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## *Chubutemys*, a New Eucryptodiran Turtle from the Early Cretaceous of Argentina, and the Relationships of the Meiolaniidae

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### ABSTRACT

*Chubutemys copelloi* is the oldest nonmarine cryptodire from South America represented by a skull. The skull and associated postcranial fragments are from the Aptian Cerro Costaño Member of the Cerro Barcino Formation of Chubut, Argentina. *Chubutemys* has a processus trochlearis oticum, showing that it is a cryptodire, and an enclosed canalis caroticus internus extending to the posterior margin of the pterygoid, showing that it is a eucryptodire. The skull of *Chubutemys* is similar to that of other primitive eucryptodires, particularly *Dracocheilus*, but also to *Hangaiemys*, *Judithemys*, *Sinemys*, and *Ordosemys*. *Chubutemys* differs from all these, however, in possessing a solidly roofed skull, formed by long, wide parietals, rather than a posterior emargination. *Chubutemys* also differs from these taxa in having no cheek emargination.

A phylogenetic analysis using PAUP\* analyzed 104 parsimony-informative characters resolving into one most parsimonious cladogram of 224 steps, a consistency index of 0.55, and a retention index of 0.74. The phylogenetic analysis weakly joins *Chubutemys* and meiolaniids on the basis of the prefrontal-postorbital contact. *Chubutemys* also has a fully roofed skull and slitlike posterior opening of the foramen caroticum laterale (foramen posterius canalis caroticus laterale), features to be expected in a meiolaniid sister taxon. *Chubutemys* provides further evidence that meiolaniids

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are related to “basal” eucryptodires (“sinemydids/macrobænid”), that is, eucryptodires outside the living Cryptodira, the Polycryptodira.

The basicranial morphology of meiolaniids, with an intrapterygoid slit, rather than being a unique feature of the group is instead a modified state of the primitive eucryptodire condition, as seen in such forms as *Chubutemys*, *Dracochelys*, *Ordosemys*, and *Sinemys*. The intrapterygoid slit of meiolaniids is homologous with the pterygoid flange associated with the foramen caroticum laterale (foramen posterius canalis caroticus laterale of Sukhanov) in non-Polycryptodiran eucryptodires like *Ordosemys*.

*Chubutemys* shows that nonmarine eucryptodires were present in South America in the Cretaceous, as they were in North America, central Asia, and Australia.

## INTRODUCTION

The record of nonmarine cryptodires in South America is very sparse, particularly in comparison to the more abundant pleurodires. There is a record of marine cryptodires from the Jurassic, but the nonmarine record has been restricted to the eucryptodiran Meiolaniidae from the late Cretaceous–Paleogene. Recent vertebrate paleontological field explorations (Rich et al., 1998) in the Early Cretaceous of the Province of Chubut, Argentina, have yielded the oldest skull of a South American cryptodire and the oldest record of a nonmarine cryptodire from South America. The only older cryptodire is the late Jurassic (Tithonian) *Neusticemys neuquina* (Fernandez and Fuente, 1993), a presumably marine form attributed to the “Plesiochelyidae-Thalassemydidae” by Gasparini and Fernandez (1997) and the “?Plesiochelyidae” by Fernandez and Fuente (1993). *Neusticemys neuquina* occurs with the pleurodire *Notoemys*. The skull and cervical vertebrae of *Neusticemys neuquina* are unknown and thus its more precise relationships are indeterminate at present. Broin (1993) listed some Jurassic localities that have yielded turtles, none identified as nonmarine cryptodires. Broin and Fuente (1993b: 182) also listed “chelyidae primitifs” from the Rio Limay Formation, thought to be Cenomanian–Turonian, but the basis of the identification is unknown and these must be considered Testudines indet. until described.

The Albian Santana Formation (Maisey, 1990, 1991) has yielded a protostegid marine cryptodire (Hirayama, 1998) that is probably later in time than the Chubut cryptodire. The University of California has a skull and partial skeleton (UCMP 38346) of an undescribed chelonoid from the vicinity of Bogota, Colombia (V 4538), that may be Aptian-

Barremian in age (Welles, 1962) and thus as old as or older than the Chubut cryptodire. However, this material has never been described and its age is not substantiated.

Later records of cryptodires in South America that postdate the Aptian Chubut cryptodire consist of meiolaniids:

1. Los Alamitos Fm., Rio Negro Province, Argentina, Campanian–Maastrichtian, described by Broin (1987).
2. Salinas de Trapalco, Rio Negro Province, Argentina, Campanian–Maastrichtian, undescribed fragments reported by Broin and Fuente (1993a,b).
3. Sarmiento Fm., Chubut Province, Argentina, Eocene, tail ring described by Fuente and Fernandez (1992).
4. *Niolamia argentina*, Cretaceous or Eocene, Chubut Province, complete skull, see Gaffney (1996) for most recent appraisal.

Another record, identified as a pleurodire: “grand Chelyidae primitif” by Broin and Fuente (1993b, see Discussion below), is probably a cryptodire similar to *Chubutemys* described here.

Although cladistic analysis has been the norm for phylogenetic work (at least in morphology) for decades, recently some have argued that there are limitations in the Linnaean classification system that require its complete abandonment in favor of an alternative, the PhyloCode, incorrectly called by some, “Phylogenetic Taxonomy” (De Queiroz and Gauthier, 1992). Although we do see some problems with the Linnaean system as an exact mirror of a cladogram, with taxon names that can change in content with every addition or subtraction of a basic taxon or character, we do not think that abandonment and creation of a new system is

the answer. We take a more traditional view, similar to that expressed by Gaffney et al. (2006; see also Nixon and Carpenter, 2000; Carpenter, 2003; Nixon et al., 2003; Schuh, 2003), that it is better to modify the Linnaean system where convenient, rather than set up a new one, particularly a rankless one. An extreme example of the abandonment of the more traditional system of turtle classification is the Joyce et al. (2004) version of the PhyloCode (q.v.) in which most of the previously named higher taxa of turtles, including the name Cryptodira, have been replaced or redefined with new content. Although this exercise claimed to improve stability in turtle nomenclature, it is obvious that the opposite is the case. In fact, the two proponents of new higher category definitions and names for turtles (Lee, 1995; Joyce et al. 2004) do not themselves agree on the taxon names or definitions. Another classification aspect is the use of geological range in naming groups, the “stem” and “crown” nomenclature, referring to whether taxa include living species. We think that since extinction is not an element of the cladogram, it should not be an element of the classification, which is cumbersome enough without the added burden of geological range. Therefore, we use the higher taxon names for cryptodires explicated in Gaffney (1996) for the taxa that are relevant in this discussion of *Chubutemys*.

The anatomical terminology used here is developed in Gaffney (1972, 1979). The term “foramen caroticum laterale” as currently used actually refers to both a more anterior foramen opening into the braincase floor and a more posterior foramen opening on the roof of the palate, with the canalis caroticus lateralis (Gaffney, 1979 and others) connecting them. Sukhanov (2000) used the term “foramen posterius canalis caroticus laterale” for the posterior foramen, and we have adopted that usage here.

The Chubut cryptodire is most similar to a series of largely Mesozoic eucryptodires usually grouped as the family Sinemydidae (Gaffney, 1996; Sukhanov, 2000), but which may also be interpreted as successive, paraphyletic, sister taxa to the Polycryptodira of Gaffney (1984, 1996). As has been done in previous literature (Brinkman and Peng,

1993a, 1993b; Brinkman and Wu, 1999; Gaffney, 1996; Gaffney and Ye, 1992; Parham and Hutchison, 2003; and Sukhanov, 2000), we refer to these early eucryptodires as “Sinemydidae/Macrobaenidae” for convenience and to indicate the inconsistent nature of phylogenetic analyses of these taxa. Earlier works that have reviewed some of these taxa are Brinkman and Peng (1993a, 1993b), Brinkman and Wu (1999), Gaffney and Ye (1992), Gaffney (1996), Parham and Hutchison (2003), and Sukhanov (2000). Specific taxa that have skulls and/or postcrania particularly relevant to the description of the Chubut cryptodire and that are referred to in this text are:

1. *Dracochelys*: Gaffney and Ye (1992), Brinkman (2001).
2. *Ordosemys*: Brinkman and Peng (1993a), Brinkman and Wu (1999).
3. *Xinjiangchelys*: Peng and Brinkman (1993b), Kaznyshkin et al. (1990).
4. *Hangaiemys*: Sukhanov and Narmandakh (1974), Sukhanov (2000), Parham and Hutchison (2003).
5. *Sinemys*: Brinkman and Peng (1993b).
6. Meiolaniidae (including *Meiolania*, *Ninjemyx*, *Warkalania*, and *Niolamia*): Gaffney (1983, 1996).
7. *Otwayemys*: Gaffney et al. (1998). See Smith (1999) for another possible Australian eucryptodire from the early Cretaceous.
8. *Judithemys*: Gaffney (1996, as TMP 87.2.1), Parham and Hutchison (2003). Skull figured in fig. 13.
9. *Macrobaena*: Tatarinov (1959).

#### INSTITUTIONAL ABBREVIATIONS

CNEA	Comisión Nacional de Energía Atómica
MACN	Museo Argentino de Ciencias Naturales
MPEF	Museo Paleontológico Egidio Feruglio
TMP	Tyrell Museum of Paleontology
UCMP	University of California at Berkeley

#### ANATOMICAL ABBREVIATIONS

bo	basioccipital
bs	basisphenoid

cci	canalis caroticus internus
ex	exoccipital
fc	foramen caroticum basisphenoidale
fpcci	foramen posterius canalis carotici interni
fpcl	foramen posterius canalis caroticus laterale
fpp	fenestra palatinum posterius
fr	frontal
ju	jugal
mx	maxilla
op	opisthotic
pa	parietal
pal	palatine
pf	prefrontal
po	postorbital
pt	pterygoid
qj	quadratojugal
qu	quadrate
so	supraoccipital
sq	squamosal
vo	vomer

### SYSTEMATICS

#### ORDER TESTUDINES LINNAEUS, 1758

#### INFRAORDER CRYPTODIRA COPE, 1864

#### PARVORDER EUCRYPTODIRA GAFFNEY, 1975

#### FAMILY INDETERMINATE ("SINEMYDIDAE/MACROBAENIDAE")

#### *Chubutemys*, new genus

TYPE SPECIES: *Chubutemys copelloi*, new genus and species.

DISTRIBUTION: Aptian, Early Cretaceous, Cerro Costaño Member, Cerro Barcino Formation.

ETYMOLOGY: Chubut, for province of Argentina in which it was found.

DIAGNOSIS: A genus of eucryptodire known only from the skull, similar to *Dracochelys*, *Hangaemys*, and *Ordosemys*; nasal-frontal contact absent in contrast to *Ordosemys*; frontal does not enter orbit in contrast to *Dracochelys*, *Ordosemys*, *Hangaemys*, and *Sinemys*; temporal roof broadly covered by parietals extending posterior to otic chamber in contrast to the deep emargination seen in *Hangaemys*, *Judithemys*, *Ordosemys*, and *Sinemys* (and probably

*Dracochelys*, although the temporal roof is incompletely known); broad parietal-squamosal contact in contrast to *Dracochelys*, *Ordosemys*, *Hangaemys*, and *Sinemys*; cheek emargination absent in contrast to *Dracochelys*, *Hangaemys*, *Judithemys*, *Ordosemys*, and *Sinemys*; triturating surface narrow as in *Ordosemys* and *Sinemys*, but not very narrow as in *Dracochelys* and *Hangaemys*; foramen palatinum posterius similar in size to that in *Ordosemys*, not very large as in *Dracochelys* and *Hangaemys*; deep pit on pterygoid absent in contrast to *Dracochelys* and *Ordosemys*; foramen posterius canalis caroticus laterale exposed in ventral view, widely separated from foramen caroticum basisphenoidale, and formed in gap between pterygoid and basisphenoid as in *Dracochelys* and *Niolamia*, in contrast to more posterior position as in *Hangaemys*, *Judithemys*, *Sinemys*, and *Ordosemys*; canalis caroticus internus only partially floored by bone along contact of basisphenoid and pterygoid as in *Dracochelys*, *Hangaemys*, *Ordosemys*, and *Sinemys*; foramen caroticum basisphenoidale formed entirely by basisphenoid and open ventrally as in *Dracochelys*, *Ordosemys*, *Hangaemys*, and *Sinemys*; basisphenoid triangular in ventral view as in *Dracochelys* and *Niolamia*, not rectangular as in *Ordosemys* and *Hangaemys*.

#### *Chubutemys copelloi*, new species

TYPE SPECIMEN: MPEF-PV1236, a partial skull lacking much of the bone from its dorsal surface, but with an internal mold of it present, ventral surfaces preserved intact with stapes in situ, atlas elements disarticulated, and a piece of presumed hyoid in right temporal fossa.

TYPE LOCALITY: "Turtle Town", 43°36'S, 68°55'W (figs. 1–3; Rich et al., 1998: fig. 1), Chubut Province, Argentina.

HORIZON: Cerro Castaño Member (fig. 3), Cerro Barcino Formation, Chubut Group, Aptian (Codignotto et al., 1978; Rich et al., 1998; Rauhut et al., 2003) based on the work of two of the authors, T. Rich and A. Constantine.

DIAGNOSIS: as for genus.

ETYMOLOGY: For Maria Copello, who discovered the holotype.

