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Otwayemys, a New Cryptodiran Turtle from the Early Cretaceous of Australia

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ABSTRACT

The Early Cretaceous Eumeralla Formation, Otway Group, of Cape Otway, Victoria, Australia, has yielded remains of a new genus of eucryptodiran turtle, *Otwayemys cunicularius*, n. gen., n. sp. *Otwayemys* is based primarily on shell material, but unassociated skull elements, cervical and caudal vertebrae, and limb elements from the type locality are attributed to this taxon. *Otwayemys cunicularius* is characterized by a carapace with an emarginate nuchal area, wide vertebral scales, and a smooth shell texture; and by a plastron with wide epiplastra, small extragular scales (scale set 2), gular scales (scale set 1) extending onto entoplastron, a small and narrow entoplastron, a large hyoplastron/hypoplastron fontanelle, and an inguinal buttress terminating on the sixth peripheral. The shell of *Otwayemys* is most similar to *Xinjiangchelys* from the Jurassic of China; both have broad epiplastra, plastral buttresses not extending onto costals, a long first thoracic rib, no inclination to the first thoracic centrum, and no mesoplastra; all these characters are primitive for the Eucryptodira. *Otwayemys* is advanced over *Xinjiangchelys* in having formed vertebral articulations in the neck. Biconvex eighth and biconcave fifth (?) cervicals in *Otwayemys* are characters found in the Early Cretaceous *Ordosemys* of central Asia.

Otwayemys differs from *Chelycarapookus*, also from the Early Cretaceous of Victoria, in being 20% larger and having a large plastral fontanelle, a smooth surface texture, and a wide posterior plastral lobe.

Otwayemys belongs in the Centrocryptodira, eucryptodires with formed vertebral articulations. A parsimony analysis of 18 taxa using 40 characters (of which only 20 are known for *Otwayemys*) produces 12 equally parsimonious trees. A consensus tree shows *Otwayemys* and Meiolaniidae in an unresolved trichotomy with Polycryptodira (consisting primarily of the living cryptodires) plus Sinemydidae.

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INTRODUCTION

Although chelid pleurodires are the dominant nonmarine turtles in the Recent Australian fauna, and were the dominant turtles through the Tertiary (Gaffney, 1981), only cryptodires have been found in the Australian Mesozoic. The cryptodiran sea turtle *Notochelone* is the best-preserved Mesozoic Australian turtle (Gaffney, 1981). The only nonmarine Australian Mesozoic turtles are represented by an internal mold, *Chelycarapookus* (Warren, 1969), and fossil fragments from Lightning Ridge, New South Wales (Molnar, 1980; Gaffney, 1981). The discovery of good turtle material from the Early Cretaceous Dinosaur Cove locality allows for the first time detailed comparison of systematically meaningful characters in an Australian nonmarine turtle from the Mesozoic.

The Dinosaur Cove material is very similar to that of primitive eucryptodires now known from central Asia. These turtles, often referred to as sinemydids or macrobaenids, include a diverse array of variably preserved forms with a complex literature, much of it in Chinese and Russian. It is not our purpose here to review this literature and its taxonomic nuances. The reader is referred to the recent reviews of Peng and Brinkman (1993), Brinkman and Peng (1993a, 1993b), and Gaffney and Ye (1992) for an introduction to this subject. For the purposes of the present paper, we have chosen the restricted use of Sinemydidae as a monophyletic group as defined by Gaffney (1996).

Although there are a number of named "macrobaenid/sinemydid" taxa that could be relevant to comparisons with *Otwayemys,* we have chosen to restrict our comparisons to taxa that are represented by well-preserved material readily available to us. Specifically, we rely on comparisons with *Xinjiangchelys, Sinemys, Ordosemys,* and *Dracochelys,* all of which have strong similarities to *Otwayemys. Xinjiangchelys* consists of material frequently referred to as Asian species of *Plesiochelys.* Recent work has shown that *Xinjiangchelys* is clearly distinct from *Plesiochelys* and that *Plesiochelys* and its close relatives do not occur outside Europe (Peng and Brinkman, 1993; Gaffney and Meylan, 1988). Nonetheless, some recent work (Ye, 1994) still refers to this taxon as *Plesiochelys. Xinjiangchelys* is known from the shell, vertebrae, and a partial skull. We rely here on Peng and Brinkman (1993) for the diagnosis and description of this taxon.

Ordosemys was described by Brinkman and Peng (1993a) on the basis of a nearly complete shell, some cervicals and other postcrania, and a few skull elements. Since then, a nearly complete, well-preserved skull (IVPP V12092) was discovered.

Dracochelys was described on the basis of a skull (Gaffney and Ye, 1992), but one of us (DB) has identified postcranials that presumably belong to *Dracochelys,* which are used here for comparison with *Otwayemys.*

Institutional Abbreviations

NMV P	Palaeontological collection of the Museum of Victoria, Melbourne
IVPP	Institute of Paleontology and Paleoanthropology, Beijing

Anatomical Abbreviations

1	first pair plastral (intergular or gular) scales
2	second pair plastral (gular or extragular) scales
ab	abdominal scale
ax	axillary scale
c	costal bone
ent	entoplastron
epip	epiplastron
fe	femoral scale
hu	humeral scale
hyo	hyoplastron
hypo	hypoplastron
inf	inframarginal scale
ing	inguinal scale
m	marginal scale
n	neural bone
pec	pectoral scale
pl	pleural scale
v	vertebral scale
xip	xiphiplastron

Acknowledgments

For assistance in collecting the specimens of *Otwayemys cunicularius,* we thank the hundreds of volunteers who contributed to the excavations at Dinosaur Cove over the past decade. For logistical, financial, and administrative support during the execution of that project, we thank Monash University, the Friends of the Museum of Victoria, the Committee for Research and Exploration of the National Geographic Society, Earthwatch, Atlas Copco Australia Pty. Ltd., ICI Australia Pty. Ltd., the Australian Research Council, and the Victorian Department of Conservation and Natural Resources.

