Brazil

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
vo	omer

SYSTEMATICS

ORDER TESTUDINES LINNAEUS, 1758

MEGAORDER PLEURODIRA COPE, 1864

HYPERFAMILY PELOMEDUSOIDES COPE, 1868

EPIFAMILY PODOCNEMIDINURA COPE, 1868

FAMILY PODOCNEMIDIDAE COPE, 1868

Caninemys, new genus

Type Species: *Caninemys tridentata*, new species.

Distribution: Late Tertiary, Miocene, of Acre, Brazil.

Etymology: Named for the bulldog appearance of the skull and the large maxillary processes in the position of mammalian canines.

Diagnosis: A podocnemidid pleurodire with a well-developed processus trochlearis pterygoidei, quadrate-basioccipital contact, and a large cavum pterygoidei; unique among podocnemidids (and all other turtles) in having greatly inflated maxillae, each with a ventral, toothlike process, which, together with a single process formed on the midline of the premaxillae, form a tridentate condition in the upper triturating surfaces, unique among pleurodires. The entire animal was probably smaller than *Stupendemys geographicus* Wood, 1976.

Caninemys tridentata, new species

Type Specimen: DNPM-MCT 1496-R, a nearly complete skull (figs. 1–4) collected by L.I. Price in 1962.

Type Locality: Locality 28 of L.I. Price, Volta de Pedra Pintada, upper Rio Juruá, Acre, Brazil (fig. 5).

Horizon: Vertebrate fossils from the upper Rio Juruá are typically found in two beds associated with the Ucayali Unconformity (Gaffney et al., 1998, Campbell et al., 2000). They come from late Miocene Red Beds of the Contamana Group that lie below the unconformity ("Huayquerian Beds" of Lapparent de Broin et al., 1993), or they come from the Acre Conglomerate unit of the Madre de Dios Formation, which overlies the unconformity (Campbell et al., 1985, 2001). Paleochannels filled with younger sediments that are known to produce vertebrate fossils elsewhere in Acre

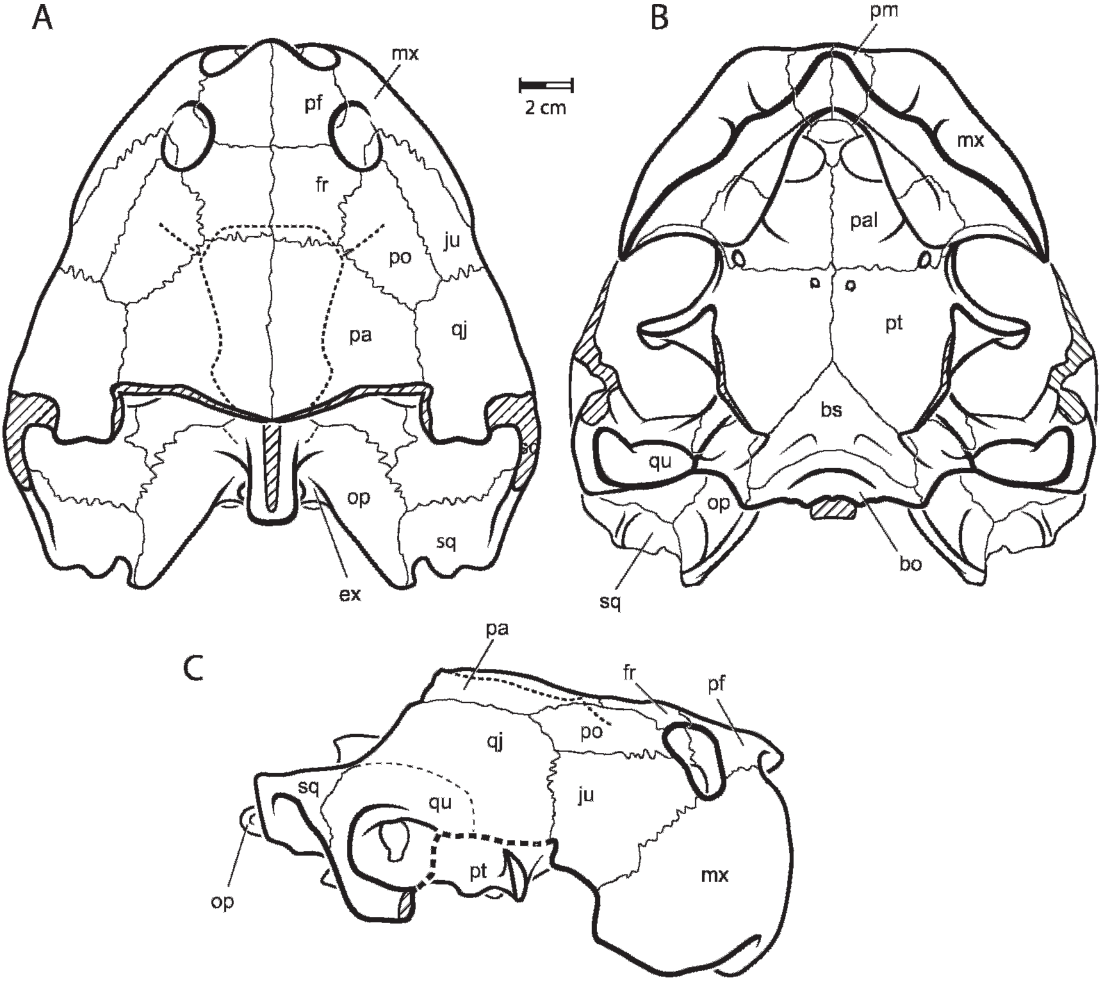

Fig. 1. *Caninemys tridentata*, new genus and species, DNPM-MCT 1496-R holotype. Partially restored views of skull. **A**, Dorsal; **B**, ventral; **C**, lateral. (B. Degner, del.)

are apparently not accessible along the upper Rio Juruá (Campbell et al., 2000). It is unlikely that this skull is from a younger horizon. The Acre Conglomerate is also considered to be of late Miocene age by Frailey (1986) and Campbell et al. (2001). Thus, we assign DNPM-MCT 1496-R to a late Miocene age, even though we do not know with certainty from which side of the Ucayali Unconformity it has come.

Lapparent de Broin et al. (1993) included this skull among turtle material they reported from "Huayquerian Beds" and referenced the work of Campos and de Broin (1981). The latter reference lists this material only as coming from the Neogene of Acre. We have not been able to confirm an origin from the "Huayquerian Beds" below the Ucayali Unconformity. Discussion of a lower jaw (see below) that might be assigned to this taxon and other geologic references are in Gaffney et al. (1998).

DIAGNOSIS: Same as for the genus.

ETYMOLOGY: The species epithet is based on the tridentate appearance of the skull that is most clearly seen in anterior view.

DISCUSSION: Although this taxon cannot be differentiated from the shell-based *Stupendemys geographicus* Wood, 1976, because there is no overlap in presently known morphology, it is likely that *Caninemys* is

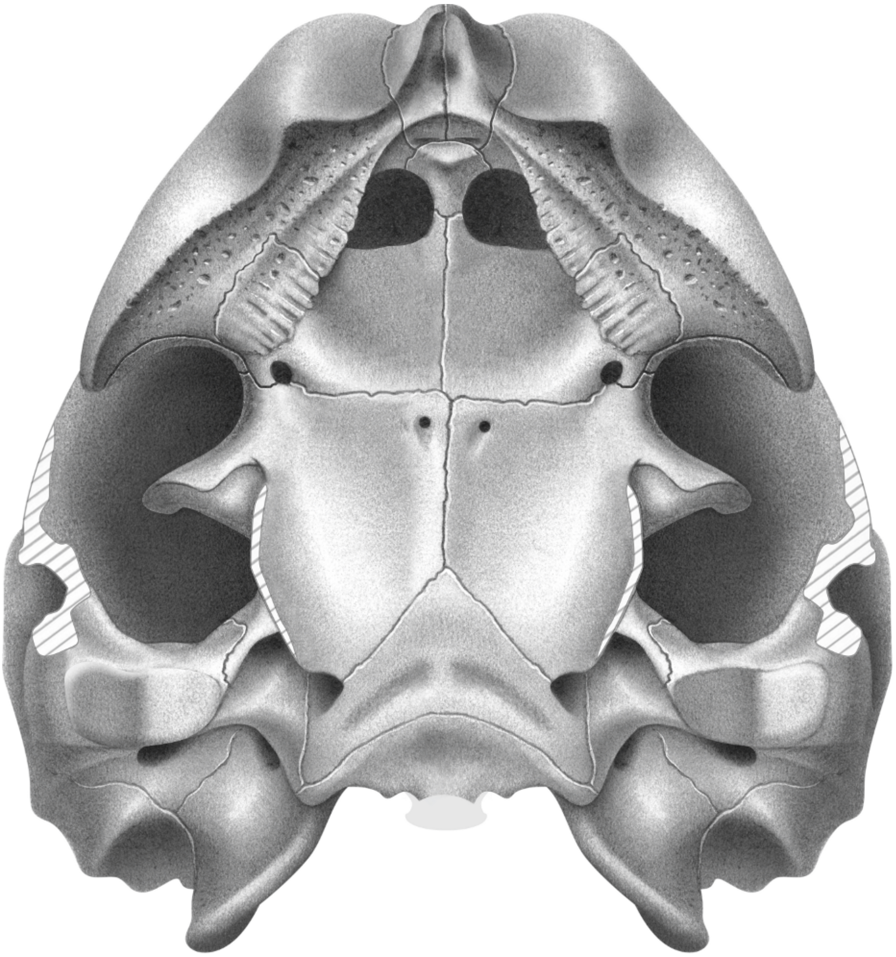

Fig. 2. *Caninemys tridentata*, new genus and species, DNPM-MCT 1496-R holotype. Partially restored ventral view. (F. Ippolito, del.)

significantly smaller than the Venezuelan *Stupendemys*. Using skull-shell ratios of recent specimens of *Podocnemis expansa* and other recent podocnemidid species, it is hypothesized that the shell of *Caninemys* would be less than 4–5 feet in length rather than the 7-foot plus length of *Stupendemys*. For comparison, the largest skulls of recent *Podocnemis expansa* have a condylobasal length of about 12 cm (Williams, 1956) and the Mio-Pliocene *Podocnemis bassleri* (Williams, 1956; very similar to *P. expansa* in morphology) is 15.7 cm in length, compared to about 16.5–17.0 cm for *Caninemys*. It is of course possible that smaller species of *Stupendemys* were present in the Acre region and that *Caninemys* is the skull of one of these, but this is only speculation.