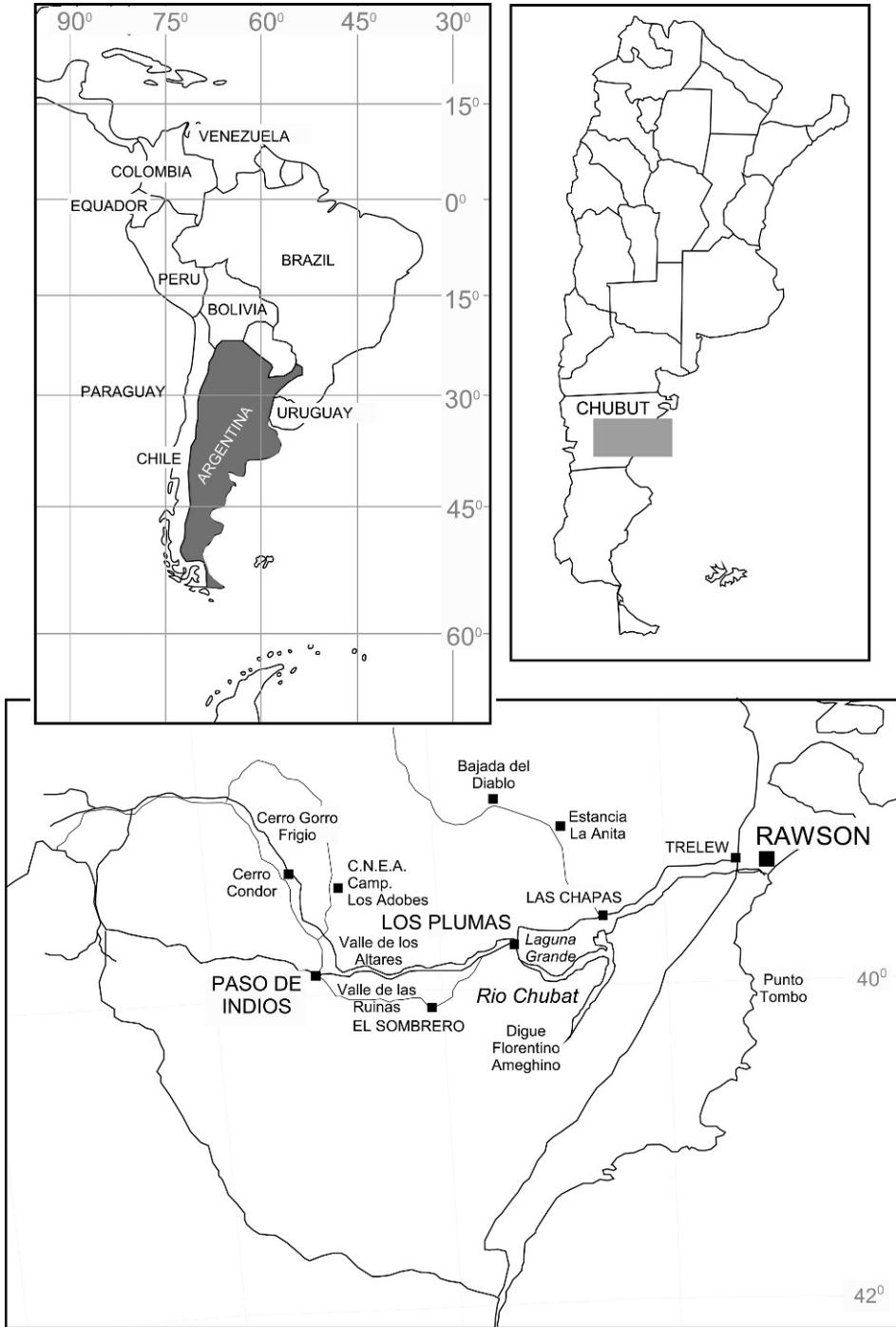


Fig. 1. Regional location maps showing the position of the type locality of *Chubutemys copelloi*, n. gen. et sp. MPEF-PV1236 (from Rich et al., 1998).

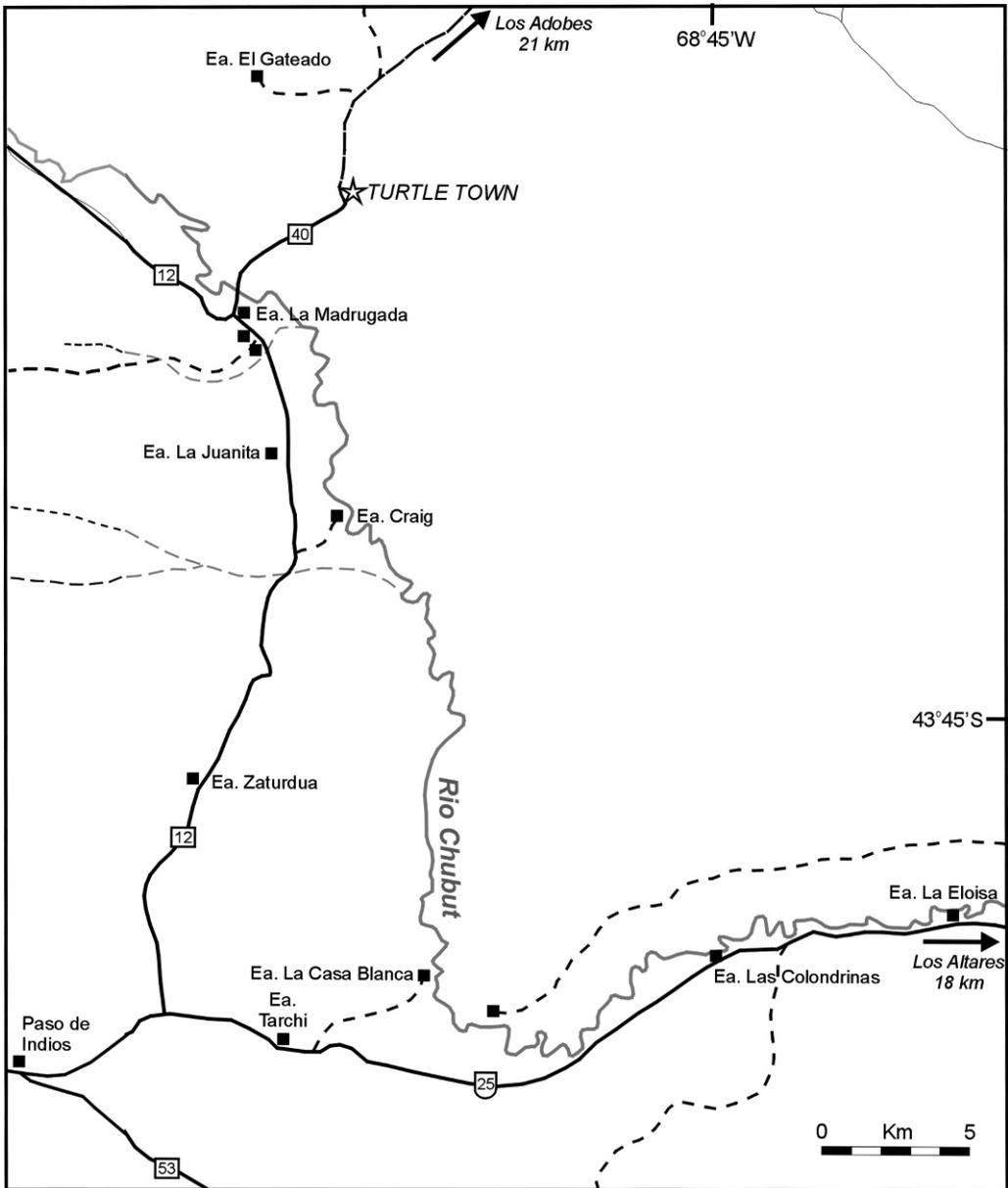


Fig. 2. Detailed location map (from 250K topographic map) showing the position of the type locality of *Chubutemys copelloi*, n. gen. et sp. MPEF-PV1236.

**REFERRED MATERIAL:** The locality that yielded the skull of *Chubutemys* also coughed up enough turtle remains to cause its giddy discoverers to call it “Turtle Town” (figs. 1–3; Rich et al., 1998: fig. 1). The fossils from the site consist of shell and postcranial fragments of cryptodires and pleurodires, as well as the

skull described here. No shell or postcranial material was found directly associated with the type skull of *Chubutemys*. However, there are postcranial elements that probably belong to *Chubutemys*. The cryptodire material is identifiable because it consists of a partial carapace with anterior thoracic centra and an

articulated eighth cervical, as well as peripherals, including bridge peripherals, that are very similar to the "sinemydid/macrobænid" postcrania described for *Dracochelys*, *Ordosemys*, *Hangaiemys*, *Judithemys*, and *Otwayemys*. The shell fragment with an eighth cervical, MPEF PV1940, is identified as a cryptodire on the basis of the widely spaced zygapophyses and the close agreement of this cervical with those of *Ordosemys* and *Dracochelys* (see below). Three sets of peripherals are also identified as cryptodire and probably belong to *Chubutemys*. These are MPEF PV1941, PV1942, and PV1943. They are very similar to peripherals figured by Brinkman (2001) for *Dracochelys*. They are relatively flat, show extensive costo-peripheral fontanelles, and have dorsally concave guttering as in *Dracochelys*.

There is at least one other species of turtle at this locality, a chelid pleurodire much smaller than *Chubutemys*. Most of these chelid bones differ from the cryptodire in being at least half the size and in having a very differently shaped shell with fused pelvis, no costo-peripheral fontanelles, and finely incised sulci.

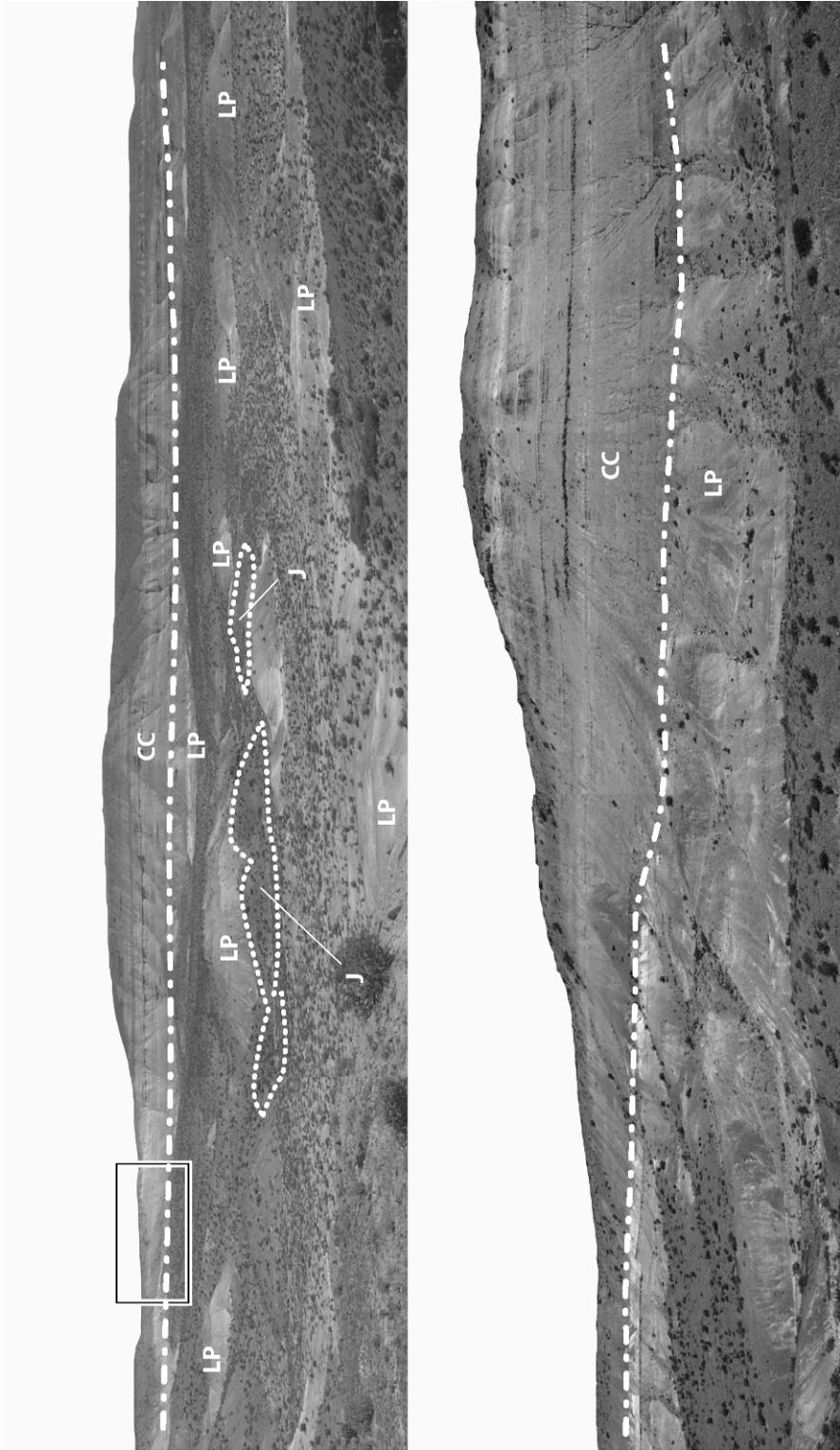
**DISCUSSION:** Discovery of a definitive, skull-based eucryptodire in the Early Cretaceous of Argentina prompts reexamination of the published record, which has generally referred nonmarine turtles to the Pleurodira or Meiolaniidae (Broin and Fuente, 1993). Much of this material is too fragmentary to reassess with confidence, but two specimens previously identified as pleurodires are probably cryptodires. These were originally identified as "grand Chelidae primitif indéterminé" (Broin and Fuente, 1993b: fig. 5, 18–19) from the Los Alamitos, Rio Negro, Late Cretaceous. Both specimens are in the Museo Argentino de Ciencias Naturales and have been examined by the senior author (E.S.G.). MACN 907 was identified as a fifth cervical, but it is very similar to the undoubted eighth cervical of MPEF PV1940. Both are biconvex with a narrowed centrum and a wide, midway positioned transverse process, distinct from any described chelid. MACN 907 lacks the neural arch as well as the zygapophyses. The principal difference between them is that the anterior central articulation of MPEF PV1940 is slightly larger than the posterior

one, whereas in MACN 907 they are closer in size. The other specimen, MACN 908, identified as an eighth cervical (Broin and Fuente, 1993), probably is an eighth; it agrees closely with MACN 907 but lacks transverse processes and a neural arch and only shows a biconvex centrum, so its identity must remain ambiguous. Nonetheless, it is very likely that MACN 908 is also a eucryptodire, along with MACN 907.

## GEOLOGY

**LOCATION:** The "Turtle Town" fossil locality (Rich et al., 1998) is situated in the center of Chubut Province approximately 32 km north of Paso de Indios, on the north side of the Rio Chubut (figs. 1–3). Most of the best turtle remains were found at a site (site A: 43°35'51"S, 68°54'37"W) approximately 150 m east of the road (Route 40) leading north to the Los Adobes Mine, while a second, less productive site (site B: 43°35'52"S, 68°54'45"W) approximately 400 m to the west of the site A, but on the opposite side of the road, has also yielded a few turtle fragments in addition to a large sauropod phalanx and a well-preserved seed cone.