For one of us (ESG) this work is a continuation of research on Australian turtles. Many individuals and institutions have significantly contributed to that research and they are credited in Gaffney (1983, 1996). Particular thanks again go to Alex Ritchie and Bob Jones of the Australian Museum. Frank Ippolito did the drawings and Steve Morton of the Museum of Victoria provided the photos. Howard Hutchison and Peter Meylan contributed to the data matrix used here.

As always, we are very grateful to those colleagues who read this paper and significantly improved it with their suggestions: Peter Meylan, Darrel Frost, George Zug, Betsy Nicholls, and Ralph Molnar. We appreciate the time they took to improve this paper.

SYSTEMATICS

ORDER TESTUDINES

GIGAORDER CASICHELYDIA

MEGAORDER CRYPTODIRA

PARVORDER EUCRYPTODIRA

Otwayemys, new genus

TYPE SPECIES: *Otwayemys cunicularius*, new species.

KNOWN DISTRIBUTION: Dinosaur Cove, 38°47′S, 143°24′E, near Cape Otway, Victoria, Australia, Albian, Early Cretaceous, Eumeralla Formation, Otway Group (Rich and Rich, 1989).

ETYMOLOGY: Otway, for Cape Otway; emys, turtle.

DIAGNOSIS

A primitive eucryptodire lacking mesoplastra, having formed vertebral articulations, and a first thoracic rib reaching to the axillary buttress. Skull poorly known, with large orbits and a flat, unexpanded triturating surface as in *Ordosemys*; lower jaws deep with an unexpanded triturating surface. Carapace outline similar to *Xinjiangchelys*, ovate with roughly parallel sides and a recessed anterior margin. Bridge peripherals guttered as in *Xinjiangchelys*, but in contrast to *Ordosemys*. Vertebral scales much wider than long in contrast to *Xinjiangchelys*, *Ordosemys*, and *Sinemys*. Plastron with broad epiplastra and a full set of extragular and gular scales as in *Xinjiangchelys*, but in contrast to *Dracochelys*; extragular scales relatively small, in contrast to *Xinjiangchelys*; entoplastron ovoid with gular scales extending onto it; strong posterolateral processes on entoplastron in contrast to *Xinjiangchelys* and *Ordosemys*; large hyoplastron/hypoplastron fontanelle in contrast to *Xinjiangchelys*; inframarginal scales reduced to three; inguinal buttress terminates on peripheral six rather than on peripheral seven or eight as in *Xinjiangchelys*, *Ordosemys*, *Dracochelys*, and *Sinemys*. Cervical vertebral formula probably)2))3))4))5((6((7((8), eighth cervical known to be biconvex and one anterior cervical (probably 5) biconcave as in *Ordosemys* but in contrast to *Xinjiangchelys*, which is amphicoelous; neural spine higher than in *Ordosemys*; transverse processes double as in *Ordosemys*. Differs from *Chelycarapookus* in being 20% larger and having a large hyoplastron/hypoplastron fontanelle, a smooth rather than rugose surface texture, and a larger posterior plastral lobe relative to the anterior plastral lobe.

Otwayemys cunicularius, new species

TYPE SPECIMEN: NMV P186116 (figs. 1–4, 10, 11), a nearly complete shell.

TYPE LOCALITY: Slippery Rock Site, Dinosaur Cove, Cape Otway, Victoria, Australia.

HORIZON: Otway Group, Aptian-Albian.

DIAGNOSIS: As for genus.

ETYMOLOGY: Cunicularius, for mining or

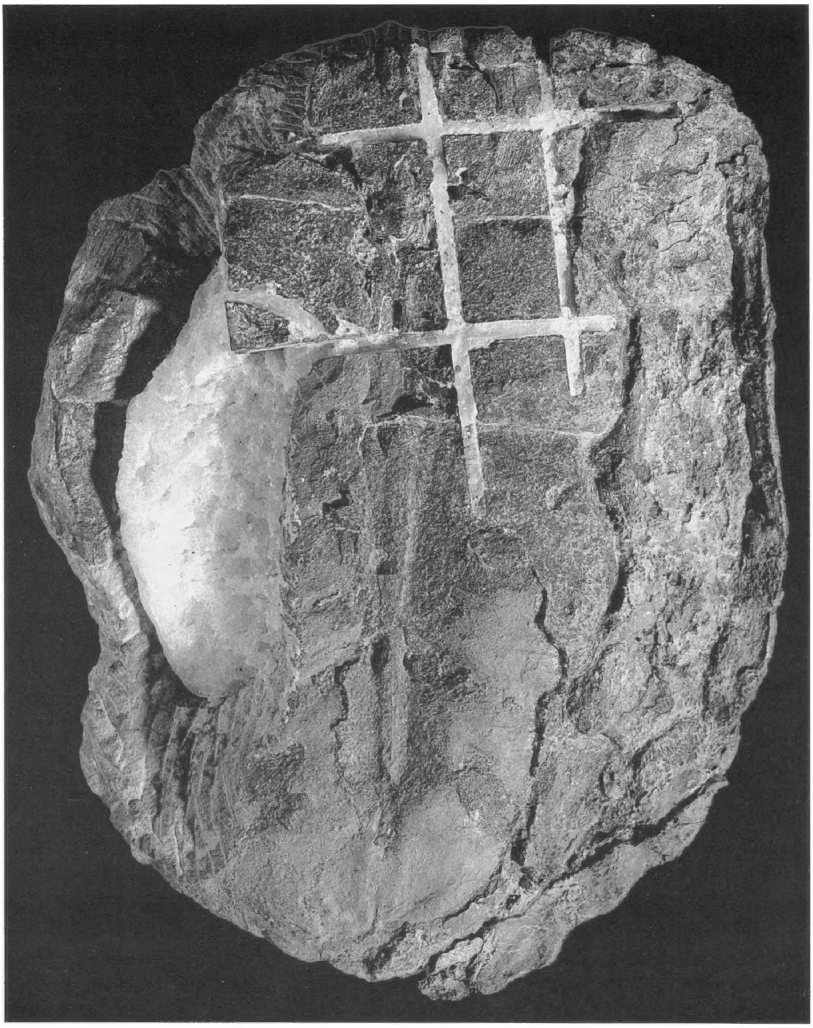

Fig. 1. *Otwayemys cunicularius,* new genus and species. NMV P186116, dorsal view of carapace. Remaining portion of carapace preserving the left posterior region is shown in fig. 4.

tunneling, in reference to the mode of collection.