DESCRIPTION

Only the skull of the type, DNPM-MCT 1496-R, is known (figs. 1–4). It is uncrushed and nearly complete. The posterior margin of the skull roof is missing on the right side. On the left side, both the otic capsule and the posterolateral part of the skull roof have been lost. However, since these areas are preserved on the right side, it is possible to give a full description of the skull of this new taxon. The

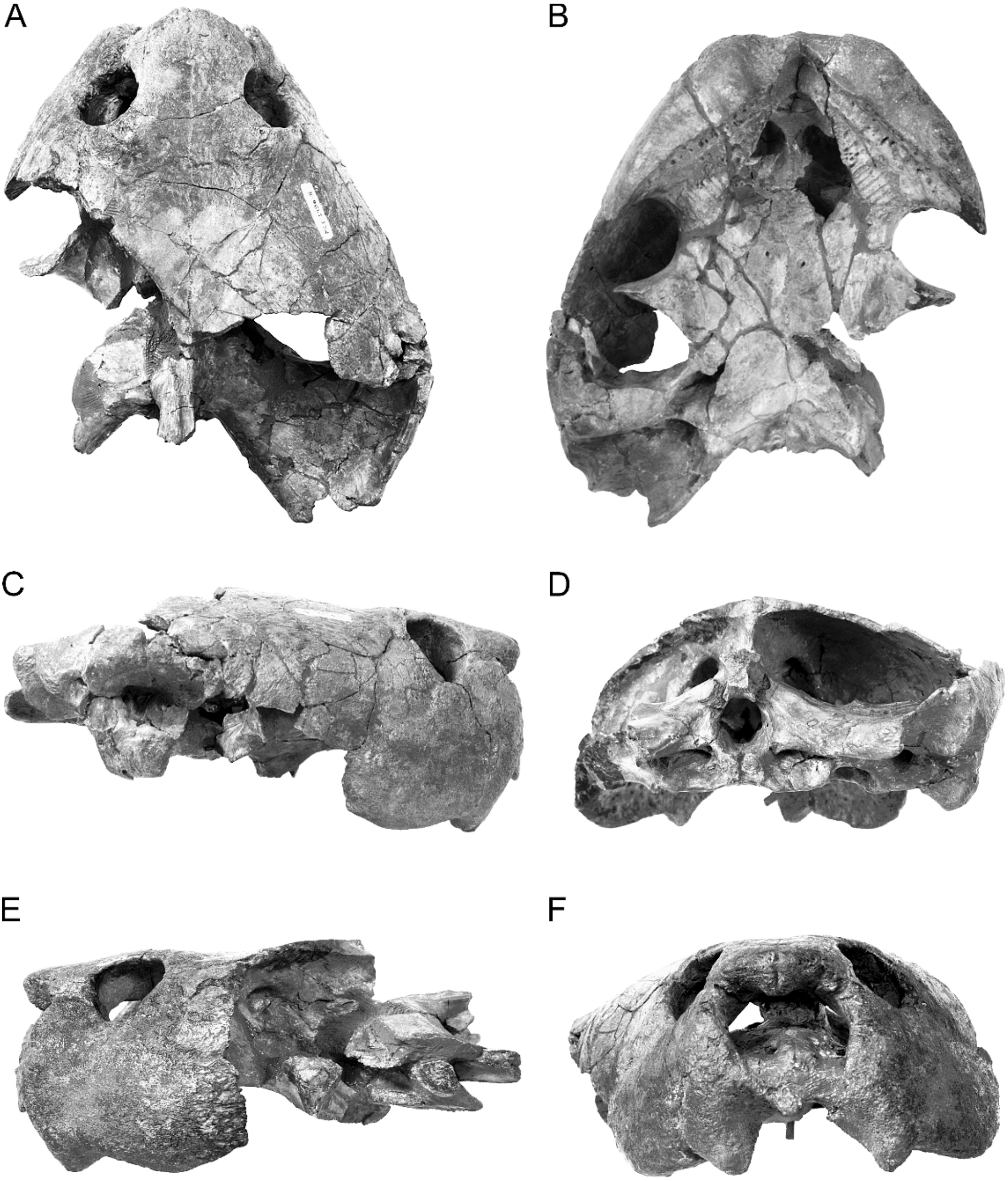

Fig. 3. *Caninemys tridentata*, new genus and species, DNPM-MCT 1496-R holotype. **A**, Dorsal; **B**, ventral; **C**, right lateral; **D**, posterior; **E**, left lateral; **F**, anterior. (B. Degner, del.)

front half of this skull is massive. The maxillae are remarkably large and thick, and the cheek emargination is reduced. In dorsal view it is clear that the temporal emargination was not extensive, but is comparable to *Podocnemis*, and that the orbits were somewhat dorsally oriented also as in *Podocnemis*. Measurements of this skull are given in table 1.

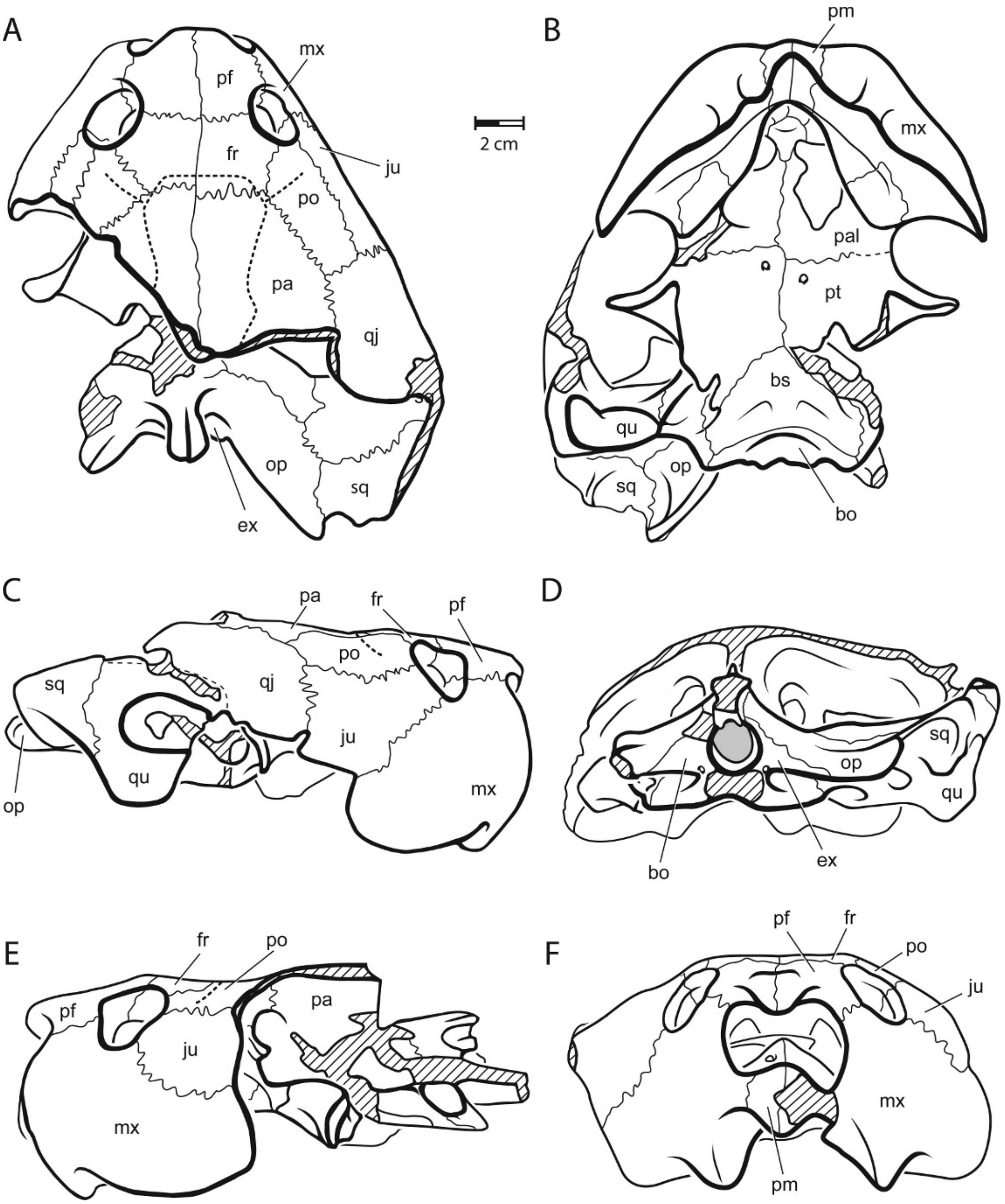

Fig. 4. *Caninemys tridentata*, new genus and species, DNPM-MCT 1496-R holotype. **A**, Dorsal; **B**, ventral; **C**, right lateral; **D**, posterior; **E**, left lateral; **F**, anterior. (B. Degner, del.)