**STRATIGRAPHY:** The Early Cretaceous Chubut Group of Argentina is a sequence of fossiliferous nonmarine epiclastic and pyroclastic sediments up to 1500 m thick (Figari and Courtade, 1993) that crop out over a large part of central Patagonia. The sediments unconformably overlie Middle–Late Jurassic volcanics and nonmarine sediments of the Cañadón Asfalto and Marafil Formations, and are unconformably overlain by latest Cretaceous (Campanian–Maastrichtian) continental to marginal marine to marine sediments of the La Colonia, Paso de Sapo, and Lefipan Formations (Figari and Courtade, 1993). The Chubut Group is presently divided into two formations called the Los Adobes Formation and Cerro Barcino Formation, based on sediment composition and depositional process. The older Los Adobes Formation is dominated by epiclastic sediments derived from the underlying Jurassic volcanic basement (unpublished CNEA report: Cerro Solo 1998, Un Proyecto Para La Produccion de Uranio y Molibdeno en la Patagonia. CAE–UAG



Geologia Economica y Regional Patagonia). It is thought to be Late Valanginian–Hauterivian in age (Cortiñas, 1996; Page et al., 1999) and is subdivided into two units called the Arroyo del Pajarito Member and Bardas Coloradas Member. The lower unit, the Arroyo del Pajarito Member, is represented by up to 150 m of yellowish-gray to orange-brown, interbedded sandstone, pebbly sandstone, pebble-cobble conglomerate, and minor shale deposited in a high-energy, low-sinuosity fluvial environment. The overlying Bardas Coloradas Member is up to 30 m thick and is composed largely of red to reddish-brown shale and minor fine-grained sand deposited in a lower energy fluvial overbank environment. Both units are well exposed at the Los Adobes Mine (43°21'43S, 68°45'22"W) approximately 32 km north-northeast of "Turtle Town", while another good exposure of the Bardas Coloradas Member can be found on the road leading up to the La Baritina Mine (43°28'35"S, 68°56'09"W) approximately 15 km to the north.

The Cerro Barcino Formation, in contrast, contains large volumes of pyroclastic sediments and is thought to be late Hauterivian to Cenomanian in age (Page et al., 1999). It is currently subdivided into five units called (in ascending stratigraphic order) the La Paloma, Cerro Castaño, Las Plumas, Puesto Manuel Arce, and Bayo Overo Members. Only two of these units crop out in the vicinity of "Turtle Town": the La Paloma Member and Cerro Castaño Member.

The La Paloma Member (fig. 3) is a sequence of interbedded pale light gray, pale bright green, and pale reddish-brown (occasionally deep red and purple) tuff, siltstone, claystone, and rare, very fine to fine-grained sandstone and limestone up to 35 m thick that conformably overlie the Bardas Coloradas Member of the Los Adobes Formation. The basal contact is well exposed at several localities on the northern (43°12'03"S, 68°52'26"W) and southwestern (43°13'32"S,

68°57'24"W) sides of Cerro Chivos approximately 45 km north of "Turtle Town".

The Cerro Castaño Member (fig. 3) is a sequence of interbedded reddish-brown, brown, and pale gray (occasionally white, yellowish brown, and pale orange-brown) tuffs, siltstone, and fine to coarse-grained sandstone in excess of 90 m thick that conformably overlie the La Paloma Member. The difference in color between these two units is quite dramatic when both are present in the same outcrop. The contact is often very sharp, and in some places, a thin lenticular coarse-grained sandstone with intraformational clasts can be found at the base of the Cerro Castaño Member.

All of the vertebrate fossils recovered from "Turtle Town" were found lying on the upper surface of outcrops of the La Paloma Member. In this area, Los Adobes Formation is absent and the La Paloma Member rests unconformably on the Jurassic Lonco Trapial Formation. The basal contact is well exposed in a 1.5-km-long section of cliffs up to 30 m in height on the northeastern side of the Rio Chubut (43°35'51"S, 68°56'44"W) approximately 2 km west of "Turtle Town". Here the La Paloma Member dips very gently (<2°) to the east and infills/blankets the top of the Lonco Trapial Formation, which can vary in relief up to 12 m over a distance of approximately 100 m (fig. 3). The basal unconformity is also exposed in the floor of a broad gully about 1.5 km northwest of "Turtle Town" (43°35'29"S, 68°57'05"W) where several small mounds of Jurassic basement can be seen protruding up to 4 m above the surrounding La Paloma Member sediments in the floor of the depression.

The depositional setting of the La Paloma Member at "Turtle Town" is difficult to assess due to the abundance of clay minerals in the sediments, which upon weathering effectively destroy all sedimentary structures. Consequently, the upper surface of the La Paloma Member on gentle to moderate slopes

←

Fig. 3. Upper, view looking west (43°35'29"S, 68°57'05"W) at outcrops of Lonco Trapial Formation (J) protruding above La Paloma Member (LP) sediments in floor of gully, Cerro Castaño Member (CC) visible in background; lower, enlarged view of area shown in box in left side of upper view, line is contact between La Paloma Member (LP) and Cerro Castaño Member (CC).

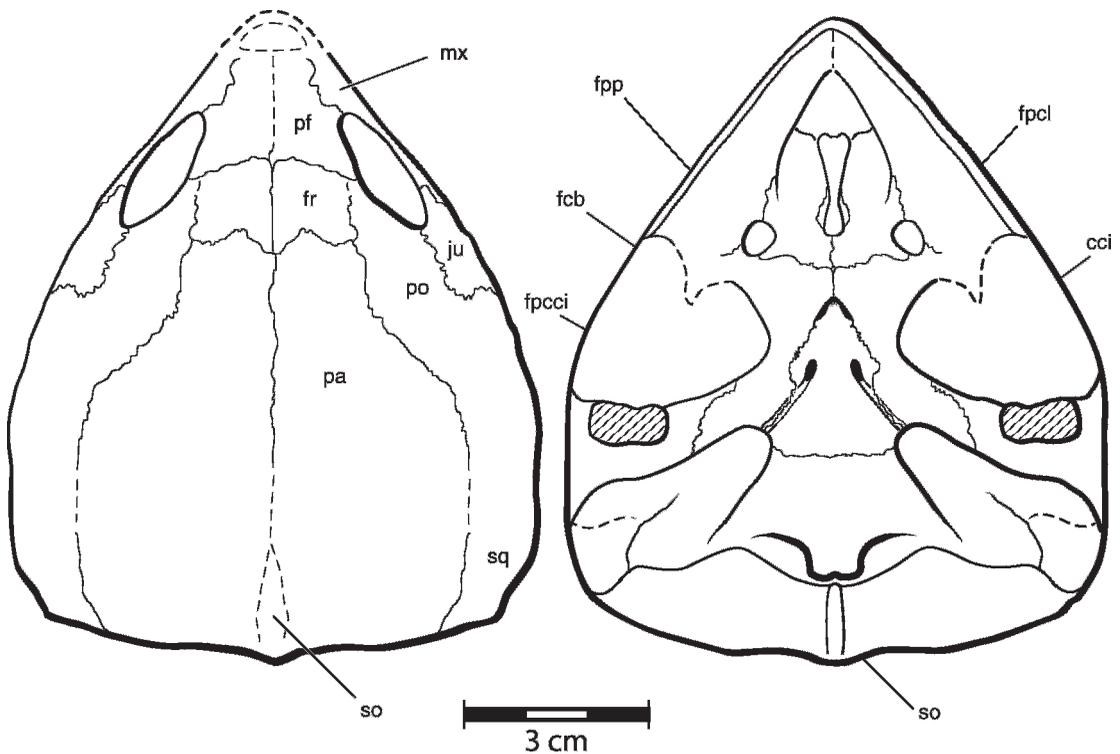


Fig. 4. *Chubutemys copelloi*, n. gen. et sp. MPEF-PV1236. Restored skull: left, dorsal; right, ventral.

(< 30°) often has a “popcorn-like” appearance with a deep weathering profile. This problem is further compounded by sediment being washed down the slopes from higher up, which masks the outcrop lower down and necessitates trenching to reveal the true color and lithology of the underlying sediments.

Mapping in the area of site A indicates that the vertebrate remains found at this location are from a thin band of silcrete less than 1 cm thick that contains abundant, randomly oriented, millimeter- to centimeter-sized pieces of silicified plant fragments and stems of branches up to 1 cm in diameter and occasionally short sections of tree trunks up to 20 cm in width. The silcrete band crops out along the top of a ridge and forms small pavement surfaces. The silcrete band occurs above a 1.8-m-thick laminated pale gray calcareous siltstone that in turn overlies an 8-m-thick bright green massive tuff. Both facies are weakly bioturbated in places, which suggests the plant matter in the fossiliferous

silcrete band probably accumulated on the floor or edge of a lake prior to cementation.

#### MORPHOLOGIC DESCRIPTION

Figure 4 is a partially restored view of the skull, figs. 5–9 are stereophotographs of the skull and fig. 10 is a key to the stereophotographs. The reader should also see tables 1 and 2.

#### NASAL

The anterior end of the skull is badly eroded; nasals could have been present or absent.

#### PREFRONTAL

The external surface of both prefrontals is badly eroded but enough remains on the right side to see a maxilla contact anterolaterally and a frontal contact posteriorly. As preserved, the

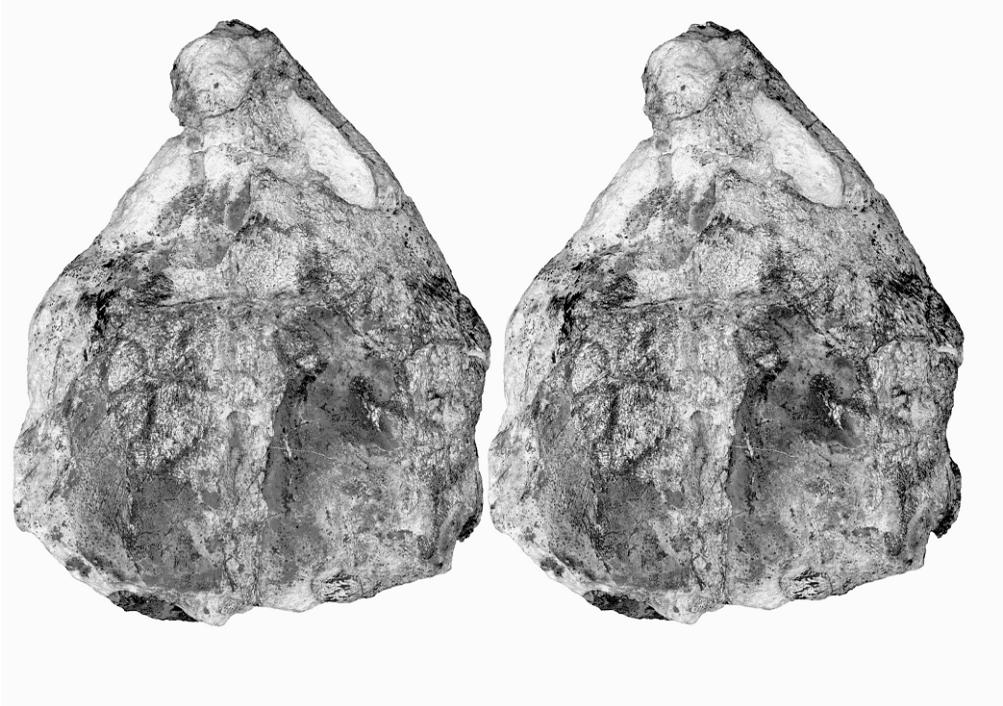


Fig. 5. *Chubutemys copelloi*, n. gen. et sp. MPEF-PV1236, holotype. Dorsal view of skull.

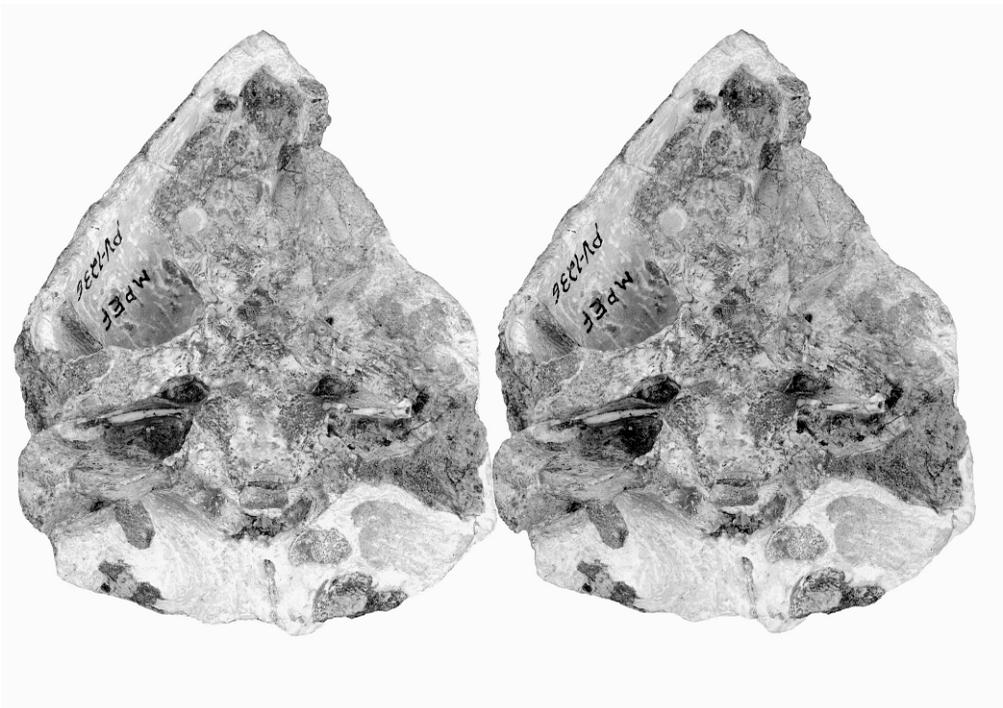


Fig. 6. *Chubutemys copelloi*, n. gen. et sp. MPEF-PV1236, holotype. Ventral view of skull.