REFERRED MATERIAL: All of these specimens were collected by T. H. Rich and party at Dinosaur Cove, Cape Otway, Victoria, Australia, except where indicated otherwise.

NMV P180900 (figs. 5–8)—left costals one to four with associated neurals and thoracic vertebrae, 20 m south of Dinosaur Cove East, on shore platform, 1984.

NMV P186234—right first costal, Slippery Rock cross tunnel, Dinosaur Cove 1989.

NMV P185883—Dinosaur Cove East, 1985.

NMV P185914—costal bone, Dinosaur Cove West.

NMV P180929—peripheral, Dinosaur Cove West.

NMV P186048—entoplastron, Slippery Rock cross tunnel, 1987.

NMV P186233—left xiphiplastron, Dinosaur Cove East, 1985.

NMV P201020—partial right hyoplastron and hypoplastron, Lake Copco Site, Dinosaur Cove East, 1986.

NMV P185952 (fig. 13)—left maxilla, Slippery Rock, 1986.

NMV P201021 (fig. 12)—right squamosal, Slippery Rock site, 1987.

NMV P186108—right quadrate, Slippery Rock site, 1989.

NMV P186124—right and left dentaries, Slippery Rock cross tunnel, 1989.

NMV P186223—right ramus dentary, Slippery Rock cross tunnel, 1989.

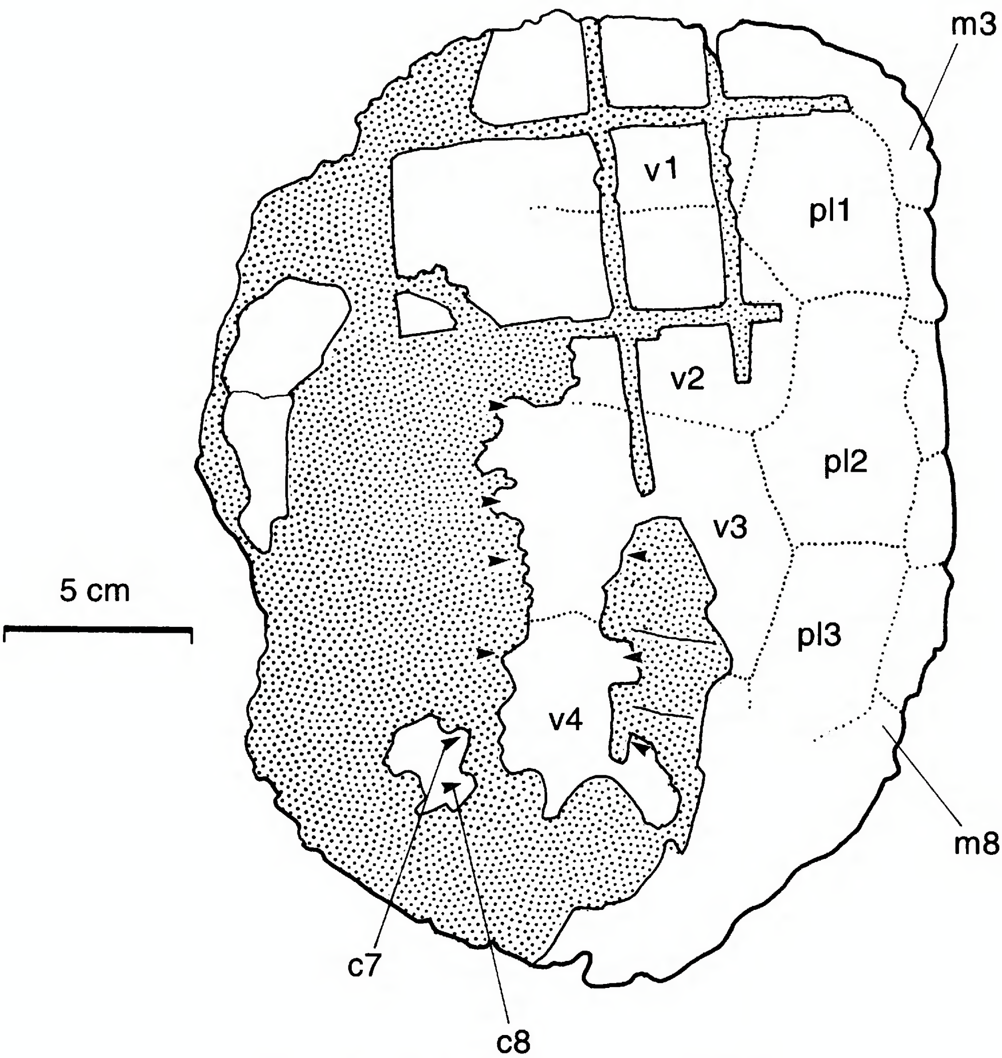

Fig. 2. Key to fig. 1. Abbreviations on page 2.

NMV P186109 (fig. 14)—right ramus dentary, Slippery Rock site, 1986.

NMV P186224—(?) fifth cervical vertebra, Lake Copco site, Dinosaur Cove East, 1989.

NMV P187261 (fig. 15)—eighth cervical vertebra, Lake Copco site, Dinosaur Cove East, 1986.

NMV P186121—first thoracic vertebra, Rock Pile Tunnel, Slippery Rock site, 1989.

NMV P197768—anterior caudal vertebra, Dinosaur Cove East, 1985.

NMV P186024—posterior caudal vertebra, Slippery Rock or Dinosaur Cove East, 1987.

NMV P186222—pelvic fragments, Slippery Rock, 1986.