DERMAL ROOFING ELEMENTS

NASALS: The snout of *Caninemys* is very well preserved, and it is clear that no nasals were present. The absence of nasals is typical of all members of the Pelomedusoides (char. 1). Nasals are present in nearly all chelids and in primitive cryptodires.

Fig. 5. Map of southwestern Amazonia showing the localities for *Caninemys* and other fossil turtles discussed in the text. **1.** Type locality of *Stupendemys geographicus* (Wood, 1976). **2.** L.I. Price locality 28, type locality of *Caninemys tridentata* (DNPM-MCT 1496-R). **3.** LACM locality 5994, source of LACM 141498, a lower jaw that might represent *Caninemys* (see "Discussion").

TABLE 1

Measurements of Skull of *Caninemys tridentata* (DNPM-MCT 1496-R) (in cm)

(For positions of measurements see Gaffney et al., 2006: fig. 315)

A. Midline length as preserved (estimated original length 16.5–17.0)	16.1[a]
B. Maximum width (right side half width doubled)	19.2
C. Width between orbits	3.9
D1. Width of left orbit	2.6
D2. Width of right orbit	2.6
E. Width of external nares	4.0
F. Width of internal nares	4.7
G. Maximum height at quadrate	9.0
H. Width of skull at middle of orbits	11.8
I. Length from anterior margin of prefrontals to posterior margin of supraoccipital	16.5[a]
J1. Height of left orbit	3.7
J2. Height of right orbit	3.6
K. Skull height at occipital condyle	7.2
L. Anterior width of triturating surface (including labial ridge)	3.4
Anterior width of triturating surface (medial to labial ridge)	2.3
M. Posterior width of triturating surface (including labial ridge)	4.2
Posterior width of triturating surface (medial to labial ridge)	3.6
N. Width of palate across foramina palatinum posterius	8.3
O. Length from front of skull to posterior edge of condylus articularis	15.6

[a] Damaged.

PREFRONTAL: The prefrontal is a relatively large element making up the anterior part of the snout. It contacts the other prefrontal medially, the frontal posteriorly, and the maxilla ventrolaterally. It forms the anterodorsal quarter of the orbit and the dorsal part of the external nares and the fossa nasalis. A strong ventral ridge on the posterior part of the prefrontal continues onto the ventral surface of the frontal and defines the lateral limits of the fossa nasalis. This element in *Caninemys* differs from *Podocnemis* but is like other podocnemidids in having no groove on the dorsal surface at the midline (see "Frontal").

FRONTAL: The frontal is relatively small but makes up much of the skull roof between the relatively small orbits. The orbits of *Caninemys* are oriented somewhat upward rather than directly outward (char. 2). This is the condition found in *Podocnemis*, *Bauruemys*, and other podocnemidids except for the clade that includes *Shweboemys*, *Stereogenys*, *Neochelys*, *Erymnochelys*, *Peltocephalus*, and *Dacquemys*.

The frontal contacts the prefrontal anteriorly, the other frontal on the midline, the postorbital laterally, and the parietal posteriorly. In addition to forming the middle part of the skull roof and the dorsal margin of the orbit, it forms the posterior part of the sulcus olfactorius and the medial part of a well-developed septum orbitotemporalis. The septum orbitotemporalis of *Caninemys* is the same relative size as in *Podocnemis*. A defining feature of the members of the genus *Podocnemis* is the presence of a groove on the dorsal surface of the frontal (char. 3). No such groove is present in *Caninemys* or other members of the Pelomedusoides.

PARIETAL: The parietals are incomplete posteriorly. This element makes up the largest part of the skull roof and contributes to the lateral wall of the braincase. It contacts the other parietal on the midline, the frontal anteriorly, the postorbital anterolaterally, and the quadratojugal posterolaterally. The contact of the parietal to the quadratojugal is broad in *Caninemys* (char. 4). This is a derived condition relative to that seen in pelomedusids, *Araripemys*, and other pleurodires, in which these elements are separated by deep temporal emargination. Narrow contact between the quadratojugal and parietal is observed in the primitive pelomedusoid, *Euraxemys*, most Taphrosphyini (Gaffney et al., 2006), *Hamadachelys*, and *Bauruemys*. The broad contact seen in *Caninemys* and all other podocnemidids is scored as a separate, further derived condition.

The posterior limits of the parietal are incompletely known but it contacts the supraoccipital posteriorly and the prootic laterally. In addition to the descending process of the parietal that makes up the lateral wall of the braincase, a more anterior projection abuts the postorbital wall and makes contact with the postorbital there. This anterior portion of the parietal forms the roof of a channel between the septum orbitotemporalis and braincase leading from the fossa temporalis superior behind the orbit into the fossa nasalis. This channel is the sulcus palatinopterygoideus (see Gaffney et al., 2006: 580). The contacts of the parietal in the area of the foramen nervi trigemini are uncertain due to breakage. However, in most podocnemidids, as in the outgroups, there is no contact between the parietal and the pterygoid just above the processus trochlearis pterygoidei (char. 5). However, such contact does occur in certain species of *Podocnemis* and in *Neochelys*, *Shweboemys*, and *Stereogenys*.

The parietal in *Caninemys* roofs much of the fossa temporalis superior. The skull roof was apparently fairly complete. Its extent is due largely to the long quadratojugal-parietal contact that is developed to the same degree as in *Podocnemis*. This is quite unlike the deep temporal emargination seen in the Pelomedusidae and *Araripemys* (char. 6).

The scales on the skull roof of *Caninemys* are best preserved on the parietal. It appears to have had an elongate, triangular interparietal scale like that seen in *Podocnemis expansa* and several other species of that genus (char. 7; Williams, 1954). A well-defined interparietal scale appears to be a feature of the Podocnemididae. However, an equilateral interparietal scale seems to have a broader distribution among the members of the family than does the elongate condition seen in *Caninemys*.

JUGAL: The jugal is a large element extending from the orbit to the cheek emargination. On the skull roof, it contacts the maxilla anteriorly, the postorbital dorsally, and the quadratojugal posteriorly. The jugal of *Caninemys* does not contact the quadrate as it does in *Peltocephalus* and *Erymnochelys* (char. 8). On the floor of the orbit there appears to be contact of the jugal to the palatine. It also makes up much of the posterior margin of the orbit and the lateral part of a robust septum orbitotemporalis.

The septum orbitotemporale (Gaffney et al., 2006) of *Caninemys* appears to be typical of podocnemidids. Most of the wall is made up of a strong medial process of the jugal, which contacts the quadratojugal dorsolaterally on the skull roof and the postorbital medially. In *Caninemys* (as in other podocnemidids except *Podocnemis*), the postorbital separates the jugal and pterygoid from the parietal. The jugal-parietal contact that is typical of *Podocnemis* (char. 9) can be seen on the septum orbitotemporalis as well as on the skull roof in members of that genus. This contact does not occur in *Caninemys*.

The jugal defines the dorsal limit of cheek emargination in most turtles. In *Caninemys* and members of the clade leading to *Shweboemys* and *Stereogenys* (other than some *Bairdemys*), the cheek emargination is less developed than it is in most podocnemidids (char. 10), and it does not reach the level of the lower rim of the orbit. In most outgroups (e.g., *Hamadachelys*, *Bauruemys*, and *Podocnemis*) it is deeper, reaching the level of the lower third of the orbit. In some Cretaceous podocnemidids (*Roxochelys* and two undescribed forms from the Peiropolis area of Brazil) the cheek emargination is deeper still, reaching close to the dorsal rim of the orbit. This character is treated via four states, with the fourth being the extensive cheek emargination found in chelids.

QUADRATOJUGAL: The area of the quadratojugal is preserved only on the right side of the skull. Although the skull roof is extensive in this area, an obvious suture between the quadrate and quadratojugal cannot be detected on the external surface of the skull. Internally, portions of the quadrate-quadratojugal suture can be seen just anterior to the cavum tympani of the quadrate. The quadrate-quadratojugal suture curves posteriorly as it reaches the dorsal aspect of the skull roof, producing a large and broadly C-shaped quadratojugal as in *Podocnemis* and *Shweboemys*. There is no evidence that the quadratojugal was excluded from the cheek margin by quadrate-jugal contact as in *Erymnochelys* and *Peltocephalus*. Along its anterior margin the quadratojugal of *Caninemys* contacts the jugal, postorbital, and parietal. It forms much of the roof of the fossa temporalis superior.

SQUAMOSAL: The squamosal is preserved only on the right side of the skull. It is a triangular element extending posteriorly from the quadrate. There is a flat lateral surface that curves posteriorly and has a weak groove along its ventral margin, probably for the M. depressor mandibulae (Gaffney, 1979: 82). The dorsal surface meets the opisthotic medially and the quadrate anteriorly. Where the dorsal and vertical portions of this element meet, there is a strong vertical flange that helps to define the fossa temporalis superior posterolaterally (char. 11).

POSTORBITAL: The postorbital is a rectangular element located just posterior to the orbit. It contacts the frontal anteromedially, the parietal posteromedially, the jugal ventrally, and the quadratojugal posteriorly. It enters the orbit anteriorly, but is excluded from the temporal emargination by a parietal-quadratojugal contact as in other podocnemidids. The postorbital is not reduced in size in this new form as it is in most species of *Podocnemis* (char. 12). In addition to contributing to the skull roof, this element forms a large portion of a thick postorbital wall.