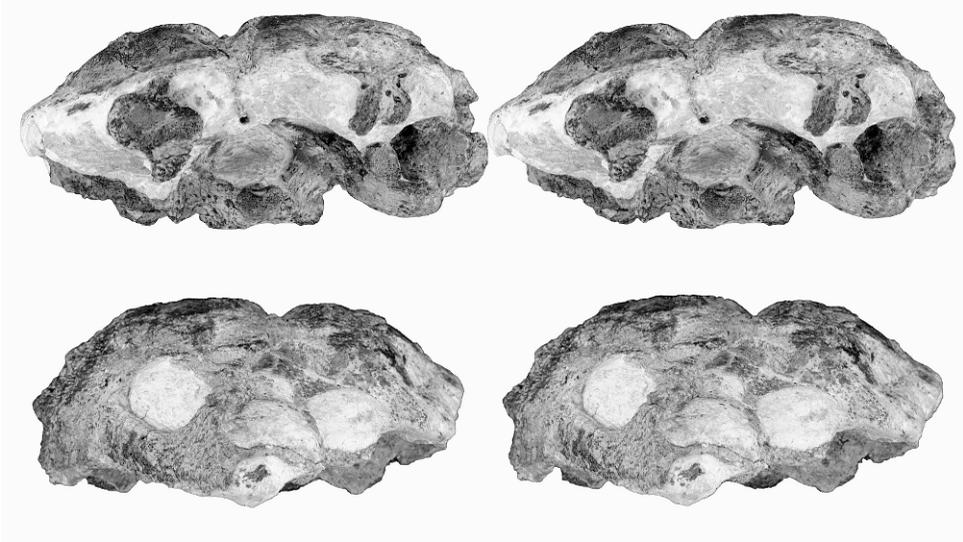


Fig. 7. *Chubutemys copelloi*, n. gen. et sp. MPEF-PV1236, holotype. Upper, posterior view of skull. Lower, anterior view of skull.

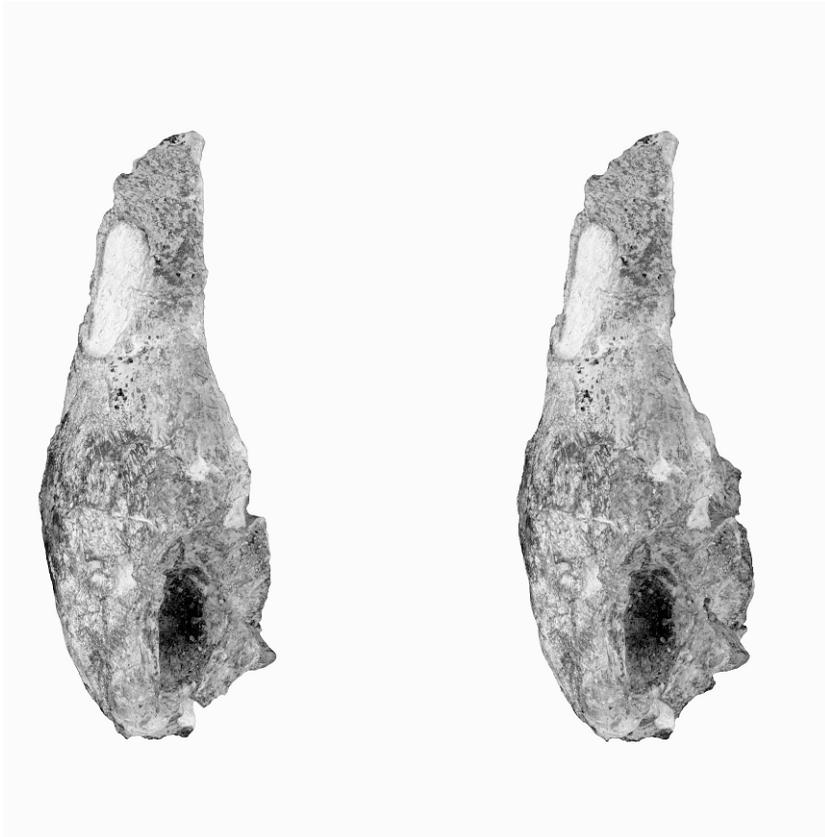


Fig. 8. *Chubutemys copelloi*, n. gen. et sp. MPEF-PV1236, holotype. Right lateral view of skull.

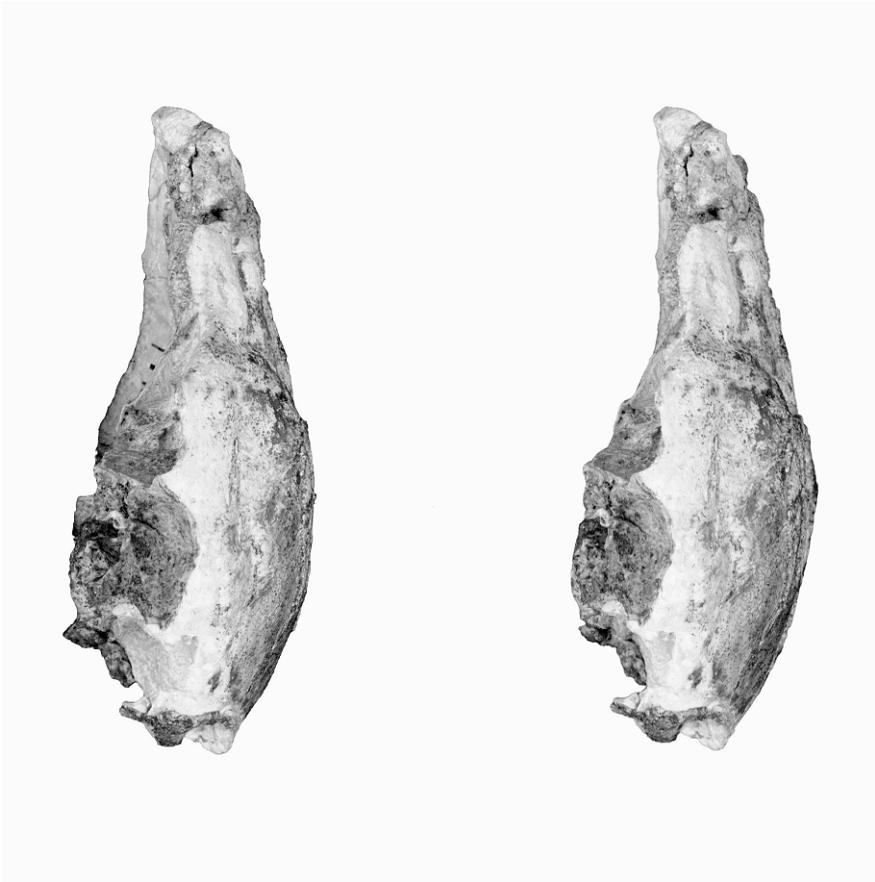


Fig. 9. *Chubutemys copelloi*, n. gen. et sp. MPEF-PV1236, holotype. Left lateral view of skull.

prefrontal meets the other prefrontal in a long midline suture completely preventing the frontal-nasal contact and anterior frontal contact seen in *Ordosemys*. The prefrontal of *Chubutemys* as preserved is consistent with both *Dracochelys* and *Hangaiemys*.

#### FRONTAL

Most of the right frontal is preserved, but the dorsal surfaces are eroded off. The left frontal is largely represented by a mold in matrix of its internal surface. The frontal of *Chubutemys* is relatively small and does not seem to reach the orbital margin due to a prefrontal-postorbital contact. Such a contact is present in *Meiolania* and absent in *Dracochelys*, *Ordosemys*, and *Hangaiemys*, although only a relatively narrow projection

of frontal reaches the orbit in those forms. However, the poor preservation of the frontal in *Chubutemys* must be kept in mind.

#### PARIETAL

Most of both parietals has been eroded off and all of their external surface is missing. However, the internal mold of the bone in the matrix retains most of the sutures (figs. 5, 10). The parietal of *Chubutemys* is a large rectangular element, contacting the frontal anteriorly and the postorbital anterolaterally. Posterolaterally, a suture with the squamosal can be made out on each side, but the postorbital-squamosal (or quadratojugal) suture is too damaged to be seen clearly.

*Chubutemys* differs significantly from the similar *Dracochelys*, as well as from the other

TABLE 1  
Comparison of *Chubutemys* and Other Eucryptodires

	Chubutemys	Dracocheyls	Ordosemys	Hangatemy	Metolamia	Nirolamia
Nasals	?	?	present	present	present	?
Nasal-frontal contact	no	?	yes	no	yes	?
Frontal enters orbit	no	yes	yes	yes	no	?
Temporal emargination	no	?	yes	yes	no	no
Broad parietal-squamosal contact	yes	no	no	no	yes	?
Squamosal-supraoccipital contact	no	no	no	no	yes	?
Parietal reaches posterior margin of otic chamber	yes	no	no	no	yes	yes
Cheek emargination	absent	present	present	present	absent	absent
Squamosal size	large	?	small	small	large	?
Triturating surface	narrow	very narrow	narrow	very narrow	wide	wide
Vomer contacts pterygoid	no	yes	yes	yes	yes	?
Foramen palatinum posterius	intermediate	very large	intermediate	very large	very small	?
Deep concavity on quadrate process of pterygoid	no	yes	yes	yes	no	no
Path of palatine artery exposed ventrally	yes	yes	yes	yes	yes	yes
Pterygoid-exoccipital contact	no	yes	yes	no (?)	yes	?
Foramen jugulare posterius closed	?	?	?	no	yes and no	?
Basioccipital	long	long	short	long	short	?
Tuberculum basioccipitale	large	small	large	small?	small	small
Basisphenoid shape	triangular	triangular	rectangular	rectangular	very small	probably triangular
Basisphenoid with posterolateral processes	no	yes	no	no	no	?
Foramen posterius canalis caroticum laterale close to foramen posterius canalis carotici interni	no	no	yes	yes	indeterminate	no

TABLE 2  
Measurements of Type Skull of *Chubutemys*,  
MPEF-PV-1236 (in mm)

Midline length from premaxilla to posterior margin of parietals	97.0
Midline length from premaxilla to occipital condyle	85.7
Maximum width	76.0
Width between orbits	18.2 <sup>a</sup>
Width of right orbit	23.3 <sup>a</sup>
Height of right orbit	10.1 <sup>a</sup>
Width of internal nares	13.2
Maximum height at quadrate	37.7 <sup>a</sup>
Skull height at occipital condyle	30.3

<sup>a</sup>Damaged.

“sinemydids/macropaenids”, *Judithemys*, *Sinemys*, *Ordosemys* and *Hangaemys*, in having no temporal emargination. The parietal of *Chubutemys* extends well posterior to the posterior edge of the otic chamber. The supraoccipital is present in part between the parietals, but the sutures are unclear. *Meiolania* has an extensive temporal roof, but this is the result of a large squamosal and a laterally expanded supraoccipital. The parietal in *Meiolania* is relatively small, nearly square, and much smaller than the parietal in *Chubutemys*. Nonetheless, the parietal of *Meiolania* does agree with *Chubutemys* in reaching the posterior edge of the otic chamber and broadly contacting the squamosal.

The skull roof in *Macrobaena* (Tatariniv, 1959) also lacks temporal emargination, but it is too poorly known for the composition of the skull roof to be determined from the literature. For this reason *Macrobaena* is not included in our data set and has not been included in other authors' data sets.

Near the posterior edge of the parietal in MPEF-PV1236 are the two atlantal neural arches, disarticulated from the atlas (fig. 10).

#### JUGAL

The jugal is present on the right cheek (figs. 8, 10), though not well defined, and is largely missing on the left. There is what appears to be the anterior contact with the maxilla and the posterior contact with the quadratojugal. The postorbital-quadratojugal

contact is unclear, and some of the dorsal suture around the jugal is presumably with the postorbital. As interpreted, the jugal is a relatively large element, making up most of the cheek. There is no cheek emargination, and the jugal makes a slight posteroventral extension comparable to the one in *Meiolania*. *Ordosemys*, *Dracochelys*, and *Hangaemys* have a cheek emargination and a much smaller jugal than that in *Chubutemys*.

#### QUADRATOJUGAL

It is likely that the bone area posterior to what we have identified as jugal on the right side of MPEF-PV1236 is the quadratojugal (fig. 10C), in which case it probably contacts the postorbital dorsally, but its relationships to the squamosal or anything else are unknown.

#### SQUAMOSAL

Very little bone representing the squamosal is present on either side, but the mold in the matrix on the right side shows what appears to be the squamosal and its broad contact with the parietal (fig. 10A, C).

#### POSTORBITAL

Much of the postorbital is present on the right side (figs. 8, 10), and an internal mold of some of it is present on the left. Sutures are probably with the prefrontal anteriorly, the frontal anteromedially, the parietal medially, and presumably the squamosal and/or quadratojugal posteriorly. The lateral and ventral contacts, for example, with the jugal, are unclear.

#### PREMAXILLA

The anteriormost end of the skull is broken off and no premaxillary sutures can be seen. The break is about where a maxilla-premaxilla suture would be expected in *Ordosemys* or one of the other eucryptodires. On the ventral surface, there is a vomer suture at its anterior end and this is most likely with the premaxilla (fig. 10B). This would indicate a premaxilla close in size and shape to that in *Ordosemys* and *Dracochelys*.