DISCUSSION

An important question concerns whether or not the Otway turtle material may be the same taxon as *Chelycarapookus* described by Warren (1969). *Chelycarapookus* consists of a natural internal mold of a shell, presumed to be from the Lower Cretaceous Merino Group, of Carapook, Victoria (see also Chapman, 1919) and is therefore close in location and age to the Otway specimens. Warren (1969) was undecided as to whether *Chelycarpookus* was a cryptodire or a pleurodire, but Gaffney (1981) referred it to the Cryp-

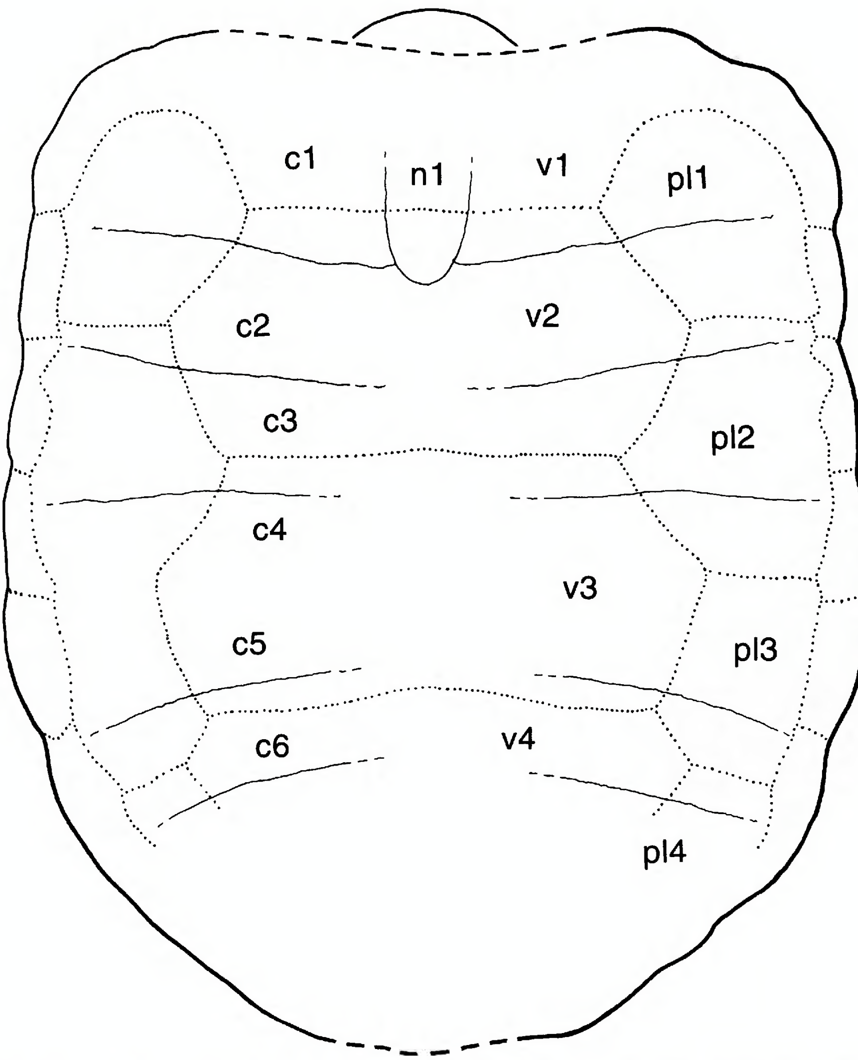

Fig. 3. *Otwayemys cunicularius.* Restored dorsal view of carapace based on NMV P186116 and NMV P180900. Abbreviations on page 2.

todira. Reexamination in the context of sinemydids and other Mesozoic eucryptodires strongly supports identification of *Chelycarapookus* as a primitive eucryptodire similar in many features to sinemydids. However, steinkerns (internal molds) are notoriously difficult to use for systematic comparisons. The *Chelycarapookus* steinkern could be referable to any number of primitive eucryptodires, as there are few characters visible in it despite the sutures found by Warren (1969, plastron) and Gaffney (1981, carapace).

There are a few characters that distinguish between *Chelycarapookus* and *Otwayemys.* The *Chelycarapookus* shell represents an animal about 76% the size of NMV P186116, based on comparable measurements of the plastron. NMV P186116, in contrast, has a very large hypoplastron/hyoplastron fontanelle. Fontanelles are found in juvenile shells and usually close up during growth. If the smaller *Chelycarapookus* shell has a small or no fontanelle and the larger NMV 186116 has a large fontanelle, it suggests that the two are probably different taxa. Variation in this feature occurs in pelomedusids, however, and it is not a particularly dependable character.