PALATAL ELEMENTS

PREMAXILLA: The premaxilla is paired and rather small relative to the size of the massive maxilla. It contacts the maxilla laterally, the vomer posteriorly, and the other premaxilla medially. The triturating surface of this element is much more complex than that of *Podocnemis* or other podocnemidids. A sharp, tall labial ridge on the maxilla extends anteromedially and then ventrally across the premaxilla to form a small but distinctive midline premaxillary toothlike process. This ridge also marks the anterior limits of the triturating surface of the premaxilla. The posterior limit is defined by the medial continuation of a median maxillary ridge from the triturating surface of the maxilla across the posterior part of the premaxilla. On the premaxilla this ridge is very sharply defined. Anterior to it, the triturating surface forms a large deep recess for a hooked lower jaw. This recess is comparable to that of *Macrochelys* in which the symphyseal hook of the dentary is twice as tall as the jaw, quite sharp, and nearly vertical. Isolated jaws fitting this general description have been described from the Miocene of western Brazil (Gaffney et al., 1998; see "Discussion").

Posterior to the median premaxillary ridge, the surface of the premaxilla extends dorsally, forming a right angle with the triturating surface, and then posteriorly to meet the vomer. The vertical surface that is formed by the premaxilla produces a steep anterior wall of a well-defined vault within the buccal cavity. Within this anterior wall an enlarged foramen praepalatinum passes through the premaxilla into the fossa nasalis. The position of this foramen, entirely surrounded by the premaxilla and below a premaxillary ridge, is typical of pelomedusoids (char. 14). In some *Podocnemis* species it is located in the maxilla-premaxilla suture, and in other genera (*Dacquemys*, *Peltocephalus*, *Stereogenys*) it is absent. In outgroups to the Podocnemididae this foramen is located on a flat area of the triturating surface, making the position under a premaxillary ridge a derived condition (char. 15).

Posterior to the foramen premaxillaris, the premaxilla, maxilla, and vomer combine to roof the most anterior part of the buccal cavity just anterior to the internal nares. This is unlike the derived condition in two species of *Podocnemis*, *Erymnochelys*, *Peltocephalus*, *Neochelys*, *Shweboemys*, and *Stereogenys* in which the paired premaxillae extend between the maxillae to reach the internal nares (char. 13). In *Caninemys*, the premaxilla is excluded from the internal nares by a vomer-maxilla contact anterior to the internal nares. Dorsally the premaxilla forms the ventral margin of the apertura narium externa and most of the floor of the fossa nasalis.

MAXILLA: The maxilla of *Caninemys* is greatly enlarged and gives the skull a "bull-dog" appearance. This element contacts the premaxilla anteromedially and the prefrontal anterodorsally, both on the skull roof and within the orbit. It contacts the jugal posteriorly on the cheek and on the postorbital wall. On the palate it contacts the palatines posteromedially and the vomer anteromedially.

The triturating surface and labial ridge of the maxilla are large and complex structures. The dominant feature is a large toothlike process on the labial ridge located about one-third of the way along the length of the maxilla and broadly similar in profile to a mammalian canine tooth (best seen in anterior view, figs. 3F, 4F). Together with the premaxillary ''tooth'', this structure gives *Caninemys* its tridentate condition. In addition to having this toothlike process, the labial ridge is massive. It is thick with a flat ventral margin, and it extends ventrally about 2 cm from the horizontal part of the triturating surface. Near the premaxilla the labial ridge curves upward, producing a wide, U-shaped notch on the midline between the maxillary teeth. The single premaxillary toothlike process extends into this notch. In external view the massive development of the labial ridge of the maxilla gives the face an inflated appearance unlike that of any turtle known.

Even with these hypertrophied maxillae, a secondary palate is not present. In certain other podocnemidids, notably *Bairdemys*, *Stereogenys*, and *Shweboemys*, a long and well-developed secondary palate is developed (chars. 16, 17). In these taxa a low thick labial ridge is present on the maxilla (char. 18).

There are three ridges on the triturating surface of the maxilla in *Caninemys*. The largest, the median maxillary ridge, is like that of *Podocnemis*, *Dacquemys*, *Erymnochelys*, and *Peltocephalus* (char. 19). It extends for the length of the maxilla along the middle of the triturating surface and then extends onto the premaxilla anterior and ventral to a well-defined foramen praepalatinum. As in *Podocnemis* and *Dacquemys* there is also a more lingual accessory ridge (char. 20). In *Caninemys* it is feebly denticulate and is less well developed than in *P. unifilis*. A third ridge is present on the interior wall of the very large labial ridge where the latter descends to form the massively inflated jaws. A similar ridge occurs only in *Podocnemis expansa*.

The maxilla joins with the palatine posteromedially to form the triturating surface. On the anterior part of the palate the maxilla contacts the vomer, forming the anterior limit of the apertura narium interna, excluding the premaxilla from that opening. There is no median contact between the maxillae at the midline, which is unlike the condition seen in *Dacquemys* and certain species of *Podocnemis* in which this contact occurs (char. 21). The maxilla forms the anterior floor of the orbit and the lateral wall of the fossa nasalis. A deep groove on the external surface of the maxilla just anterior to the suture with the jugal suggests that the upper jaw was covered by a broad, thick rhamphotheca on the external surface as is the case in living *Podocnemis*.

VOMER: *Caninemys* has a small but distinct vomer. It is a short, triangular, midline element with broad anterior contact to the premaxilla and maxilla and narrow posterior contact to the palatines. It forms the anteromedial margin of the apertura narium interna and the floor of the fossa nasalis. It appears that the vomer has been lost three times within the Pelomedusoides (char. 22), once in the Pelomedusidae plus *Araripemys* (the magnafamily Pelomedusera of Gaffney et al., 2006), once within *Podocnemis*, and once within the lineage that gives rise to the *Shweboemys* group.

PALATINE: The palatine is a rectangular element in the anterior part of the palate. It contacts the vomer anteromedially, the maxilla laterally, the pterygoid posteriorly, and the other palatine on the midline of the palate. The palatine roofs the anterior part of a vaulted buccal cavity. It forms a long posterior margin of the apertura narium interna that is partially hidden in ventral view by a medially expanded triturating surface. It contributes to the posteromedial part of the triturating surface as it does in *Podocnemis* and other podocnemidids. The palatine encloses a small foramen palatinum posterius along the lateralmost part of its suture with the pterygoid, which is typical for podocnemidids and all Pelomedusoides. Only in *Shweboemys* and *Stereogenys* is the posterior palatine foramen absent (char. 23).

Dorsally in *Caninemys* the palatine forms a thin continuous floor below the foramen interorbitale. Posterolaterally it forms a significant contribution to the upper triturating surface, which appears to be a derived condition for podocnemidids (char. 25) that also occurs in the Bothremydidae. In *Stereogenys* and *Shweboemys* the contribution of the palatines to the triturating surface is especially large, and their free medial margins form parallel edges along a midline cleft (chars. 24, 25). The significantly enlarged condition of the palatines in *Stereogenys* and *Shweboemys* is further indicated by their dorsal contact to the parietal (char. 26) and their posterior contact with the basisphenoid (char. 27) in these two genera.

PALATOQUADRATE ELEMENTS

QUADRATE: The quadrate is preserved only on the right side. On the skull roof it contacts the quadratojugal anteriorly and squamosal posteriorly. In ventral view it can be seen to contact the pterygoid anteromedially, the basisphenoid and basioccipital medially, and the opisthotic and squamosal posteriorly. Medial contact of quadrate to the basioccipital is a derived condition shared by members of the Bothremydidae and Podocnemididae (char. 31; Gaffney et al., 2006). The quadrate-prootic contact on the anterior wall of the otic chamber cannot be seen because of the loss of bone in this area, but a long suture with the opisthotic is clearly visible on the dorsal surface of the otic chamber.

In *Caninemys* the quadrate forms a relatively small, conical cavum tympani. It is closed posteriorly as in all living pleurodire families (char. 30) but not in *Araripemys*, *Euraxemys*, or primitive bothremydids. The anterior wall of the cavum tympani is incompletely preserved, but the preserved portions suggest that no precolumellar fossa was present (char. 29). This appears to fit a pattern of reduction of this structure seen in such related forms as *Dacquemys*, *Peltocephalus*, *Neochelys*, and *Stereogenys*. Reduction of this structure also occurs within *Podocnemis*.

The posterior part of the cavum tympani includes a very small antrum postoticum. It is only a few millimeters wide and a few millimeters deep, and it is therefore relatively smaller than that of most podocnemidids. However, the antrum postoticum of podocnemidids is already small relative to the large antrum seen in various outgroups, so this is treated as a further derived condition in our analyses (char. 28).

Ventral to the cavum tympani a very short, stout processus articularis extends ventrally to a broad condylus mandibularis. The condylus is three times wider than long and is dorsally concave, a feature of nearly all pleurodires. The area articularis extends laterally from the quadrate process of the pterygoid with which the quadrate forms a broad suture. Posterior to the suture with the pterygoid the quadrate extends medially where it forms the posterodorsal limits of the cavum pterygoidei. It contacts the basisphenoid and basioccipital medially.

In posterior view the quadrate forms most of the ventral margin, as well as the lateral part of the dorsal margin of a wide fenestra postotica. At the lateral limits of the fenestra postotica it surrounds the common opening for the eustachian tube and stapes. Along with the opisthotic and squamosal it also forms a broad shelf dorsal to the fenestra postotica. Laterally, a well-developed dorsal ridge on the quadrate marks the lateral limit of the fossa temporalis superior. Medial to this ridge the quadrate forms the dorsal and anterior part of the otic chamber lateral to the prootic.