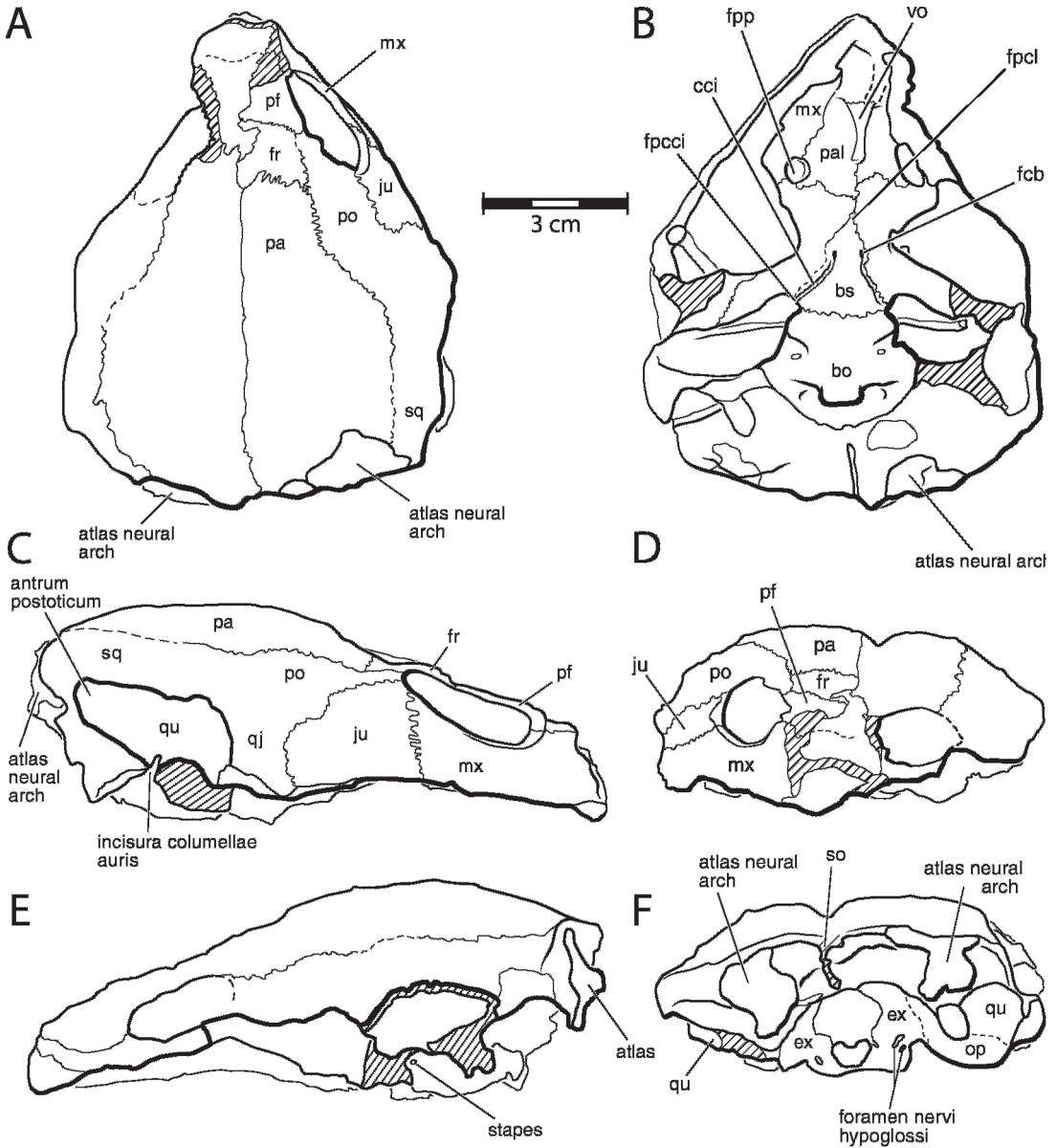


Fig. 10. *Chubutemys copelloi*, n. gen. et sp. MPEF-PV1236, holotype. Line drawings of skull views shown in figs. 2-6. A, Dorsal; B, ventral; C, right lateral; D, anterior; E, left lateral; F, posterior.

MAXILLA

The maxilla (figs. 6, 8, 10) is best preserved on the right side, but some of the triturating surface is present on the left. Its external surface is present on the right as well as most of its ventral surface.

The labial ridge of *Chubutemys* is a straight, narrow sheet, similar to that in *Dracocheyls*, *Ordosemys*, and *Hangaitemys*. There is no evidence of the cusps seen near the pre-maxillary contact in *Dracocheyls*. The depth of the ridge is similar to *Ordosemys* and *Dracocheyls*. The labial ridge is low and

parallels the lingual ridge as in *Ordosemys*, *Dracochelys*, and *Hangaemys*. The width of the triturating surface in *Chubutemys* is very similar to that in *Ordosemys*, that is, wider than the very narrow surface of *Hangaemys* and *Dracochelys*, but narrower than that in meiolaniids.

The apertura narium interna in *Chubutemys* is very similar in position and size to that in *Ordosemys*, *Dracochelys*, and *Hangaemys*. The foramen palatinum posterius is unusually large in *Hangaemys* and *Dracochelys*, but it is smaller, about as in *Chelydra*, in *Chubutemys* and *Ordosemys*. In *Meiolania* the foramen is unusually small.

#### VOMER

The vomer in *Chubutemys* (figs. 6, 10) is relatively well preserved, broken in the middle but with good contacts. The vomer in *Chubutemys* is similar to that bone in other non-polycryptodiran eucryptodires. Its contacts are with the premaxilla anteriorly, the prefrontal (questionably) anterolaterally, and the palatine laterally. In contrast to *Dracochelys*, *Ordosemys*, *Hangaemys*, and *Meiolania*, there is no posterior contact with the pterygoid. The vomer in *Meiolania* is usually wide, forming the parasagittal choanal grooves characteristic of this genus. The vomer has a midline, sagittal ridge that appears to be relatively wide in *Chubutemys* as in *Dracochelys*, not narrow as in *Hangaemys* and *Ordosemys*, although this could be the result of poor preservation.

#### PALATINE

The palatine in *Chubutemys* (figs. 6, 10) is present on both sides and has sutures showing most of its limits. It has the usual cryptodiran contacts of vomer medially, pterygoid posteriorly, and maxilla laterally. An anterior prefrontal contact is likely but not clear. *Chubutemys* differs from *Ordosemys*, *Dracochelys*, *Hangaemys*, and *Meiolania* because the palatines meet in the midline and are not separated by the vomer. The shape of the palatine is similar in *Chubutemys*, *Dracochelys*, *Hangaemys*, and *Ordosemys*. The bone is much smaller in *Meiolania*.

#### QUADRATE

The right quadrate in *Chubutemys* (figs. 6, 8, 10) preserves the cavum tympani, but the processus articularis is broken off. The left quadrate is less complete, lacking much of the cavum tympani as well as the processus articularis. Quadrate sutures are generally unclear, but on the right side one can be interpreted as a quadratojugal and squamosal contact. In ventral view, the quadrate-ptyergoid suture is visible on the right side as well as the contact with the squamosal and opisthotic.

As preserved, the cavum tympani in *Chubutemys* is very deep and has a large dorsal overhang. This condition, however, is probably exaggerated by dorsoventral crushing in this specimen. Nonetheless, the dorsal part of the cavum tympani probably was much deeper than the anterior area. The ventral area is missing. The dorsal area leads into the antrum postoticum, which is mostly missing, but appears to have been comparable in size and shape to that in *Ordosemys*. The incisura columellae auris is preserved almost completely on the right side and partially on the left. It is narrow but posteroventrally open as in *Ordosemys* and *Dracochelys* (unclear in *Hangaemys*). In *Meiolania* it is similar but closed laterally to include the eustachian tube by approximation of the quadratojugal and quadrate. It is possible that this was also the case in *Chubutemys*, but the lateralmost parts of the quadrate are missing. The processus trochlearis oticum can be seen on both sides. It seems to be comparable in size to that in *Ordosemys* and *Dracochelys*.

Both stapes are preserved in place in *Chubutemys* from the incisura columellae auris to the fenestra ovalis. The stapes is thicker in *Chubutemys* than in *Chelydra* with a similar-sized skull. The footplate is conical rather than disc-shaped, a feature of baenids, meiolaniids, and some trionychoids (see Gaffney, 1983: 449). It is unknown in the other eucryptodires compared here.

#### EPIPTERYGOID

A small section of what appears to be the epipterygoid is preserved on the right side

anterodorsal to the cavum epipterygoidei, in its usual eucryptodiran position.

#### PTERYGOID

The pterygoid is preserved almost completely on both sides (figs. 6, 10). Its surface is eroded in some areas and some of the thin web of bone that usually stretches medially from the quadrate ramus has been lost on both sides, revealing the cavum acusticojugulare in ventral view. The pterygoid of *Chubutemys* meets the palatine anteriorly, the other pterygoid in a short suture anteromedially, the basisphenoid medially, and the quadrate posterolaterally. The pterygoid, along with the maxilla and palatine, forms the foramen palatinum posterius. The processus pterygoideus externus in *Dracochelys* is characteristically very large, but both processes are mostly missing in *Chubutemys*, and its size is unknown. In *Dracochelys*, *Hangaemys*, and *Ordosemys* there is a deep fossa just posterior to the quadrate ramus of the pterygoid. Much of this area in *Chubutemys* has been eroded but enough is preserved to show that a deep fossa was absent, making *Chubutemys* more like *Chelydra* in this feature. *Meiolania* also lacks a fossa in this position. *Ordosemys* and *Dracochelys* also have a distinct ridge paralleling the bone margin laterally, presumed to be for pterygoideus muscle attachment. This ridge is absent in *Chubutemys* and also in *Meiolania*.

The medial margin of the pterygoid in *Chubutemys* contacts the basisphenoid, and on the right side the anterior part of this suture is expanded to form a foramen, just lateral to the midline. On the left side, the foramen is present but damaged by crushing. In *Dracochelys* this foramen was identified as the foramen caroticum laterale (Gaffney and Ye, 1992), being the entry of the palatine artery into the cavum cranii. *Chubutemys* appears to have this foramen in the identical position as it is in *Dracochelys*. In *Hangaemys* and *Ordosemys* the basisphenoid is much shorter than in *Chubutemys* and *Dracochelys*, and the foramen is positioned farther posteriorly, close to the foramen caroticum basisphenoidale. The difference is due to a thin, posteromedial sheet of pterygoid that covers

the basisphenoid in *Hangaemys* and *Ordosemys*.

The term foramen caroticum laterale as currently used actually refers to both a more anterior foramen opening into the braincase floor and a more posterior foramen opening on the roof of the palate, with the canalis caroticus lateralis (Gaffney, 1979 and others) connecting them. Sukhanov (2000) used the term "foramen posterius canalis caroticus laterale" for the posterior foramen, and we have adopted that usage here.

#### SUPRAOCCIPITAL

Only a small part of the supraoccipital is preserved (figs. 7, 10). On the dorsal surface some of the bone on the midline portion of the temporal roof is probably supraoccipital. In occipital and ventral view a portion of the crista supraoccipitalis is visible. It is comparable in size and shape with those seen in other non-polycryptodiran eucryptodires. Although very little bone is present on the posterior part of the temporal roof, the internal mold of the ventral surface does show other sutures and there is no indication of a laterally expanded supraoccipital as seen in *Meiolania*.

#### EXOCCIPITAL

Both exoccipitals are preserved and some sutures are visible (figs. 7, 10). Laterally, the exoccipital contacts the opisthotic and ventrally the basisphenoid. As preserved there is no pterygoid contact as seen in *Dracochelys*, *Ordosemys*, and *Meiolania*. *Hangaemys* seems to lack the contact, but it is hard to be sure. It is possible that *Chubutemys* had a pterygoid-exoccipital contact because clearly some of the posterior portion of the pterygoid is missing due to damage. However, it is difficult to say how much is missing.

The foramen magnum in *Chubutemys* is about as wide as high, not as narrow as in *Dracochelys* and *Ordosemys*, but this could be due to crushing. The two foramen nervi hypoglossi can be seen on the right side and one on the left. The area is not well preserved, but it is possible that the medial margin of the foramen jugulare posterius is preserved on the

right side. As preserved the foramen is not enclosed, but its margin could easily be missing. However, neither *Dracochelys* nor *Ordosemys* seems to have a definitive foramen jugulare posterius, so the situation is ambiguous. The condylus occipitalis has no sutures preserved on it, but it is presumed to be formed by the exoccipitals and basioccipital as is usual in cryptodires.

#### BASIOCCIPITAL

The basioccipital (figs. 6, 10) is nearly complete in MPEF-PV1236, but seems at least slightly eroded along its lateral edges. There is a clear anterior suture with the basisphenoid, but the exoccipital sutures are visible in only a few places. As preserved, there is no pterygoid contact as seen in *Dracochelys*. The basioccipital in *Chubutemys* is relatively long as in *Hangaemys* and *Dracochelys*, not short as in *Ordosemys*, although this comparison is somewhat subjective. The tuberculum basioccipitale in *Chubutemys* is distinct as in *Ordosemys*, and much larger than in *Dracochelys*.

#### PROOTIC

Although both prootics are probably complete in MPEF-PV1236, they are mostly covered by matrix. The bone is best seen on the right side where the anterior surface of the otic chamber is exposed, but no sutures are apparent, so the bone is not identified in the figures. The processus trochlearis oticum is comparable in size to that in *Dracochelys* and *Ordosemys*. The foramen nervi trigemini, also presumably formed in part by the prootic, is visible on the right but no sutures can be seen. Its position and size are similar to *Chelydra*.

#### OPISTHOTIC

Most of both opisthotics are preserved in MPEF-PV1236, but sutures are visible only on the right side (fig. 10). Only the ventral and occipital surfaces of the opisthotic are visible in MPEF-PV1236; the dorsal surfaces are covered with matrix. The opisthotic in *Chubutemys* is basically similar to that in other cryptodires, as this bone does not vary

much within this group. In ventral view it lies between the quadrate and squamosal laterally and the exoccipital medially. As preserved the floor of the cavum acustico-jugulare is largely missing. This reveals the stapes and the fenestra ovalis being formed posteriorly by the processus interfenestralis of the opisthotic. The fenestra ovalis is not visible in ventral view in other eucryptodires. Its visibility in *Chubutemys* may be due to missing bone in MPEF-PV1236. In MPEF-PV1236 the foramen externum nervi glossopharyngei is visible at the base of the processus interfenestralis as well as the foramen jugulare anterius.

#### BASISPHENOID

The entire basisphenoid is preserved and visible in ventral view in MPEF-PV1236 (fig. 10). Sutures are present for most of its margins. The basisphenoid is triangular and lies between the pterygoids anterolaterally. A posterior transverse suture is with the basioccipital. As preserved in *Chubutemys* the pterygoid does not reach the basioccipital as in *Ordosemys*, and the basisphenoid has a free lateral edge just anterior to its contact with the basioccipital. *Hangaemys* (Sukhanov and Narmandakh, 1974; Sukhanov, 2000) seems to have a similar condition in which the pterygoid barely reaches the basioccipital. If the pterygoid were only slightly eroded it would produce a free edge for the basisphenoid.