A fragment of shell is present on the *Che-*

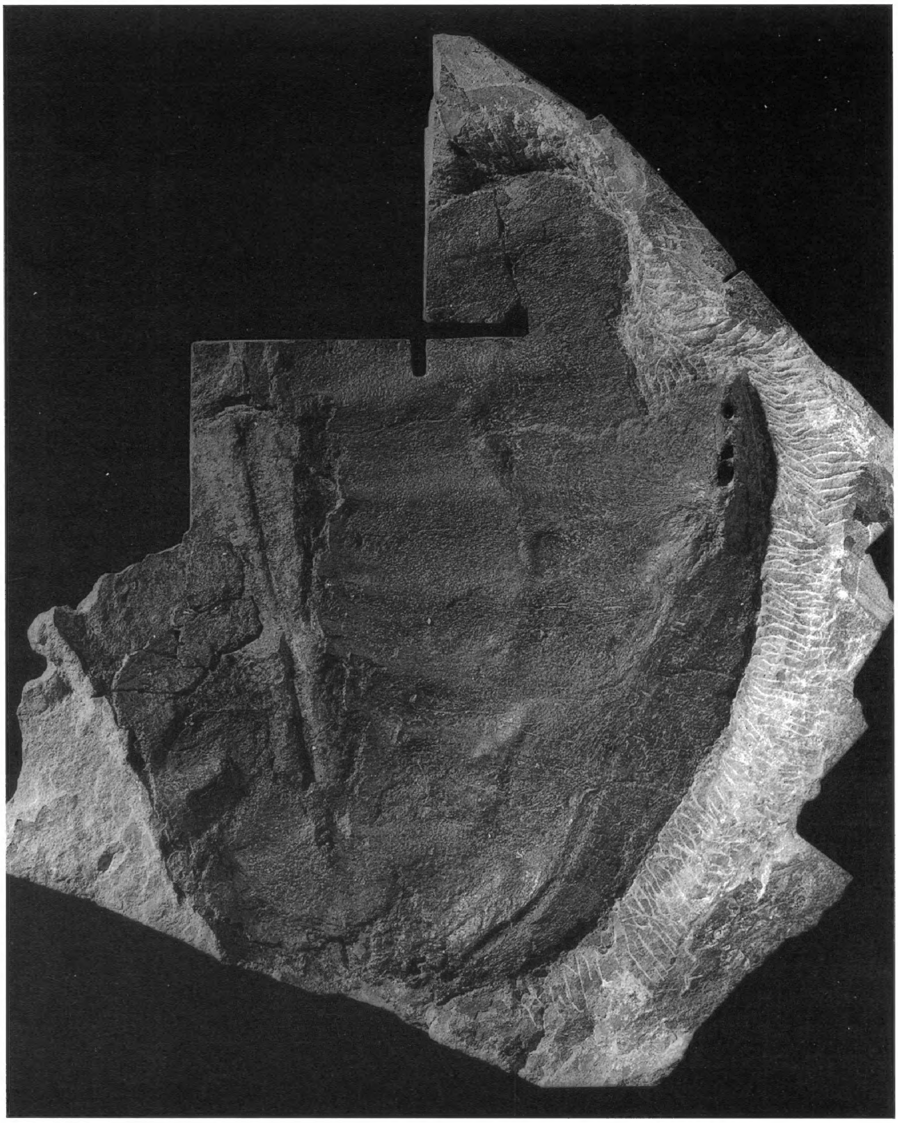

Fig. 4. *Otwayemys cunicularius.* NMV P186116, ventral view of carapace preserved as counterpart to rest of shell, shown in fig. 1.

lycarapookus steinkern and this seems to show a surface texture that is moderately rugose, in contrast to the smooth surface in *Otwayemys.* However, bone preservation in *Chelycarapookus* is poor and this may not be characteristic of the whole carapace. The base of the posterior lobe of the plastron in NMV P186116 appears to be distinctively wider than the base of the posterior lobe in *Chelycarapookus* when both are compared relative to the anterior lobe.

It is likely that *Otwayemys* is distinct from *Chelycarapookus,* based on this pattern of characters. However, owing to the inadequacy of the type specimen of *Chelycarapookus,* it may never be positively determinable which specimens actually belong to that taxon.

Description

Carapace (figs. 1–8)

The type specimen, NMV P186116 (fig. 1), consists of a nearly complete shell with a

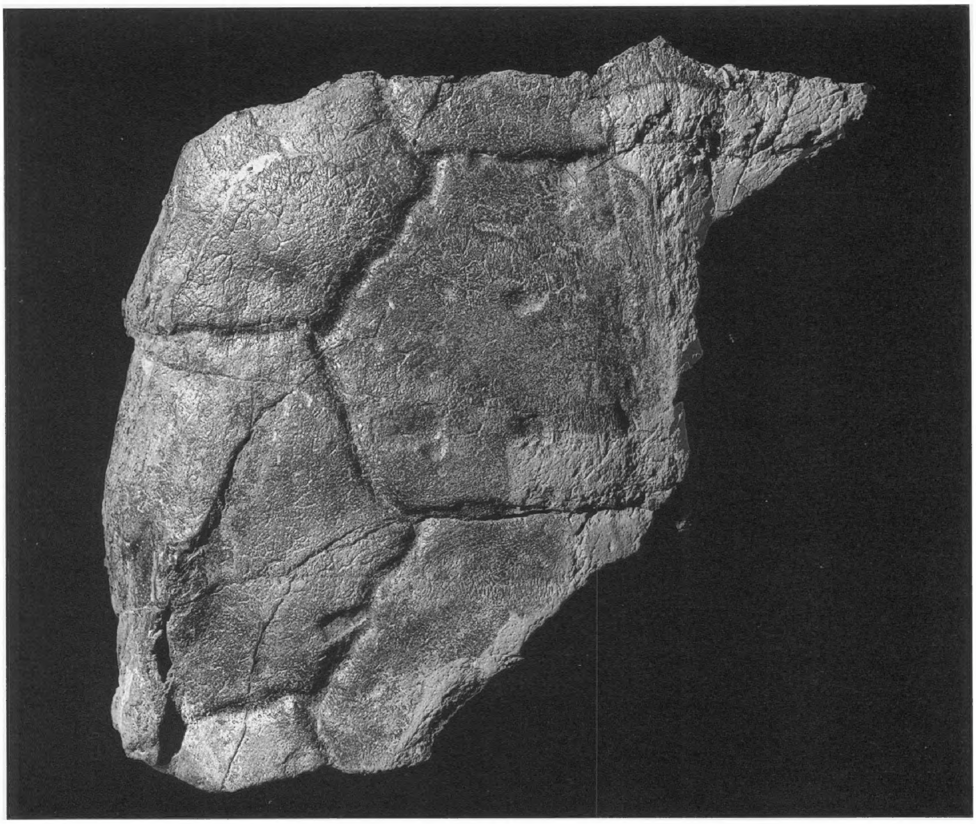

Fig. 5. *Otwayemys cunicularius.* NMV P180900, dorsal view of partial carapace with costals 1–4.

well-preserved plastron. The carapace, although most of it is present, has not survived the rigors of collection and preparation as well as it might. In addition to the four neat little incisions ornamenting the anterior half of the carapace, the entire carapace was split through the bone exposing much of the internal surface but very little of the external surface. The central and left lateral portions of the carapace are in the counterpart piece, whereas the anterior and right lateral portions are in the larger piece containing the plastron.

TABLE 1
Comparison of *Otwayemys* and *Chelycarapookus*

	Otwayemys	*Chelycarapookus*
Size comparison (estimated shell length at midline)	100%	76%
Hyoplastral/Hypoplastral fontanelle	large	absent (or very small)
Surface texture	smooth	rugose
Posterior lobe of plastron relatively wide at base	yes	no

NMV P186116 is the basis for the restored outline and scale markings (fig. 3), although it appears that there was some preservational distortion, particularly along the right side. Other carapace specimens add to our understanding of the morphology. NMV P180900 (figs. 5–8) is an articulated set of costals 1–4 with associated neurals and thoracic vertebrae. NMV P185883 is a sixth costal with well-preserved sulci. NMV P186234 is a partial first costal, NMV P185914 is an indeterminant costal, and NMV P180929 is a peripheral. The smooth surface texture, conformity to NMV P186116, and the consistency with expected eucryptodiran morphology support identification of these other specimens as *Otwayemys*.