PTERYGOID: All of the right and most of the left pterygoid are preserved but both are broken. The pterygoid contacts the palatine anteriorly and the jugal and postorbital anterolaterally on the posterior surface of the septum orbitotemporale. Posteriorly there is a strong quadrate process that makes broad contact to the quadrate, and a long diagonal suture with the basisphenoid. Dorsal contact to the prootic cannot be determined because much bone is missing from the trigeminal region. Anterior to the foramen nervi trigemini the pterygoid makes broad contact with the parietal. In ventral view the most salient feature of the pterygoid is the large processus trochlearis pterygoidei. It is laterally directed with the trochlear surface oriented in a vertical plane and very strongly buttressed. A single nutritive foramen (possibly enlarged by preparation?) is present anteromedially.

In *Caninemys*, the pterygoid forms the anterior wall of a wide cavum pterygoidei that extends medially from the quadrate nearly to the midline. A cavum pterygoidei that opens medially into the cavum cranii is an important derived feature of the Podocnemididae (char. 33). The cavum pterygoidei is only partially formed in *Hamadachelys*. Unfortunately, the medial limit of the cavum pterygoidei is not preserved in *Caninemys*, so systematically useful information about the size and structure of the opening from this chamber into the cavum cranii (char. 32) is unavailable for this new taxon. Within the Podocnemididae, *Erymnochelys*, *Peltocephalus*, *Neochelys*, *Shweboemys*, and *Stereogenys* have a very wide opening into the cavum cranii. Within the genus *Podocnemis*, the medial limit of the cavum pterygoidei is reduced to a few small foramina in some species.

In posterior view a strong ridge extends medially and anteriorly from the processus trochlearis pterygoidei to produce the posteromedial part of a massive septum orbitotemporale. This buttress reaches the jugal laterally and the postorbital medially. The parietal contacts the pterygoid medial to the sulcus palatinopterygoideus, a broad channel that passes from the fossa temporalis superior anteriorly into the medial part of the orbit (Gaffney et al., 2006: 122, 580).

Along the lateral margin of the pterygoid in *Caninemys*, extending from the base of the processus trochlearis pterygoidei beyond the quadrate process of the pterygoid, there are the remains of a ventral flange of the pterygoid (char. 34). Such a flange is present in all podocnemidids (see Gaffney, 1979: figs. 129, 131, 134, 136; Gaffney et al., 2006) but they are frequently broken off in both fossil and recent specimens.

Braincase Elements

Supraoccipital: Only the most anterior part of the supraoccipital spine is preserved in *Caninemys*. This element is incomplete dorsally and posteriorly. It contacts the exoccipital ventrally, the opisthotic laterally, and the parietal dorsally. It forms the dorsal margin of the foramen magnum and a stout supraoccipital spine of unknown length. The dorsal exposure of the supraoccipital on the skull roof may be systematically informative. In all members of the genus *Podocnemis*, and in *Bauruemys* and *Euraxemys*, this element forms a small but significant contribution to the skull roof (char. 35). In *Dacquemys* this elements makes a very large contribution to the skull roof.

Exoccipital: The exoccipitals are complete on both sides of the foramen magnum. This element contacts the supraoccipital dorsally, the opisthotic laterally, and the basioccipital ventrally. It forms the lateral margin of the dorsoventrally oval foramen magnum and extends posterolaterally along the medial surface of the paroccipital process of the opisthotic. It forms the dorsal margin of the foramen jugular posterius and all of the single foramen nervi hypoglossi. The occipital condyle is broken off and thus it is not possible to determine the relative contribution of the exoccipitals to this structure. In the Pelomedusidae and many Bothremydidae, the occipital condyle is made up by the exoccipitals alone without contribution from the basioccipital (char. 36).

In *Caninemys* the foramen jugulare posterius is formed medially by the exoccipital and laterally by the opisthotic and basioccipital. As in all podocnemidids, other than *Hamadachelys* and *Bauruemys*, this lateral bar of bone completely isolates the foramen jugulare posterius from the fenestra postotica (char. 37). This is a derived condition relative to the open nature of this foramen in *Araripemys* and *Euraxemys*.

Basioccipital: The basioccipital is a narrow element exposed ventrally between the basisphenoid and quadrates. It contacts the exoccipital medial to, and the opisthotic lateral to, the foramen jugulare posterius. It contacts the quadrate on the distal part of the tuberculum basioccipitale. The extent of its contribution to the occipital condyle cannot be determined. Well lateral to the occipital condyle on either side this element forms a well-defined tuberculum basioccipitale (char. 40). These structures in *Caninemys* and most other podocnemidids differ from those in *Hamadachelys* and *Bauruemys*, which are much smaller and more medially located. Although the basioccipital is short in *Caninemys*, it is not as short as it is in *Stereogenys* and *Shweboemys* (char. 39).

Prootic: The anterior wall of the otic chamber is only preserved on the right side, and a significant amount of bone is missing between the parietal and quadrate, so the exact extent of the prootic cannot be determined. On the left side only the posterior part of the prootic is present. It is clear that the prootic contacts the quadrate laterally, the opisthotic posteriorly, the parietal medially, and the pterygoid ventrally. The palatoquadrate region of the skull is preserved adequately to determine that, as in all bothremydids and podocnemidids, the prootic was not exposed ventrally in this species (char. 41). Furthermore, *Caninemys* appears to share a feature of all podocnemidids in having the prootic covered ventrally by the pterygoid (char. 42).

Few structures are visible on the prootic. The area of the foramen stapedio-temporale is not preserved and the structures formed by this element in the wall of the braincase are not visible. There is a distinct tubercle on the prootic just lateral to the parietal contact. A similarly placed but smaller tubercle is also present just medial to the foramen stapedio-temporale in *Podocnemis expansa* and in *Peltocephalus*. It is also quite clear that the foramen posterius canalis carotici interni did not enter the skull via the prootic (char. 43), which is the primitive condition for the Pelomedusoides.

OPISTHOTIC: The opisthotic appears to be complete on the right side. It contacts the exoccipital and supraoccipital medially, the prootic anteriorly, and the quadrate and squamosal laterally. It forms the posteromedial portion of the otic chamber. In posterior view the opisthotic forms the medial wall of the fenestra postotica, separating this structure completely from the foramen jugulare posterius (char. 45). Along with the squamosal and quadrate, it forms a broad shelf over the fenestra postotica. The opisthotic extends farther posteriorly on this shelf than the squamosal and forms a distinct medial ridge to the shelf. A slightly lower ridge on the squamosal forms the lateral limit of this shelf. The processus interfenestralis of the opisthotic is not visible ventrally in *Caninemys* (char. 44). This is a feature of all Pelomedusoides other than members of the Pelomedusidae and *Araripemys*.

BASISPHENOID: The basisphenoid is complete, but only the ventral surface is visible. It contacts the basioccipital posteriorly, the quadrate laterally, and the pterygoid anteriorly. It forms the medial wall of the cavum pterygoidei and the floor of the cavum cranii. On the ventral surface of the basisphenoid there is a pair of small depressions extending posterolaterally from the midline along the suture with the basioccipital. It is not possible to discern the condition of the foramen nervi abducentis on the dorsal surface of the basisphenoid in *Caninemys*. Reduction of the diameter of this foramen appears at present to be an autapomorphy for the genus *Podocnemis* (char. 46). It would be useful to be able to score this character for *Caninemys*.

DISCUSSION

There is no doubt that DNPM-MCT 1496-R is a pelomedusoid pleurodire. The most striking feature in ventral view is the large processus trochlearis pterygoidei, a classic pleurodire character (Gaffney, 1975, 1979; Gaffney et al., 2006). Furthermore, the arrangement of the elements of the ear region relative to those of the braincase is also diagnostic of pleurodires, and the pterygoid does not intervene between the quadrate and the basicranial elements as it does in cryptodires. Further evidence that this skull is that of a pleurodire can be derived from the many characters that suggest that its closest relatives lie well within the pleurodiran clade. Within the Pleurodira there are two major groups with Cenozoic representatives, the Cheloides (family Chelidae) and the Pelomedusoides. The absence of nasal bones and the presence of a large quadratojugal show that *Caninemys* is a pelomedusoid and not a chelid.

In the most primitive of the Pelomedusoides, the prootic is exposed ventrally between the quadrate and basisphenoid. In more advanced forms this element is covered by the pterygoid and/or quadrate and the latter element contacts the basisphenoid (Gaffney et al., 2006). Thus, the presence of a quadrate-basisphenoid and quadrate-basioccipital contact in *Caninemys* indicates that this is not a basal pelomedusoid. Furthermore, in the most primitive pelomedusoids such as *Pelomedusa*, *Pelusios*, and *Araripemys*, the postorbital is exposed by extensive temporal emargination. In more advanced pelomedusoids including *Caninemys*, there is broad quadratojugal-parietal contact excluding the postorbital from temporal emargination.

An important set of features suggests that within the Pelomedusoides, a monophyletic group is formed by the families Euraxemydidae, Bothremydidae, and Podocnemididae (Magnafamily Podocnemidera of Gaffney et al., 2006). Monophyly of this group is suggested by the presence of a quadratojugal-parietal contact, the foramen posterius canalis carotici interni not entering the skull via the prootic, the processus interfenestralis of the opisthotic covered in ventral view, the fenestra postotica at least partially closed off by a quadrate-basioccipital contact, and the prootic covered ventrally. All of these characters can be seen in *Caninemys*. Another feature of this group, the presence in the lower jaw of a retroarticular process, cannot be evaluated in DNPM-MCT 1496-R. However, a lower jaw (LACM 141498) that might represent this taxon or a close relative was described by Gaffney et al. (1998), and it has a well-developed retroarticular process.