Midway along the length of the basisphenoid is the paired foramen caroticum basisphenoidale (figs. 4, 10). In MPEF-PV1236 this foramen is preserved on both sides with a poorly preserved canalis caroticus internus extending posterolaterally from it. The canalis is only a poorly defined groove on the right, but on the left a small portion of floor is preserved showing that it was a canal (fig. 6). The canal closely follows the pterygoid-basisphenoid suture where that is visible. The foramen posterius canalis carotici interni is interpreted to lie at the posterior end of the groove, formed in or near the pterygoid-basisphenoid suture as in *Dracochelys*, *Ordosemys*, and probably *Hangaemys*. In *Meiolania* and *Niolamia* (Gaffney, 1983) the canalis caroticus internus is deeper within the pterygoid and basisphenoid but still close to

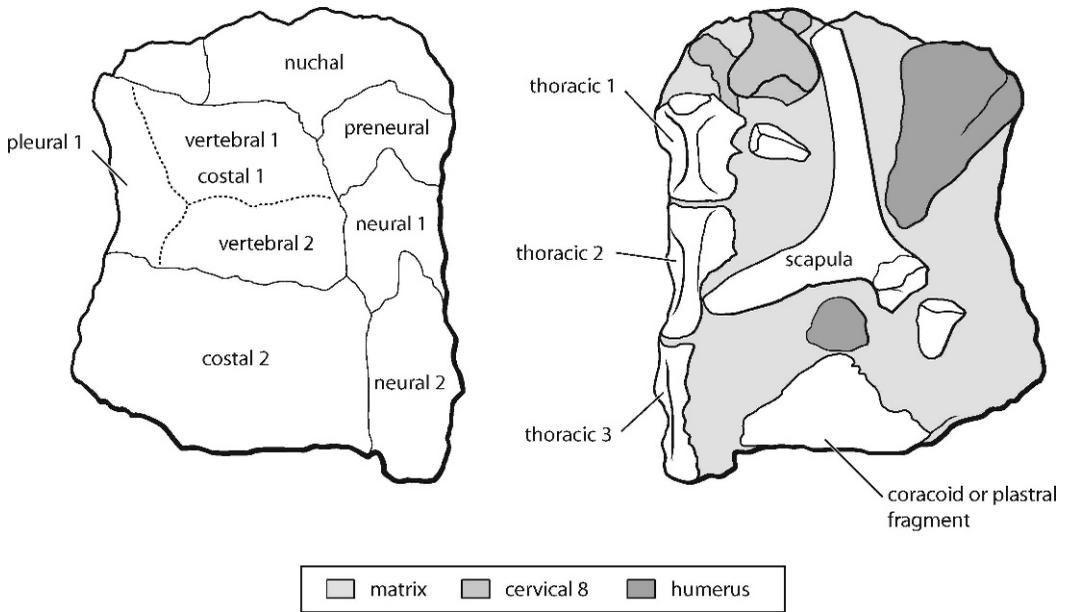


Fig. 11. *Chubutemys copelloi*, n. gen. et sp. MPEF-PV1940. Anterior portion of carapace. Left, dorsal view; right, ventral view. Anterior to top of page. In dorsal view, solid lines are sutures, dotted lines are scale sulci. Cervical eight is shown in more detail in fig. 12.

the sutural contact of those bones. In *Ordosemys*, *Dracochelys*, *Hangaemys*, and *Chubutemys* there is both an open foramen basisphenoidale and ventrally open foramen caroticum laterale, leading Gaffney (1996: 139) to suggest that the branching of the palatine artery from the carotid was unenclosed by bone. Gaffney (1983, 1996) also argued that the condition in *Niolamia* (and its modified form in *Meiolania*) was very similar to that in *Dracochelys*, now known in *Ordosemys*, *Hangaemys*, and *Chubutemys*. The pterygoid of *Niolamia* (Simpson, 1938; Gaffney, 1983: fig. 60) is very similar to the pterygoid in *Dracochelys* and *Chubutemys*, apparently differing only in the greater thickness of the canalis caroticus internus floor in *Niolamia*. This is further evidence that the gap in the suture between the basisphenoid and pterygoid in *Dracochelys* and *Chubutemys* is the homologue of the intrapterygoid slit of meiolaniids, as suggested by Gaffney (1996).

#### CARAPACE

The left anterior fragment of a carapace (fig. 11) is preserved along with postcranial

elements in MPEF PV1940. The dorsal surface consists of some bone along with the underlying mold of the missing bone. The medial ends of costals one and two, the posterior edge of the nuchal, neurals one and two, and a presumed preneural are present on the dorsal surface. The nuchal is relatively broad, similar to that in *Ordosemys*, *Dracochelys*, and other non-polycryptodire eucryptodires. Costals one and two also vary little among these taxa, and *Chubutemys* agrees with them. The neurals are not well preserved and the bone surface is eroded off, but sutures are visible. If correctly interpreted, *Chubutemys* has a preneural between the nuchal and neural one. *Ordosemys* (Brinkman and Peng, 1993a) is another non-polycryptodire eucryptodire with this element. In *Ordosemys* it is longer than wide; in *Chubutemys* it is wider than long.

The only dorsal surface preserved in MPEF PV1940 is in the area of the first costal. This shows sulci of the triple junction between vertebral scale one and two and pleural scale one. The position of this junction in *Chubutemys* is very similar to that in *Ordosemys* and the other early eucryptodires. The first vertebral does not seem to be much

larger than the second as in these forms and *Kirgizemys*. The bone surface as preserved is smooth, lacking a textured pattern. The sulci are broadly incised, forming wide troughs.

On the ventral surface of MPEF PV1940 are the first three thoracic vertebrae, the eighth cervical, the left humerus and scapula, and a flat bone fragment that could be a piece of plastron or coracoid. The first thoracic has an anterior central articulation facing anteriorly as in *Ordosemys*, *Xinjiangchelys*, *Meiolania*, *Sinemys*, and *Dracochelys*, and it is interpreted as the primitive cryptodiran condition (Gaffney, 1996). The rib head for this centrum is visible, but the distal part of the rib is covered by matrix, thus preventing determination of its length.

#### CERVICAL EIGHT

An eighth cervical vertebra (figs. 11, 12) is in articulation in the partial carapace, MPEF PV1940. As the eighth cervical figures importantly in previous analyses of eucryptodire relationships, it is important to describe that bone in *Chubutemys*. The eighth cervical is also known in *Dracochelys* (Brinkman, 2001), *Ordosemys* (Brinkman and Peng, 1993a), *Otwayemys* (Gaffney et al., 1998), *Sinemys* (Brinkman and Peng, 1993b), *Xinjiangchelys* (Kaznyshkin et al., 1990), and *Meiolania* (Gaffney, 1985, 1996). Phylogenetic analyses using eighth cervical morphology that include discussion of characters are Gaffney (1996) and Brinkman and Wu (1999). The eighth cervical of MPEF PV1940 is not completely preserved. Figure 12 has been partially restored by assuming bilateral symmetry. The centrum, transverse processes, and right zygopophyses are visible, but nothing of the neural arch or spine can be seen. The ventral edge of the centrum is eroded off and there has been dorsoventral crushing. The crushing has pressed the postzygapophyses so far ventrally that the neural canal is nearly obliterated. Anteriorly, the crushing is much less and may be nonexistent, but this is difficult to determine.

The eighth cervical of MPEF PV1940 as preserved is generally similar to those in other early Cretaceous eucryptodires. The centrum is biconvex as in *Dracochelys*, *Ordosemys*,

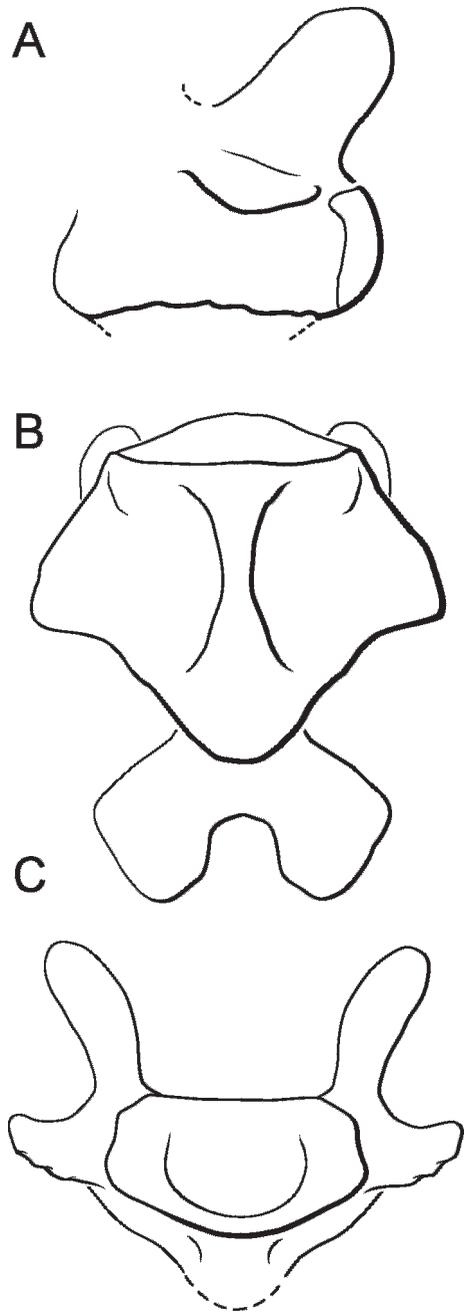


Fig. 12. *Chubutemys copelloi*, n. gen. et sp. MPEF-PV1940. Partially restored eighth cervical vertebra. **A**, Right lateral; **B**, ventral, anterior to top of page; **C**, anterior.

*Otwayemys*, and *Sinemys*, in contrast to the procoelous condition of *Meiolania* and the Polycryptodira. The posterior articulation in *Chubutemys* is relatively narrow and hemispherical, while the anterior articulation is much wider. This condition can also be seen in *Otwayemys*, but the wider distribution of this feature is unclear. The transverse processes in *Chubutemys* are single as in *Chelydra* and the Polycryptodira, not double as in *Dracochelys*, *Otwayemys*, *Ordosemys*, *Sinemys*, and *Meiolania*. The transverse process in *Chubutemys* is also placed more anteriorly than the middle of the centrum. This condition is also as in the above genera and the Polycryptodira. There is no evidence of cervical ribs. The ventral surface of the centrum is eroded, and the presence or absence of a keel or process is not determinable.

The prezygapophyses in *Chubutemys* are only represented by the right one, and it is placed much more laterally than in *Otwayemys*, *Dracochelys*, *Ordosemys*, and *Meiolania*. This may be due to deformation. Its position could have been very similar to those in *Ordosemys* and *Dracochelys*, which are farther apart than in *Otwayemys*. The postzygapophyses in *Chubutemys* are also widely placed as in *Ordosemys*, not narrow as in *Otwayemys*. The eighth cervical in MPEF PV1940 is positioned anterior and lateral with respect to the first dorsal. It also underlies the nuchal. There is no sign on the nuchal of a neural spine pushed through or crushed beneath it. The implication is that *Chubutemys* does not have a tall neural spine as in *Otwayemys* and *Meiolania*, but this is just a guess.

#### PHYLOGENETIC ANALYSIS

*Chubutemys* is a cryptodire similar to other cryptodires that have been referred to as "sinemydids" and "macrobaenids" (see Gaffney and Yeh, 1992; Gaffney, 1996; Brinkman and Peng, 1993a; Brinkman and Wu 1999; Brinkman, 2001; Sukhanov, 2000, for references), and it is among these extinct cryptodire groups that its relationships are to be sought. The present analysis is based on an analysis developed in 1992 in a joint effort by Don Brinkman, Gene Gaffney, Howard Hutchison, and Peter Meylan. The major part

of this analysis was published in Gaffney (1996). Once again, the senior author is very grateful to his three colleagues for sharing their knowledge. Analyzing relationships of the extinct eucryptodires is hampered by the fact that the terminal taxa being analyzed are something of a moving target. Many named taxa are inadequately described in the literature but are known firsthand by some workers, making corroboration of some published character distributions more difficult than usual.

Although the matrix of 111 characters (appendix 1) is based on the 40 characters in Gaffney (1996), it has obviously been greatly altered by the addition of new ones. In Gaffney (1996) the specific-level taxa in the family Meiolaniidae were analyzed separately from the family Meiolaniidae among turtles, so two data sets were used. We have incorporated some of the characters from the within-group data set here. Brinkman and Wu (1999) made significant additions, and their characters are also added here (except for parsimony uninformative ones due to non-overlapping terminal taxa). Characters are also added from Rougier et al. (1995) and Gaffney et al. (2006).

Hirayama et al. (2000) proposed a cladogram showing eucryptodires to be nonmonophyletic, with meiolaniids allied with *Mongolochelys* and outside most other cryptodires. The Hirayama et al. (2000) cladogram is based on a 69 character data set, including the 40 characters from Gaffney (1996), modified in Gaffney et al. (1998), and characters from Parham and Hutchison (2003). We have used at least a version of all the characters in the Hirayama et al. (2000) data set that are parsimony-informative. Because we have deleted some terminal taxa (that in our opinion are not firmly based) from Hirayama et al. (2000), some characters from Hirayama et al. (2000) that were parsimony-informative in that analysis are no longer parsimony-informative in our analysis and have been deleted. A few characters have been altered either in definition or distribution. The altered characters relevant to meiolaniid relationships in particular are as follows:

1. "(10) Prominent enlargement of squamosal reaching supraoccipital." This character is

unchanged here, but we have added another character, supraoccipital with horizontal plate, to reflect the different conditions of the contact. In both *Mongolochelys* and meiolaniids, there is a large squamosal forming most of a posteriorly directed temporal margin. However, in *Meiolania* much of this margin is formed by a horizontal plate of the supraoccipital, which is absent in *Mongolochelys*. In the latter the squamosals meet on the midline, a condition not seen in meiolaniids.

2. Hirayama et al. (2000) united meiolaniids and *Mongolochelys* on the common presence of “(13) Prominent lingual ridge on maxilla”, or “accessory ridge on the triturating surface” in our usage. Although this ridge is present in *Meiolania* and *Ninjemyx*, the sister taxon of these, *Niolamia*, lacks the ridge. In the cladogram and data set for Meiolaniidae developed by Gaffney (1996) and used here, the absence of the ridge is primitive for Meiolaniidae and does not unite Meiolaniidae and *Mongolochelys*.