The anterior margin of the carapace is pre-

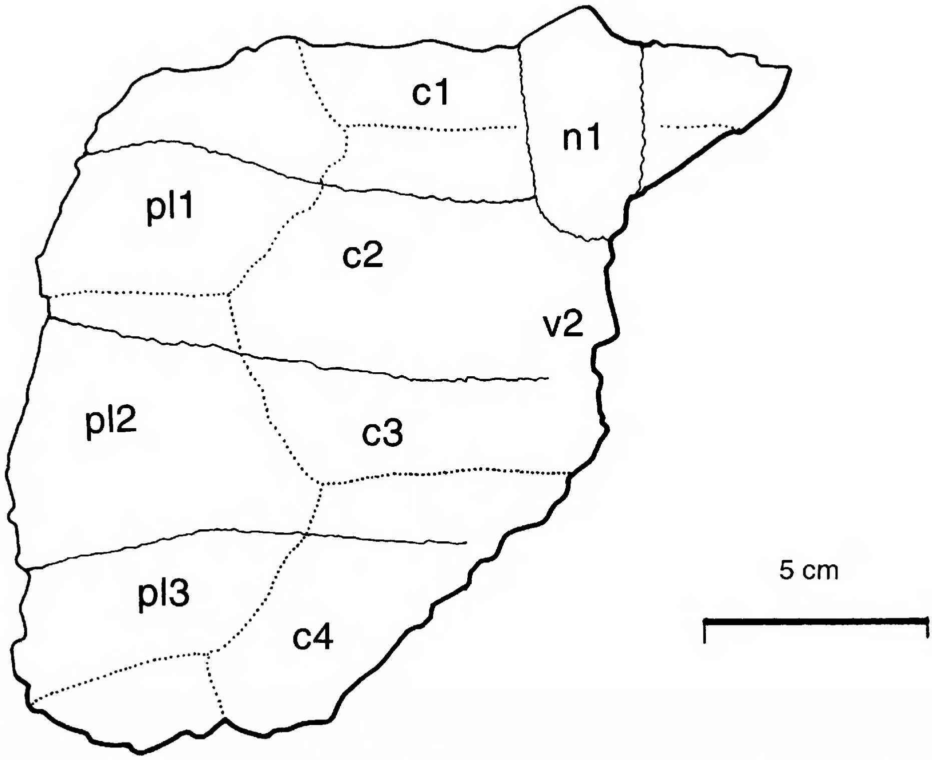

Fig. 6. *Otwayemys cunicularius.* NMV P180900, key to fig. 5. Abbreviations on page 2.

served only in NMV P186116 and it is badly damaged in this specimen. Sutures have not been determined in this carapace (although they are clear in the plastron of the same specimen) and the limits of nuchal bone and peripherals are not known. Nonetheless, this specimen does show the shouldered anterior margin with recessed nuchal area that is also seen in *Ordosemys* (Brinkman and Peng, 1993a) and *Xinjiangchelys* (Peng and Brinkman, 1993). *Otwayemys* appears to differ from these taxa (except *Xinjiangchelys latimarginalis*) in being much broader along its anterior margin and not having anteriorly converging sides.

Otwayemys seems to have guttered peripherals (NMV P186116), developed in the pleural/marginal sulcus along the bridge. Damage may have exaggerated or even produced this appearance of a trough, however. Guttered peripherals are also found in *Xinjiangchelys* and *Ordosemys,* although weakly developed in the latter.

NMV P186116 has clear vertebral and pleural sulci and these show that *Otwayemys* has relatively broad vertebrals with small pleurals, in contrast to the small vertebrals of *Xinjiangchelys* and *Ordosemys.* This feature varies a great deal in turtles, but distinguishes *Otwayemys* from Asian forms. Broad vertebrals tend to be primitive in turtles, occurring in *Proganochelys, Kayentachelys,* and baenids.

An articulated partial carapace, NMV P180900 (figs. 5–8), consists of costals 1–4 and their associated neurals and thoracic vertebrae. This specimen is the basis for the sutures shown in the central carapace of the restoration (fig. 3). NMV P180900 and NMV P186116 agree closely in morphology, particularly the large vertebrals, smooth surface texture, and deeply incised scale sulci. The sutures of the first neural and part of the second are visible. None of the other neurals nor the total number of neurals are determinable in this or any other specimens.

A disarticulated costal bone, NMV P185883, is identified as a sixth left costal. This bone has clearly incised sulci on it that separate pleurals 3 and 4 and vertebrals 3 and

TABLE 2
Comparison of Carapace in Some Primitive Eucryptodires

	Otwayemys	*Xinjiangchelys*	*Ordosemys*	*Dracochelys*	*Chelycarapookus*
Emarginated nuchal area	present	present	present	indet.	indet.
Carapace surface texture	smooth	smooth	smooth	smooth	rugose
Bridge peripherals guttered	yes	yes	no	variable	indet.
Vertebrals	wider	narrower	narrower	narrower	indet.
Shell shape	broad anteriorly	variable	narrow anteriorly	narrow anteriorly	indet.

4. This is somewhat unusual because the sulci between vertebrals 3 and 4 usually lie on costal 5.

The posterior margin of the carapace is only preserved in NMV P186116 and that is poorly preserved. Sutures are not determinable. On the ventral surface of the counterpart, the portion of the peripherals extending beyond the ridge marking the body wall attachment becomes smaller posteriorly.