The Bothremydidae and Podocnemididae plus two podocnemidid relatives, *Brasilemys* and *Hamadachelys*, are considered to form the superfamily Podocnemidoidea (Gaffney et al., 2006). Evidence for this group is available from the present study in the form of three characters. Members of both families have a quadrate-basioccipital contact, the prootic is at least partially covered ventrally, and the dentaries are fused. The dentaries are sutured and not fused on the midline in *Euraxemys*, *Araripemys*, *Pelomedusa*, and some *Pelusios*. Both of the skull characters listed above are clearly visible in *Caninemys*.

The families Bothremydidae and Podocnemididae are far more diverse than has been previously recognized (Gaffney et al., 2006). The family Bothremydidae includes a diverse group of pleurodires in which the eustachian tube passes through the quadrate in a separate passage from the stapes, and the maxillary-quadratojugal contact and exoccipital-quadrate contact are typically present. Our work suggests that monophyly of the Podocnemididae is supported by a significant list of features including: the position of the orbits facing more upward than outward (reversed within the family); the position of the foramen praepalatinum under a ridge on the premaxilla (foramen absent in some forms); moderate to extensive contribution by the palatine to the triturating surface; small to very small antrum postoticum; incisura columellae auris enclosing stapes and eustachian tube; presence of a cavum pterygoidei that opens anteriorly into the cavum cranii; the foramen jugulare posterius at least partially isolated from the fenestra postotica (occurs also in some bothremydids); pterygoid covering the prootic at least in part; and pectoral scales of the plastron in contact with the entoplastron. *Caninemys* has all of the skull characters of the Podocnemididae. Thus, it is clearly a member of this family.

Caninemys was included in a phylogenetic analysis of pleurodiran taxa with particular emphasis on relationships among the Podocnemididae (fig. 7). The data set includes 63 characters (appendix 1) for 21 pleurodiran taxa plus a hypothetical outgroup based on *Proganochelys* (appendix 2). The data set includes all eight living podocnemidid species plus the extinct genera *Bauruemys*, "*Roxochelys*", *Dacquemys*, *Neochelys*, *Shweboemys*, and *Stereogenys*. All of these are included based on first-hand study of fossil specimens. The term "*Roxochelys*" is used to indicate that the type of this genus is shell material, and the skulls that we have used to score this taxon (AMNH 14444, THUg 2160) are only tentatively referred to the genus, although they include associated shells, so the identification is probably accurate.

The data set was analyzed in PAUP*4.0b10 using the branch-and-bound search option. Seven characters (4, 25, 28, 33, 34, 37, and 48) were run ordered. Characters 7, 14, and 29 could not be objectively scored and were not used in the results presented herein. Analysis using the settings above produced 11 equally parsimonious trees of 123 steps, the strict consensus for which is shown in figure 7.

This preliminary analysis suggests that *Caninemys* nests well within the Podocnemididae as the sister group to a clade (*Dacquemys* ((*Peltocephalus*, *Erymnochelys*) (*Neochelys* (*Shweboemys*, *Stereogenys*)))). That clade plus *Caninemys* is the sister group to the living genus *Podocnemis*. Evidence for the monophyly of this entire group (including *Caninemys* and *Podocnemis*) includes the presence of a well-developed median maxillary ridge (secondarily lost in *Neochelys*, *Shweboemys*, and *Stereogenys*), accessory ridges on the maxilla (secondarily lost in *Peltocephalus*, *Erymnochelys*, *Neochelys*, *Shweboemys*, and *Stereogenys*), and pectoral scales of the plastron not in contact with the mesoplastra and in contact with the epiplastra. The *Podocnemis*-like characters of the maxillary triturating surface are clearly visible in *Caninemys*.

Characters that suggest the close relationship of *Caninemys* and the clade leading to the *Shweboemys* group include a reduced precolumellar fossa (absent in *Caninemys*, and a dimple or absent in other members of this group except *Erymnochelys*), a vertical flange on the squamosal, and reduced cheek emargination. However, additional evidence for this phylogenetic position may come from the isolated jaw, LACM 141498, described by Gaffney et al. (1998) that is probably assignable to *Caninemys*.

Gaffney et al. (1998) expressed doubts that the heavy pleurodire jaw (LACM 141498) that they described from Amazonia, Brazil, could represent the same taxon as DNPM-MCT 1496-R. However, reexamination and reinterpretation of the skull and jaw suggest that they probably do represent the same taxon. The skull of *Caninemys* has a marked dorsal recess in the premaxilla that is emphasized by dorsal curvature of the maxillae. Such a depression in the upper triturating surface occurs in such living turtles as *Macrochelys*, *Claudius*, and *Staurotypus*. All of these genera also have lower jaws with a well-developed symphyseal hook similar to that of LACM 141498. LACM 141498 is just slightly too large to fit the type skull of *Caninemys*, DNPM-MCT 1496-R. However, the labial ridge of the jaw matches the dorsoventral line formed by the maxilla and premaxilla very closely. Furthermore, the labial ridge of the dentary fits closely between the labial ridge and the median maxillary ridge of the maxilla. The lingual ridge of the dentary passes along the inner edge of the palatine where the latter element contributes to the upper triturating surface, and the dorsal process on the lingual ridge fits medial to the maxilla. Laterally on the jaw there is a well-developed depression from the anterior one-third of the dentary posterior to the level of the coronoid. This depressed area allows passage of the very tall labial ridge of the maxilla outside of the lower jaw.

Although there is not an exact correspondence between the upper triturating surface of the skull, DNPM-MCT 1496-R, and that of the lower jaw, LACM 14198, they are sufficiently complementary to suggest that they are from closely related taxa. If this is in fact the jaw of *Caninemys*, then, in addition to having massive upper jaws, it also had very heavy lower jaws with a well-developed symphyseal hook, making *Caninemys* a kind of pleurodiran snapping turtle. DNPM-MCT 1496-R and LACM 14198 were used to model the skull and jaws of *Stupendemys* for a restored complete skeleton on exhibit at the AMNH (fig. 6). Interestingly, in order to make the skull of *Caninemys* fit with the shell of *Stupendemys* at the same ratio of skull to shell seen in *Podocnemis expansa*, the model of the skull, as well as the lower jaws, had to be made more than twice the size of DNPM-MCT 1496-R. The *Stupendemys* shell, cervicals, and limbs in this mount were cast from the Venezuelan specimens of *Stupendemys geographicus* (Wood, 1976).

The very heavy upper and lower jaws of *Caninemys* are roughly similar to those of such living forms as *Macrochelys* and *Caretta*. However, the most apparent modifications of the jaws are not crushing surfaces but the three large ‘‘teeth’’ on the upper surface. This type of skull morphology is known elsewhere among turtles only in the small kinosternid turtle, *Claudius*. The diet of *Claudius* is not well known but it is included in a group of turtles that uses the hyoid apparatus for vacuum feeding (Lauder and Prendergast, 1992), an adaptation for capturing highly mobile prey. The symphyseal hook and dorsal processes of the lingual ridge of the dentary in LACM 141498 would make a complementary three-hooked surface to the three ‘‘teeth’’ in the skull of *Caninemys*. The three toothlike structures in the jaws of this massive head, if combined with a vacuum feeding system, would have made this turtle capable of capturing and holding prey of very large size. It could have had a lifestyle like living snapping turtles, walking on the bottom and snapping up passing fish, caimans, and ana-