3. Another character of more general distribution that breaks up the Eucryptodira in Hirayama et al. (2000) is the “lower cheek emargination”. In Hirayama et al. (2000) the complete absence or presence of a shallow cheek emargination is one state, but we see three states: 0 = absent, shallow, with a large jugal; 1 = absent, shallow, with a large quadratojugal; 2 = moderate to deep. We have used these to reflect what we see as a significant difference when the solid cheek is formed by a large jugal as in *Proganochelys*, *Australochelys*, *Kayentachelys*, as well as *Mongolochelys*. This condition is common and seems to be primitive at the level of Testudines as well as Cryptodira. *Meiolania* has a solid cheek formed in part by an unusually large quadratojugal, which seems to be a different character state. This state may be best interpreted as the secondary filling of an emarginate cheek.

4. We have also used four rather than three states for the Hirayama et al. (2000) “Posterior temporal emargination” character. We have added a state, unique to meiolaniids for a fully covered skull roof, but with an unusually small parietal, a condition that is different from the much larger parietal seen in *Proganochelys* and other non-Casichelydians

as well as in the extensively roofed *Mongolochelys*, *Kallokibotion*, and *Chubutemyx*. The implication of the unique cheek and temporal roof structure in meiolaniids is that these areas may be secondarily solid from a more emarginated ancestor, similar to the conditions in taxa such as *Dracochelys* and *Ordosemys*.

5. The Hirayama et al. (2000) character “(34) Cervical ribs of large size” also breaks up the Eucryptodira of Gaffney and other authors. Gaffney and others have used the simple presence or absence of cervical ribs as a character. The problem here is that cervical ribs in turtles show a great deal of variation, much of it described in Gaffney (1985, 1990), Brinkman and Peng (1993a), and Brinkman and Nicholls (1993), with a discussion of the problem in Gaffney (1996: 149). Hirayama et al. (2000) tried to use some of this diversity, but as discussed previously we think that the diversity does not show discrete states. It is true that there is a considerable difference in the relatively large ribs of *Proganochelys* (Gaffney, 1990) and the small ribs of some later cryptodires, such as baenids. However, the ribs in *Meiolania* (Gaffney 1985, 1990) do not agree with the morphology of the ribs in *Proganochelys* and are, in fact, unique among turtles in shape, as well as in their relative size. Therefore, we use only the presence/absence of ribs and not their size or other aspects of morphology.

Corrections to the data matrix in Gaffney et al. (1998) for characters referring to *Hangaiemyx* are from Parham and Hutchison (2003). Parham and Hutchison (2003) also changed some characters for *Judithemyx* (the unnamed TMP 87.2.1 of Gaffney, 1996). However, the senior author has corroborated some of the earlier codings and thinks that the original states for characters 3 (visible on broken edge of prefrontal on right side) and 18 (sutures visible on left side) are correct. Parham and Hutchison (2003) also change characters 4 and 5 in appendix 1, but this may be an error. We use the original codings from Gaffney (1996). Character 25, presence of chevrons, was reported absent by Parham and Hutchison (2003), but chevrons are clearly present on the anterior caudals preserved in TMP 87.2.1 (Parham and Hutchison, 2003: fig. 8D). In order to clarify the senior author's

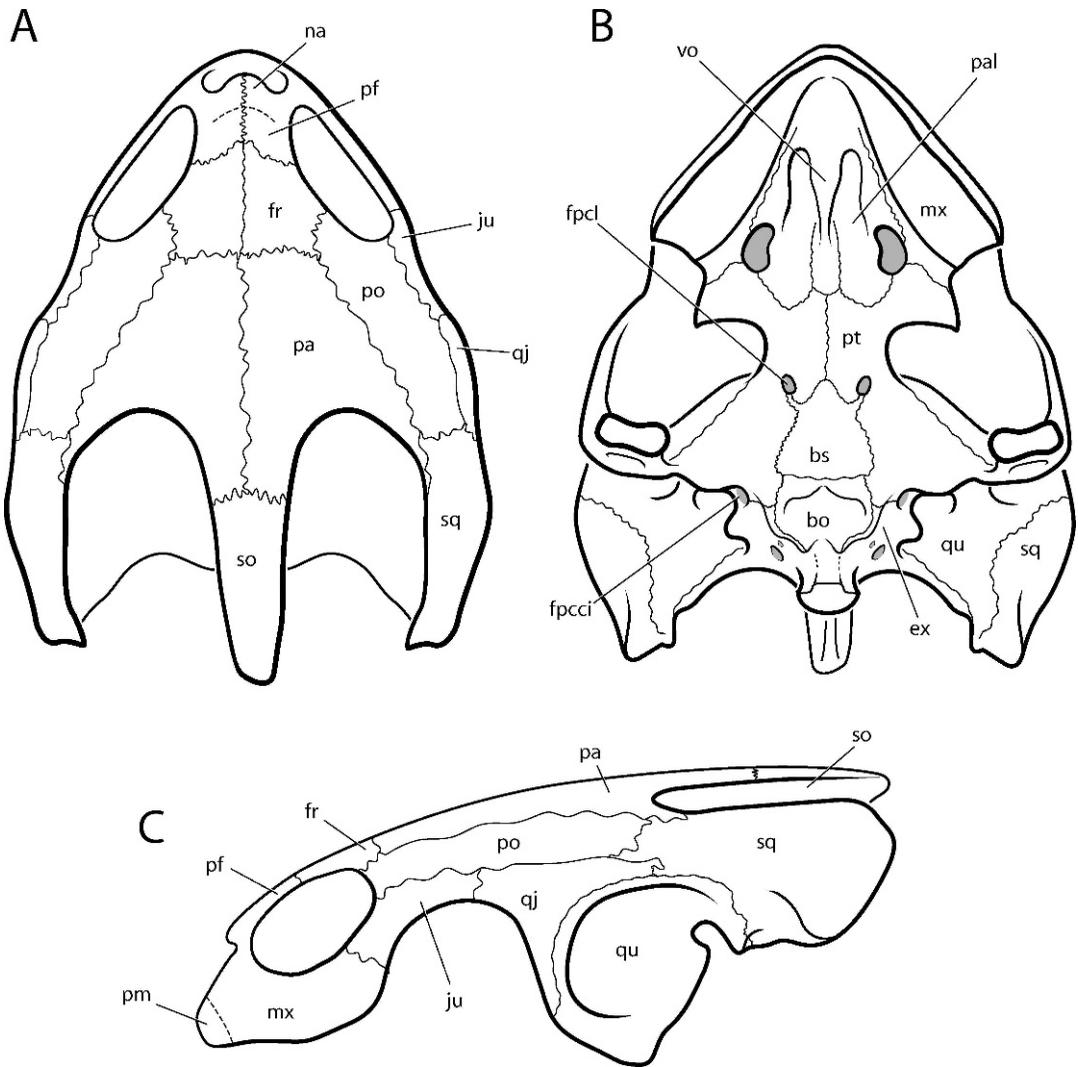


Fig. 13. *Judithemys sukhanovi* Parham and Hutchison, 2003, TMP 87.2.1. Partially restored views of the skull. **A**, Dorsal; **B**, ventral; **C**, left lateral.

interpretations of the skull of *Judithemys* (TMP 87.2.1), a set of partially restored views are provided as fig. 13.

The terminal taxa used here are mostly the “usual suspects” from Gaffney (1996), with some additions. As it became apparent that *Chubutemys* may be related to meiolaniids and that the position of meiolaniids has been called into question by Hirayama et al. (2000), the better known meiolaniid taxa were added to the analysis. The discovery of associated postcranial material of *Solnhofia*

(Joyce, 2000; see also Broin, 1994; Lapparent de Broin et al., 1996) has allowed this taxon to be added. On the other hand, the relationships of the living cryptodire groups are beyond the scope of this analysis, and only a few characters and larger, more inclusive taxa are used. The molecular evidence that the family Trionychidae is the sister taxon to all other living cryptodires is a hypothesis well beyond the scope of this paper, and we continue to use Trionychoidea. We do not think that this lumping of the recent taxa significantly affects

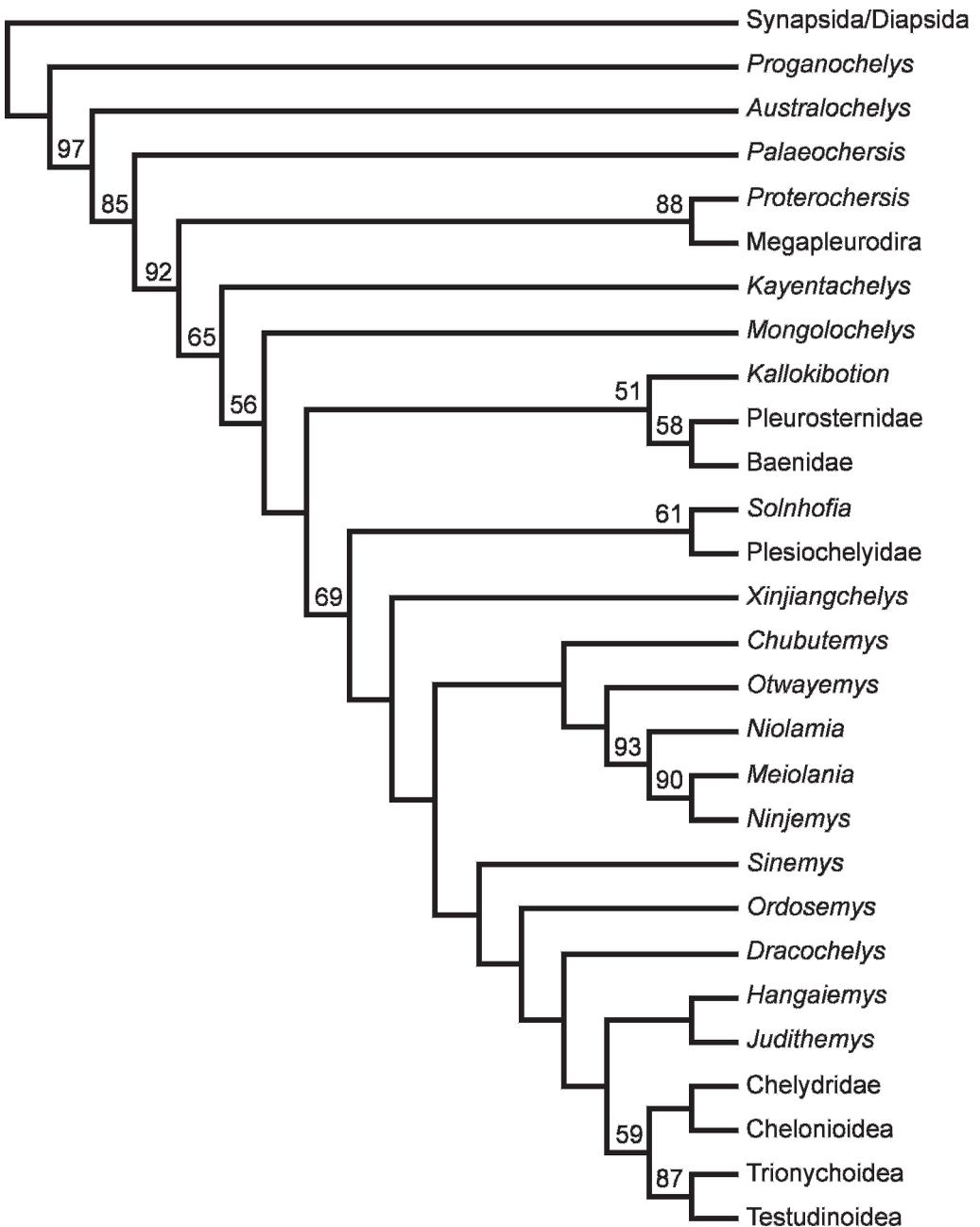


Fig. 14. Most parsimonious cladogram (MPC) based on data set shown in appendix 2. Numbers at nodes show result of bootstrapping. Higher taxon names are as in Gaffney (1996).

cladograms of the extinct cryptodires we have chosen.

The phylogenetic analysis corroborates the eucryptodiran nature of meiolaniids and contradicts the hypothesis of Hirayama et al.

(2000). It also supports monophyly of the Centrocryptodira of Gaffney (1996), which has formed central articulations as one of its synapomorphies. The Sinemydidae of Gaffney (1996), supported by the biconvex eighth

cervical in the earlier analysis, is not supported in the present analysis; instead, the extinct eucryptodire taxa often referred to as “sine-myids” and/or “macrobaenids” are resolved as a paraphyletic group of successive sister taxa to the Polycryptodira. The biconvex eighth cervical in this resolution becomes a synapomorphy for Centrocryptodira, lost in Meiolaniidae, *Judithemys*, (?*Hangaiemys*), and most of the Polycryptodira. The Centrocryptodira is also supported by the biconvex fourth cervical, which does occur in meiolaniids, as well as in the other Centrocryptodira, except *Sinemys* and trionychoids. The number of unambiguous synapomorphies and the bootstrap test (fig. 14) show Cryptodira and Eucryptodira to be well supported, but the resolution of extinct cryptodires breaks down in bootstrapping. Nonetheless, the most parsimonious tree (fig. 14) shows six unambiguous synapomorphies for the node containing Polycryptodires, *Judithemys*, *Hangaiemys*, *Dracochelys*, *Sinemys*, and *Ordosemys*. The particularly interesting result of this data set resolution is that the sister taxon to the above listed group consists of the meiolaniids plus *Otwayemys* and the subject of the present paper, *Chubutemys*. This is a little surprising because *Chubutemys* is similar to *Dracochelys* in much of its skull. It also does not rely on the fully roofed skull found in both *Chubutemys* and meiolaniids, because this is interpreted here as separate characters in these two taxa, and is not used as a character uniting *Chubutemys* and meiolaniids. A previous analysis of the Early Cretaceous Australian cryptodire *Otwayemys* (Gaffney et al., 1998) allied that form with meiolaniids, and the present analysis also found that relationship, adding *Chubutemys* as well.