The anterior portion of the internal surface of the carapace is well-preserved in NMV P180900 (figs. 7, 8). NMV P186116 shows the rib heads and rib ridges posteriorly. The disarticulated first costal, NMV P186234, also has a well-preserved ventral surface. *Otwayemys* has a long first thoracic rib (fig. 7), a primitive feature for cryptodires, found in *Kayentachelys,* baenids, and plesiochelyids, as well as in sinemydids and meiolani-

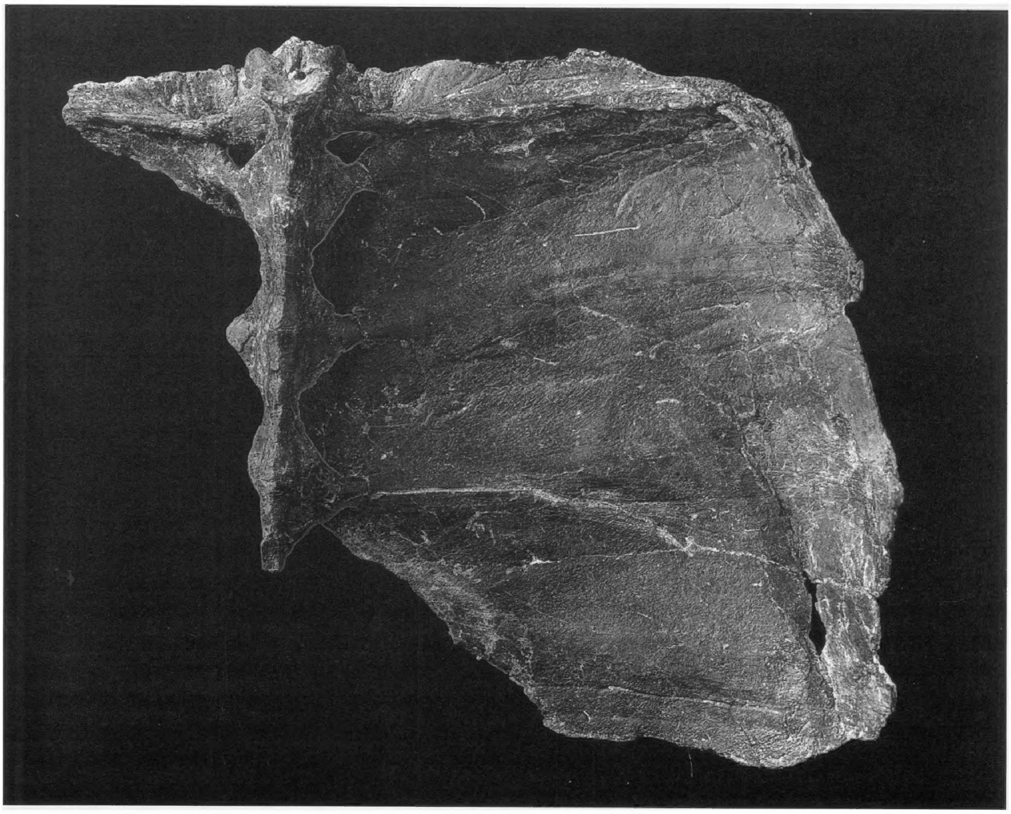

Fig. 7. *Otwayemys cunicularius.* NMV P180900, ventral view of partial carapace with costals 1–4.

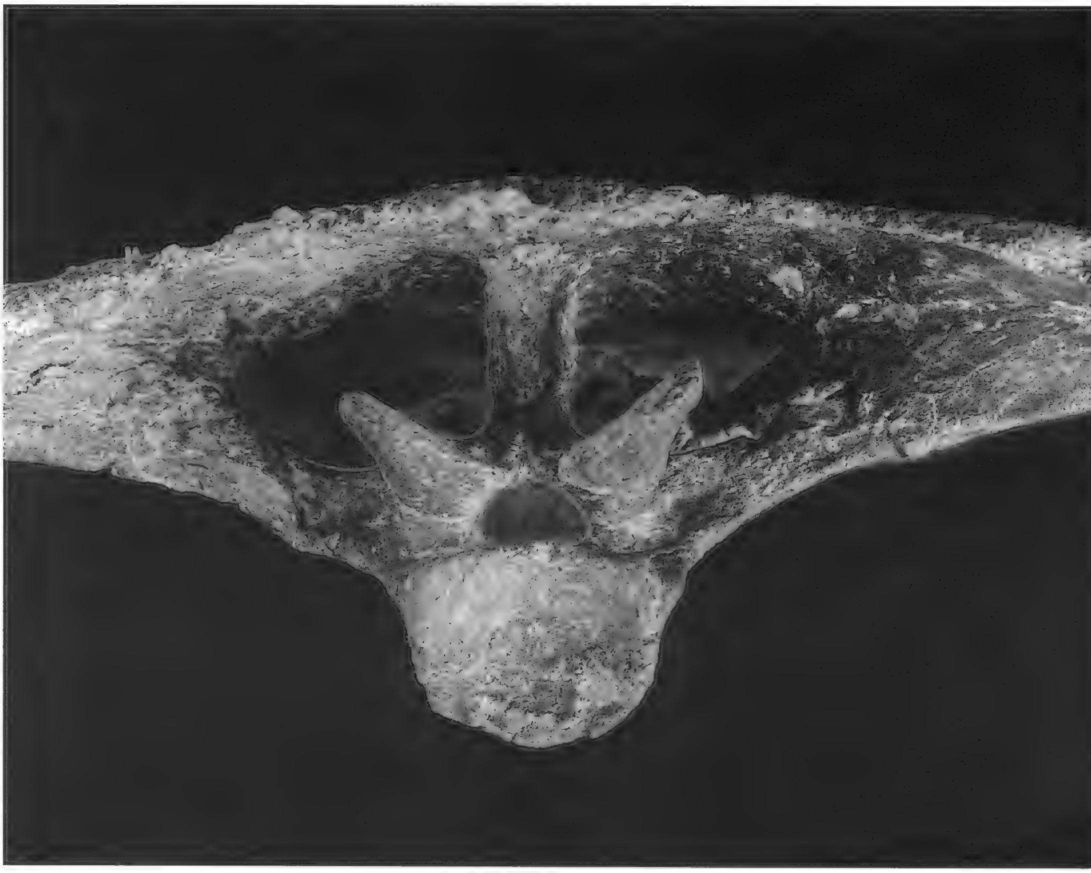

Fig. 8. *Otwayemys cunicularius.* NMV P180900, anterior view of first thoracic vertebra as articulated in partial carapace seen in fig. 7.

ids. This character was used by Gaffney and Meylan (1988) and Gaffney (1996) for systematic relationships among eucryptodires.