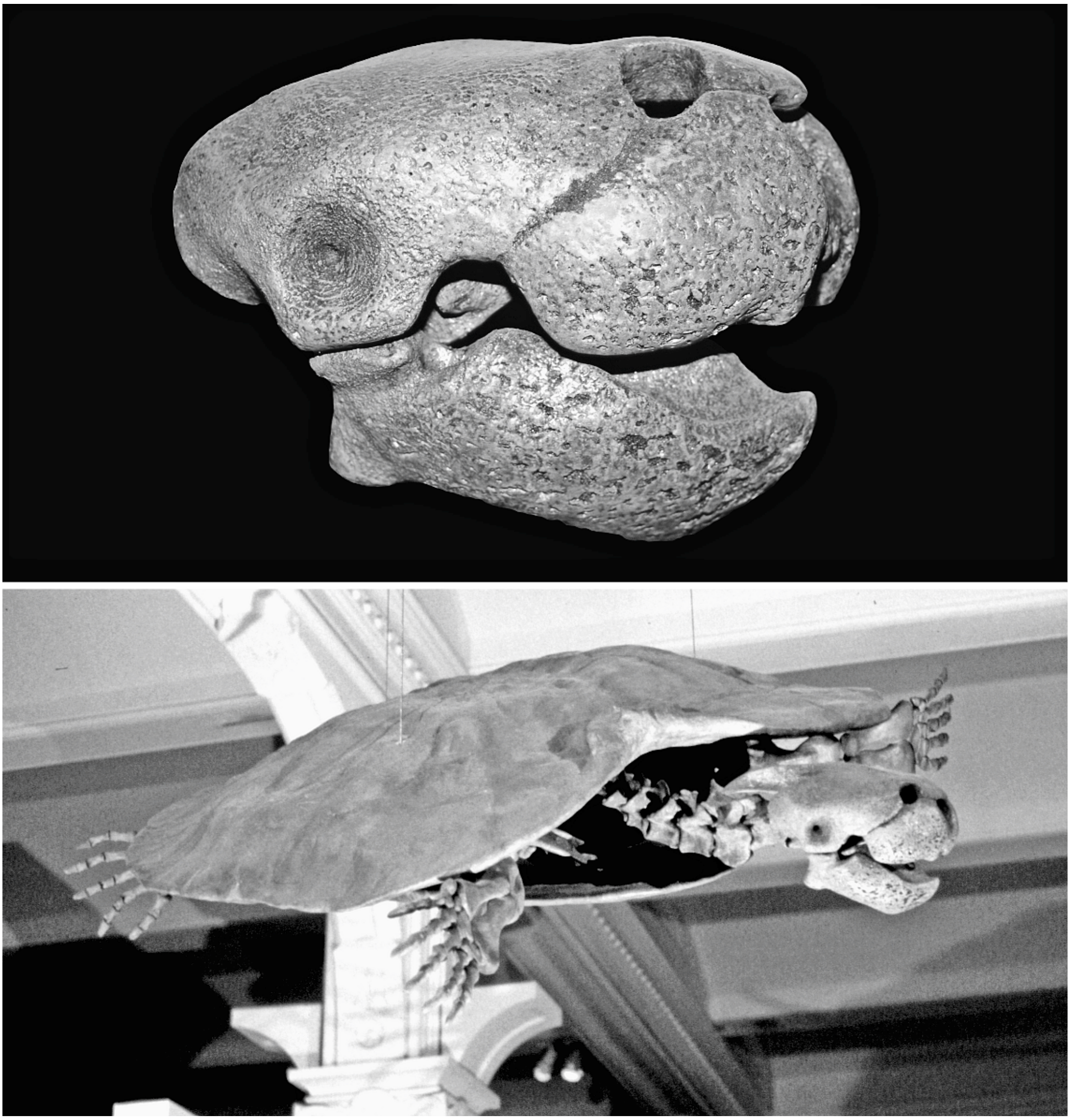

Fig. 6. Skeleton of *Stupendemys geographicus* Wood, 1976, as mounted in the American Museum of Natural History under the direction of E.S. Gaffney, using the enlarged skull of *Caninemys* (DNPM-MCT 1496-R) and lower jaws (LACM 141498) in the restoration. **Upper**, Restored model of *Caninemys* skull (based on DNPM-MCT 1496-R) with lower jaw (based on LACM 141498, described in Gaffney et al., 1998). Both skull and jaw enlarged about twice original size to roughly agree with the shell. **Lower**, The world's largest turtle, *Stupendemys geographicus* Wood, 1976 (Urumaco, Venezuela, AMNH 29077; this cast is of a shell that is 7 feet 2 inches in length; the largest known shell is 7 feet 7 inches; see Wood, 1976).

condas. It was very likely a significant predator in the large Mio-Pliocene river systems of Amazonia.

The relationships among the living podocnemidids suggested by our analysis of skeletal data differ from those suggested by molecular evidence. Based on morphological data, *Peltocephalus* and *Erymnochelys* are sister taxa and members of the clade that leads to *Shweboemys* and *Stereogenys* (Noonan, 2000;

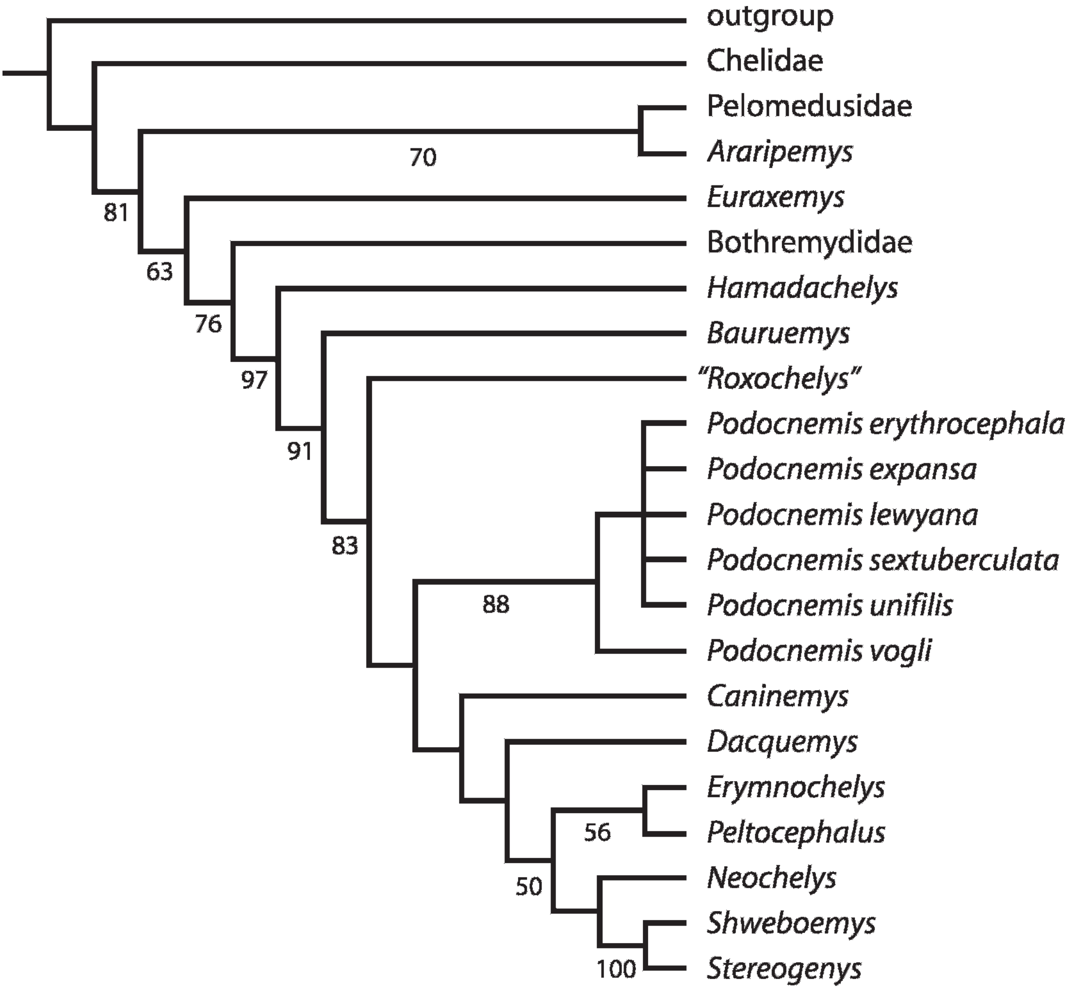

Fig. 7. Cladogram of selected podocnemidid taxa and relevant outgroups. The data set (appendix 2) was analyzed in PAUP*4.0b10 using the branch-and-bound search option. Seven characters (4, 25, 28, 33, 34, 37, and 48) were run ordered. Characters 7, 14, and 29 were not used in the results presented here. This figure is a consensus tree of 11 equally parsimonious trees of 123 steps. Bootstrap values are based on 1000 replicates.

França and Langer, 2006; but see Gaffney and Meylan, 1988; Lapparent de Broin, 2000). Molecular data have suggested that *Erymnochelys* is the sister group to *Podocnemis* (Seddon et al., 1997; Georges et al., 1998; Noonan, 2000). Morphological evidence for a sister group relationship of these two genera includes jugal-quadrate contact below the quadratojugal, and the presence of axillary musk ducts in the axillary buttress rather than in the bridge peripherals.

Evidence for the inclusion of *Peltocephalus* and *Erymnochelys* in the clade leading to *Shweboemys* and *Stereogenys* includes the presence of a small degree of cheek emargination, a cavum pterygoidei that is widely open medially, no dorsal exposure of the supraoccipital, foramen nervi chorda tympani enclosed in retroarticular process of lower jaw, and reduction in the ridges of the triturating surface. In *Peltocephalus*, *Erymnochelys*, *Neochelys*, *Shweboemys*, and *Stereogenys*, accessory ridges are absent. In *Neochelys*, *Shweboemys*, and *Stereogenys* there is the additional loss of the median maxillary ridge.

BIOGEOGRAPHICAL IMPLICATIONS OF THE PHYLOGENY

The distribution of fossil and living pleurodiran turtles in relationship to the breakup of Gondwanaland has been of recent interest to biogeographers (Noonan, 2000; Noonan and Chippendale, 2006; Romano and Azevado, 2006; Yoder and Nowak, 2006). The fundamental question is whether a vicariance model can explain current distributions. Noonan (2000) and Noonan and Chippendale (2006) argued that a molecular phylogeny of the living genera of the Pelomedusoides is consistent with a vicariance model for present distributions. However, few fossils are included in these studies, and Noonan (2000:1249) suggested that they "do not unequivocally support cladogenesis associated with continentral drift". Romano and Azevadeo (2006) focused on fossil taxa, particularly the South American genus *Bauruemys*, but their study is limited by the treatment of the Podocnemididae as three taxa, the South American *Bauruemys*, a South American Podocnemidinae, and an African Erymnochelyinae. None of these studies considered the full diversity of the Podocnemididae nor did they cite the emerging understanding that the Pelomedusoides includes at least three clades that contain species that apparently occupied near-shore marine environments. Two of these clades are bothremydids, Bothremydini and Taphrosphyini (Gaffney et al., 2006), and one is a podocnemidid, the clade that includes *Shweboemys*, *Stereogenys*, and *Bairdemys* (Gaffney and Wood, 2002; MacPhee and Wyss, 1990). The capacity of members of the Pelomedusoides, including the Podocnemididae, for oceanic dispersal is likely greater than has been previously appreciated.