Neither *Chubutemys* nor *Otwayemys* is strongly supported as a sister taxon to meiolaniids, but the most problematic element of this resolution is that both taxa have lots of missing data: *Chubutemys*, 49%; *Otwayemys*, 68%. PAUP fills in the missing characters consistent with the most parsimonious cladogram (MPC), which probably masks contradictory characters. There is only one unambiguous character uniting *Chubutemys* with meiolaniids, and that is the prefrontal-post-orbital contact that prevents orbital exposure

of the frontal. This is actually a rare character among the extinct cryptodire groups; it occurs in *Mongolochelys* and Polycryptodira, but it is indeterminate in *Otwayemys*. The sole character uniting *Otwayemys* and meiolaniids is the transverse process of the cervicals in the middle of the centrum, which is absent in all other Centrocryptodira except *Dracochelys*.

One could argue that the solid temporal roof of *Chubutemys* is the primitive condition for meiolaniids. The large parietal of *Chubutemys* certainly seems to be the primitive condition for cryptodires, although many Paracryptodira and Plesiochelyidae have some degree of emargination. Within Eucryptodira, only meiolaniids and *Chubutemys* (outside a few Polycryptodira) have a fully roofed skull, and the present MPC suggests this may not be a homoplasy. However, if the meiolaniid condition is re-coded as “0” (agreeing with *Mongolochelys* and *Kallokibotian*), the same MPC results.

The carotid morphology of *Chubutemys* makes a good primitive condition for meiolaniids. Jamniczky et al. (2006) gave a summary of carotid canal hypotheses (see also Jamniczky and Russell, 2004) and proposed an evolutionary progression consistent with our character states. The enclosed canalis caroticus internus posterior to the foramen basisphenoidale has been divided into two character states by Gaffney (1996), Gaffney et al. (1998), and Parham and Hutchison (2003), among others. One state is a thin or partial floor and the other is a thick floor. The senior author now thinks that this might be better changed to present/absent. After looking at a large number of specimens, both recent and fossil, the distinction is beginning to become blurred with a number of specimens within some species showing a fair amount of variation. However, changing the data set to present/absent results in the same MPC. For meiolaniids the carotid is embedded deeply in the pterygoid in *Meiolania*, but it is just covered by it in *Niolamia* (= *Crossochelys*, see Simpson, 1938: fig. 7), so a thin condition is probably primitive for the group.

The morphology of the canalis caroticus lateralis, the presumed path of the palatine artery, in *Chubutemys* is also primitive for the condition in meiolaniids. In *Chubutemys* and

*Dracochelys* there is a step in the basisphenoid-pterygoid suture that opens up on each side very close to the midline to form the foramen posterius canalis caroticus laterale (the posterior opening of the foramen caroticum laterale), the presumed entry point of the palatine artery into the skull. In these two taxa the two openings form a V-shaped suture at the apex of the basisphenoid. In *Hangaemys* (Sukhanov, 2000) the pterygoid-basisphenoid shelf forming the ventral margin of the foramen posterius canalis caroticus laterale is transverse rather than V-shaped, but it is otherwise apparently very similar. However, in *Sinemys*, *Judithemys*, and *Ordosemys* there is no shelf or foramina at the apex of the basisphenoid; instead, the foramen posterius canalis caroticus laterale is placed more laterally from the midline and more posteriorly. Although it is still formed by both pterygoid and basisphenoid, the basisphenoid is exposed as a short anterolateral process reaching the foramen posterius canalis caroticus laterale. The foramen is also a more oval foramen rather than the slit seen in *Dracochelys* and *Chubutemys*. The disarticulated pterygoid of *Niolamia* (AMNH 3161) figured by Simpson (1938: fig. 7) is clearly very similar to the pterygoid in *Chubutemys* and *Dracochelys* (and probably *Hangaemys*, although the senior author has not seen this material). The primitive nature of the *Niolamia* (= *Crossochelys* Simpson) pterygoid was argued by Gaffney (1983: fig. 60). However, even in *Meiolania platyceps*, the likely homology of the meiolaniid intrapterygoid slit with the foramen posterius canalis caroticus laterale and canalis caroticus lateralis in the extinct eucryptodires is substantiated by comparison of fig. 55 (upper) in Gaffney (1983) showing *Meiolania* with figure 6A, C in Brinkman and Peng (1993a) showing *Ordosemys*. These figures show that the intrapterygoid slit in *Meiolania* actually has paired canals lying laterally formed by basisphenoid and pterygoid, as in *Ordosemys* and other non-polycryptodiran eucryptodires.

Therefore, *Chubutemys* provides further evidence that meiolaniids are related to "basal" eucryptodires or "sinemydids/macrobaenids", that is, eucryptodires outside the Polycryptodira. The basicranial morphology

of meiolaniids, rather than being a unique feature of the group, is instead a modified state of the morphology seen in such "sinemydids/macrobaenids" as *Chubutemys*, *Dracochelys*, *Ordosemys*, and *Sinemys*.

*Chubutemys* shows that terrestrial eucryptodires were present in South America in the Cretaceous, as they were in North America, Asia, and Australia. At present, the distribution of the (probably paraphyletic) non-polycryptodiran eucryptodires seems to be relatively widespread: North and South America, central Asia, and Australia, but apparently not Africa (although the record is poor) or Europe. *Chubutemys* itself, if it does prove to be a meiolaniid sister taxon, would represent the Mesozoic distribution of the more restricted monophyletic group in Australia and South America that evolved into the meiolaniids with their characteristic skull roof synapomorphies. Others of the paraphyletic "sinemydids/macrobaenids" were more closely related to the living eucryptodires, the Polycryptodira.

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#### APPENDIX 1 CHARACTER LIST

1. NA, nasals  
0: present  
1: absent
2. NA, size  
0: small, absent  
1: very large
3. NA, nares divided  
0: yes  
1: no
4. NA, nasomaxillary sinus  
0: absent  
1: present
5. LA, lacrimal bone  
0: present  
1: absent
6. LA, lacrimal foramen  
0: present  
1: absent
7. PF, meet on midline  
0: no, separated by na-fr contact  
1: yes
8. PF, pf-po contact  
0: present  
1: absent (fr to orbit)
9. PF, pf-vo contact  
0: absent  
1: present
10. PA, processus inferior parietalis  
0: small to absent  
1: large
11. PA, pa-sq contact  
0: present  
1: absent
12. PA, temporal emargination  
0: fully roofed skull  
1: shallow emargination  
2: deep emargination
13. ST, supratemporal  
0: present  
1: absent
14. JU, cheek emargination  
0: absent, shallow, large ju  
1: absent, shallow, large qj  
2: moderate to deep
15. SQ, meet on midline  
0: no  
1: yes
16. SQ, posterolateral process  
0: no  
1: yes
17. SQ, sq-so contact  
0: absent  
1: present
18. SQ, broad sq-qj contact  
0: absent, narrow  
1: broad contact below cavum tympani
19. PO, length  
0: short  
1: long
20. PO, po-sq contact  
0: present  
1: absent
21. PM, premaxillary hook  
0: absent  
1: present
22. MX, accessory ridge on triturating surface  
0: absent  
1: present

23. MX, length of facial region  
0: shorter, equal to orbit length  
1: longer than orbit
24. VO, vomer  
0: double  
1: single
25. VO, teeth  
0: present  
1: absent
26. PAL, teeth  
0: present  
1: absent
27. PAL, foramen palatinum posterius large  
0: small–moderate  
1: very large
28. PT, vertical flange on proc pter ext  
0: absent  
1: present
29. PT, interpterygoid vacuity  
0: widely, slightly open  
1: completely closed by medial extension of pt
30. PT, canalis caroticus internus, posterior to foramen basisphenoidale  
0: absent  
1: at least partially covered by bs-pt  
2: covered by prootic
31. PT, canalis caroticus internus at least partially formed by pt  
0: no  
1: yes, distal to foramen basisphenoidale
32. PT, canalis caroticus lateralis vs canalis caroticus internus  
0: lateralis equal to, larger than internus  
1: lateralis smaller than internus
33. PT, foramen posterius canalis carotici interni  
0: not formed by bs and pt  
1: formed by bs and pt, and located midway along bs
34. PT, middle ear with ossified floor formed by posteromedial pterygoid process  
0: process absent  
1: present
35. PT, pt-bo contact  
0: absent  
1: present
36. PT, deep concavity on qu ramus  
0: absent  
1: present
37. PT, bs-pt space  
0: interpterygoid vacuity widely open  
1: distinct space, perhaps a foramen posterius caroticum laterale, present  
2: closed pt-bs suture, foramen basisphenoidale possibly present
38. PT, intrapterygoid slit  
0: absent, small  
1: extensive, completely covering foramen basisphenoidale
39. QU, posterior pocket for stapes  
0: present  
1: absent
40. QU, cavum tympani  
0: absent  
1: present
41. QU, middle ear with complete lateral wall  
0: not complete  
1: complete
42. QU, cavum tympani curved dorsally  
0: absent  
1: present
43. QU, acute posterior margin  
0: no  
1: yes
44. QU, incisura columellae auris  
0: separated from eustachian tube  
1: with eustachian tube
45. QU, antrum postoticum  
0: absent  
1: present
46. QU, covers op laterally  
0: no  
1: yes
47. QU, cranioquadrate space  
0: relatively open  
1: a well-defined canal
48. OP, processus paroccipitalis  
0: loosely articulated  
1: tightly fused
49. OP, fenestra perilymphatica  
0: relatively large  
1: relatively small
50. PR, anterior surface otic chamber  
0: faces more anterodorsally  
1: faces more anteriorly, anteroven-  
trally (processus trochlearis oticum)
51. PR, otic chamber thickness

- 0: anterior wall thin  
1: anterior wall thick
52. SO, crista supraoccipitalis  
0: low to absent  
1: distinct sagittal plate
53. SO, wide occipital plate  
0: wide occipital plate with depressions  
1: absent
54. SO, supraoccipital with horizontal plate  
0: no  
1: yes
55. EX, recessus scalae tympani  
0: not formed in bone  
1: formed in bone with fenestra perilymphatica
56. BS, basiptyergoid articulation  
0: open articulation  
1: sutured joint
57. BS, foramen anterius canalis carotici interni  
0: widely separated  
1: close together
58. BS, foramen basisphenoidale  
0: formed by bs, equals fpcci  
1: formed by bs+pt, equals fpcci  
2: formed by bs+pt, more posterior fpcci present  
3: absent due to prootic forming fpcci  
4: absent due to solid pterygoid covering
59. BS, foramen posterius canalis carotici interni  
0: equals foramen basisphenoidale  
1: formed in part by bs  
2: formed entirely by pt  
3: formed by prootic
60. BS, paired pits  
0: absent  
1: present
61. BS, ventral bs/bo tubercle  
0: single  
1: paired  
2: absent
62. CA, columella auris  
0: thick, without distinct footplate  
1: thin, with distinct wide footplate
63. JW, splenial  
0: present  
1: absent
64. CE, proportions  
0: as high as wide  
1: wider than high for posterior cervicals
65. CE, central articulations  
0: unformed  
1: formed
66. CE, anterior end of 8th cervical  
0: unformed  
1: cotyle  
2: condyle
67. CE, ribs  
0: present  
1: absent
68. CE, transverse processes  
0: middle of centrum  
1: anterior edge of centrum
69. CE, doubled transverse processes  
0: present on any cervical  
1: absent on all
70. CE, 4th cervical articulation  
0: amphicoelous  
1: biconvex  
2: opisthocoelous
71. CE, double articulation between 5th and 6th  
0: absent  
1: present
72. CE, double articulation between 6th and 7th  
0: absent  
1: present
73. CE, double articulation between 7th and 8th  
0: absent  
1: present
74. CE, strong ventral process  
0: absent on all centra  
1: present on posterior centra
75. CE, neural spine on 8th cervical  
0: high  
1: low
76. CE, 8th cervical centrum  
0: amphicoelous  
1: procoelous  
2: biconvex
77. CAU, tail rings  
0: absent  
1: present

78. CAU, tail club  
0: absent  
1: present
79. CAU, biconcave caudal near base of tail  
0: absent  
1: present
80. CAU, central articulations  
0: posterior not procoelous  
1: all centra procoelous
81. CAU, chevrons  
0: well developed and present on nearly all caudals  
1: small or present on only a few caudals
82. SH, coracoid foramen  
0: present  
1: absent
83. SH, coracoid columnar  
0: no, flat plate  
1: yes
84. POSTC, paddles formed by limbs  
0: absent  
1: present
85. PEL, pelvis sutured to shell  
0: not sutured to shell  
1: sutured to shell
86. PEL, pelvis narrow  
0: pelvis widely placed  
1: ilia close to midline
87. CAR, first thoracic rib  
0: extends, nearly extends to peripherals  
1: extends less than halfway across costal
88. CAR, anterior articulation of first thoracic centrum  
0: faces anteriorly to slightly anteroventrally  
1: faces strongly anteroventrally
89. CAR, knob on ventral surface of nuchal that articulates with 8th cervical  
0: absent  
1: present
90. CAR, 10th thoracic rib  
0: reaches 8th costal  
1: free from costal
91. CAR, sacrum with dorsal 10  
0: no  
1: yes
92. CAR, 9th costal bone  
0: present  
1: absent
93. CAR, suprapygal  
0: nearly equally subdivided into two  
1: first suprapygal much smaller than second  
2: only one suprapygal  
3: second suprapygal absent or much smaller than first  
4: second suprapygal divided by first  
5: no suprapygal  
6: three suprapygals
94. CAR, supramarginal scales  
0: 12  
1: 3  
2: none
95. PLA, plastral fontanelles surrounded by hyo-hypoplastra  
0: absent  
1: retained in adult
96. PLA, carapace-plastron attachment  
0: sutured  
1: ligamentous
97. PLA, plastral buttresses  
0: reaching peripherals  
1: reaching costals
98. PLA, entoplastron separating epiplastra  
0: yes  
1: no
99. PLA, dorsal process on epiplastron  
0: large, reaches carapace  
1: smaller than length of epiplastron  
2: absent
100. PLA, epiplastron  
0: broad  
1: narrow
101. PLA, epiplastral beak  
0: absent  
1: present
102. PLA, bridge of plastron  
0: broad  
1: narrow
103. PLA, mesoplastra  
0: present  
1: absent
104. PLA, xiphiplastron  
0: moderately broad  
1: narrow



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*Niolamia*

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*Chubutemys*

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*Otwayemys*

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*Hangaiemys*

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*Dracochelys*

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Chelydridae

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Chelonioidea

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Trionychoidea

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Testudinoidea

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