Although our cladogram for the Podocnemidinura (fig. 7) is likely to be modified by the inclusion of additional taxa and characters, the interspersion of African and South American forms makes it highly unlikely that it might be revised in such a way that a series of vicariant events will ultimately explain the distribution of all fossil and living podocnemidids. The origin of the family Podocnemididae in South America may very well be the result of a Cretaceous split between Africa and South America that left its sister group, represented by *Hamadachelys*, across the Atlantic in Morocco (Romano and Azevado, 2006). The subsequent appearance of *Dacquemys* and *Erymnochelys* on the African continent and Madagascar could be a result of dispersal across a narrow Atlantic or, alternatively, the result of a link to Madagascar via Antarctica (Noonan and Chippendale, 2006). However, when one realizes that *Shweboemys* and *Stereogenys* belong to a clade whose members must have used the Tethys Sea and Atlantic Ocean to extend their distribution from Venezuela to Burma (including Puerto Rico, South Carolina, Egypt, and Pakistan), it is easier to visualize other members of the Podocnemididae appearing on the east side of the Atlantic as a result of dispersal. Thus, it seems clear that the distribution of podocnemidid turtles will not ultimately be explained by ancient vicariant events alone. A better explanation might include one or two early vicariant events followed by multiple subsequent dispersal events in a lineage that included some estuarine or near-shore marine forms. Further exploration of the diversity and relationships of the Podocnemididae will provide the opportunity to explore which events are most likely due to vicariance and which to dispersal.

ACKNOWLEDGMENTS

We refer the reader to the Acknowledgments section of Gaffney et al. (2006) for a complete list of people who aided our research in pleurodires. For this paper in particular we thank Brittany Degner and Frank Ippolito for the figures, and Ken Campbell, Pat Holroyd, and Haiyan Tong for comments on the manuscript. This paper was submitted on August 22, 2007, and was accepted for publication on Jan 15, 2008.

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APPENDIX 1

Character list (using same conventions as in Gaffney et al., 2006)

1. Nasal, nasal bones: present = 0; absent = 1.
2. Frontal, orbital position: facing out = 0; facing up = 1.
3. Frontal, frontal groove: absent = 0; present = 1.
4. Parietal, quadratojugal-parietal contact: absent = 0; short contact = 1; long contact = 2.
5. Parietal, parietal-pterygoid contact: absent = 0; present above processus trochlearis pterygoidei = 1.

6. Parietal, temporal emargination: moderate to absent = 0; extreme = 1.
7. Parietal, interparietal scale: absent = 0; equilateral triangle = 1; elongate triangle = 2; parallel-sided = 3; broad posteriorly = 4.
8. Jugal, jugal-quadrate contact: absent = 0; present = 1.
9. Jugal, jugal-parietal contact: absent = 0; present = 1.
10. Jugal, cheek emargination: slight = 0; above lower margin orbit = 1; near top of orbit = 2.
11. Squamosal, vertical flange on ventral surface: absent = 0; present = 1; very large = 2.
12. Postorbital, size of postorbital: equal to or larger than orbit = 0; smaller than orbit = 1.
13. Premaxilla, premaxilla reaches internal nares in palate: absent = 0; present = 1.
14. Premaxilla, foramen prepalatinum in suture with maxilla: in premaxilla only = 0; in premaxillamaxillary suture = 1; absent = 2.
15. Premaxilla, foramen prepalatinum relative to triturating ridge: on flat surface = 0; under triturating ridge = 1; absent = 2.
16. Maxilla, secondary palate: absent = 0; present = 1.
17. Maxilla, secondary palate long: no = 0; yes = 1.
18. Maxilla, labial ridge: high and narrow = 0; low and thick = 1.
19. Maxilla, median maxillary ridge: absent = 0; present = 1.
20. Maxilla, accessory ridge(s): absent = 0; one or two = 1.
21. Maxilla, maxillae meet broadly on midline: absent = 0; present = 1.
22. Vomer: present = 0; absent = 1.
23. Palatine, foramen palatinum posterius: present = 0; absent = 1.
24. Palatine, median edges of cleft palate: absent = 0; parallel = 1; curved.
25. Palatine, extent of palatine contribution to triturating surface: narrow or absent = 0; moderate = 1; large = 2.
26. Palatine, dorsal process extends to parietal: absent = 0; contact made in anterior wall of fossa temporalis = 1.
27. Palatine, palatine-basisphenoid contact separates pterygoids: absent = 0; present = 1.
28. Quadrate, antrum postoticum: large = 0; smaller = 1; very small = 2.
29. Quadrate, precolumellar fossa: absent = 0; moderate = 1; deep = 2; dimple = 3.
30. Quadrate, incisura columellae auris: open = 0; closed = 1.
31. Quadrate, quadrate-basioccipital contact: absent = 0; present = 1.
32. Pterygoid, cavum pterygoidei open medially: absent = 0; small foramen = 1; small opening = 2; wide open = 3.
33. Pterygoid, cavum pterygoidei development: absent = 0; partial = 1; complete = 2.
34. Pterygoid, pterygoid flange: absent = 0; partial = 1; complete = 2.
35. Supraoccipital, exposure of supraoccipital on skull roof: none = 0; small = 1; large = 2.
36. Exoccipital, formation of occipital condyle: formed by exoccipitals and basioccipital = 0; formed by exoccipitals only = 1.
37. Exoccipital, foramen jugulare posterius: open = 0; partially closed = 1; closed by well-developed bar = 3.
38. Exoccipital, foramen nervi hypoglossi: separated = 0; combined and in a single depression = 1.
39. Basioccipital, basioccipital very short: no = 0; yes = 1.
40. Basioccipital, basa tubera: more medially located = 0; more laterally located = 1.
41. Prootic, ventral exposure of prootic: completely exposed = 0; at least partially covered = 1.
42. Prootic, pterygoid covers prootic: no = 0; at least in part = 1.
43. Prootic, foramen posterius canalis carotici interni: in prootic = 0; not in prootic = 1.
44. Opisthotic, ventral exposure of processus interfenestralis: exposed = 0; covered = 1.
45. Opisthotic, fenestra postotica: open = 0; at least partially closed = 1.
46. Basisphenoid, foramen nervi abducentis: minute = 0; moderate to large = 1.
47. Dentary, dentaries sutured at symphysis: no, fused = 0; yes = 1.

48. Articular, retroarticular process: not visible dorsally = 0; small = 1; large = 2.
49. Articular, foramen nervi chorda tympani: not enclosed in retroarticular process = 0; enclosed in retroarticular process = 1.
50. Splenial, splenial bone: present = 0; absent = 1.
51. Vertebrae, cervical central condyle shape: not saddle-shaped = 0; saddle-shaped = 1.
52. Vertebrae, biconvex cervical centrum: not second cervical = 0; second cervical = 1.
53. Vertebrae, cervical posterior zygapophyses: not fused in any cervicals = 0; fused in some cervicals = 1.
54. Shell, cervical scute: present = 0; absent = 1.
55. Shell, neurals continuous to suprapygal: present = 0; absent, some costals meet on midline = 1.
56. Shell, keeled neurals: none = 0; some = 1.
57. Shell, axillary buttress: reaches peripheral 3 = 0; reaches peripheral 2 = 1.
58. Shell, axillary musk duct location: in buttress = 0; not in buttress = 1.
59. Shell, axillary musk duct openings: not in bridge = 0; one opening in bridge = 1; three openings in bridge = 2; four openings in bridge = 3.
60. Shell, mesoplastra: meet medially = 0; reduced and lateral = 1; absent = 2.
61. Shell, pectoral scutes contact mesoplastron: yes = 0; no = 1.
62. Shell, pectoral scutes contact entoplastron: no = 0; yes = 1.
63. Shell, pectoral scutes contact epiplastron: no = 0; yes = 1.

APPENDIX 2

Data matrix for 22 taxa used to estimate the phylogenetic position of *Caninemys*.

Characters 7, 14, and 29 were not used in the final analysis. Characters 4, 25, 28, 33, 34, 37, and 48 were run ordered. Characters and character states are in appendix 1.

Outgroup
00000000000000000000000000000000000000000000000??0000000???00??

Chelidae
0(01)000000030001000000010000000110000101000000000(01)000000010???2?11

Pelomedusidae
100001100100122000000100(01)00021000001100000000(01)001010110???1000

Araripemys
10000100010010000000001000000100000000000000000?10010111(01)0???2?00

Euraxemys
10010000010000000000000000001000000100000000111?1111011100???1000

Bothremydidae
1(01)0(01)000(01)0000000000000000(01)00(01)00100001(01)00110111?02?101?1(01)0???10(01)?

Hamadachelys
110100200100???00000?0000001111111?0100011111?0??1?????????1???

Bauruemys
?1010?1001100010000000001001011122101000111110?1010??110???1111

Podocnemis erythrocephala
1112001011011010001101001001111322102001111111010111011010 21111

Podocnemis expansa
111210201111011000111100100131122210200111111101011101101111111

Podocnemis lewyana
1112102011010010001101001001111122102001111111010111011 01?31111

Podocnemis sextuberculata
111210201101111000110100100131122210200111111101011101111121111

Podocnemis unifilis
111200201100001000111100100111112210200111111101011101111121111

Podocnemis vogli
111200101101001000110000100111112210200111111101011101100131111

Erymnochelys
100200210000101000100100100111132200200111111001110101101001111

Peltocephalus
1002004100001220001001001001311322 0(01)2001111110011111011 00001111

“*Roxochelys*”
1102101002100010000000001001311122002001111110010?1?01100??10??

Neochelys
10021010001010100000010010013113220?2?0111111?011????1100??1???

Caninemys
1102?02000100010001100001002011?22?0200111111??????????????????

Dacquemys
1002?01000?00220001111001001311?22202001111110?????????????????

Shweboemys
100?10?????0100111000111211???1?22?02111111110?????????????????

Stereogenys
1002103??0?0?22111000111211?011?22?02111111110021??????????????