The orientation of the central articulation of the first thoracic vertebra is also significant in cryptodire systematics (Gaffney and Meylan 1988; Brinkman and Peng 1993a, 1993b; Gaffney 1996). NMV P180900 (fig. 8) preserves the anterior thoracics and NMV P186121 is a disarticulated first thoracic. Both of these show the primitive cryptodiran condition in which the central articulation faces anteriorly rather than anteroventrally or ventrally. This is the same as in the Asian sinemydids, *Xinjiangchelys,* plesiochelyids, and meiolaniids.

PLASTRON (figs. 9–11)

The plastron of *Otwayemys* is based primarily on NMV P186116, the type specimen, which is well-preserved and has clear sutures and sulci. There are also useful disarticulated specimens. NMV P186048 is an entoplastron, and NMV P186233 is a xiphiplastron used to restore the missing xiphiplastra in the composite based on NMV P186116 (fig. 9).

In general the plastron of *Otwayemys* is very similar to the plastron of *Xinjiangchelys* (Peng and Brinkman, 1993), differing primarily in the narrow entoplastron, small extragular scales, and large central fontanelle.

The epiplastra of *Otwayemys* are relatively broad, as in *Xinjiangchelys*, in contrast to the relatively small, splintlike epiplastra of *Dracochelys, Hangaiemys,* and chelydrids. These splintlike epiplastra also lack the extragular scales, scale set 2 of Hutchison and Bramble (1981), which are present in *Otwayemys.* It is hypothesized that the narrow epiplastra are present in *Ordosemys* and the Sinemydidae as defined by Gaffney (1996). The dorsal surface is not visible so the presence or ab-

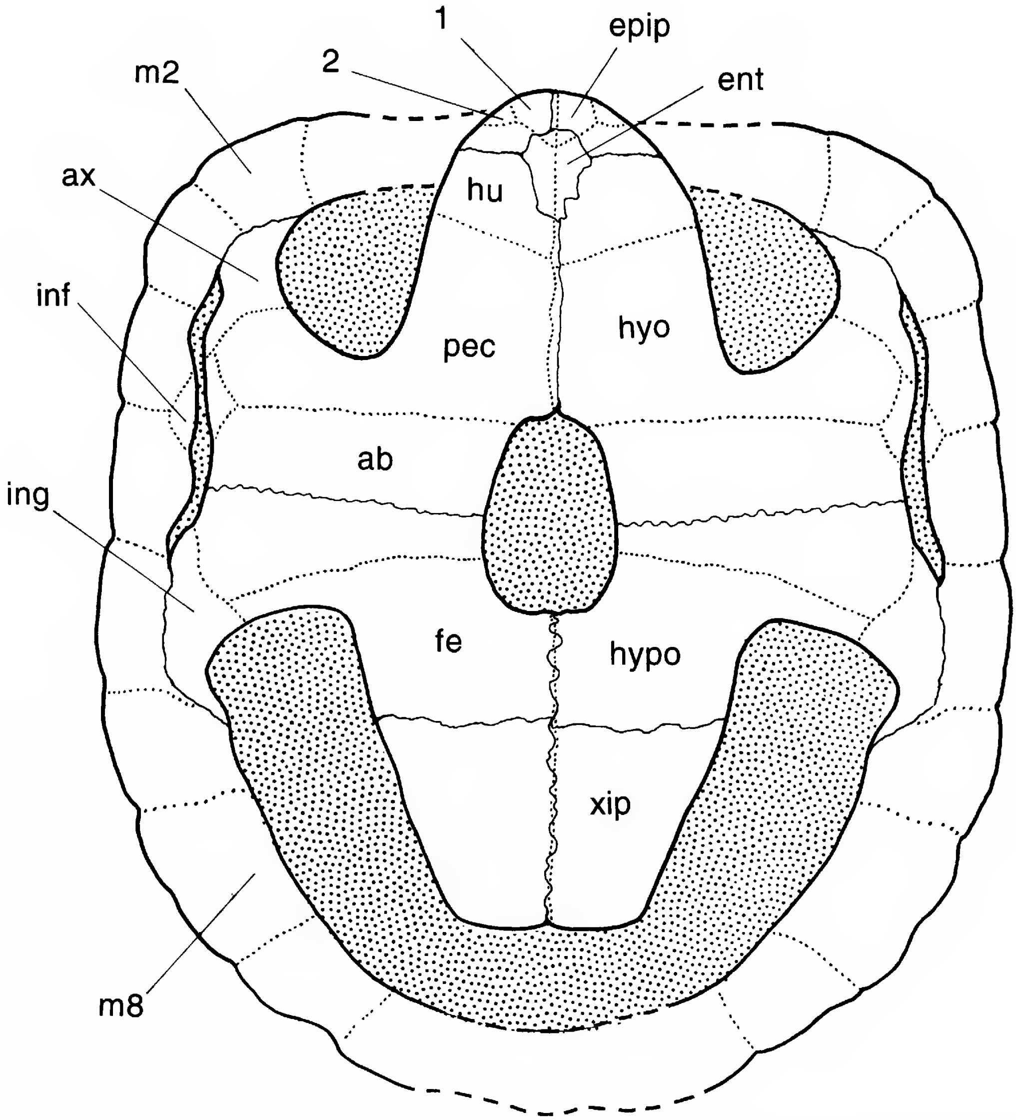

Fig. 9. *Otwayemys cunicularius.* Restored plastron in ventral view based primarily on NMV P186116 with xiphiplastron from NMV P186233. Abbreviations on page 2.

sence of dorsal processes of the epiplastra in *Otwayemys* is not determinable.

The extragular scales, scale set 2, are relatively small in *Otwayemys* and lie on the anterior edge of the epiplastron. The gular scales, scale set 1, are paired and are distinctly larger than the extragulars. The gulars lie mostly on the epiplastra but do extend onto the entoplastron for a short distance, in contrast to the gulars in *Xinjiangchelys,* which do not extend onto the entoplastron at all.

The entoplastron of *Otwayemys* is generally similar to that seen in *Xinjiangchelys.* It is longer than wide with a clear midline sulcus. In *Otwayemys* the entoplastron is relatively smaller and narrower than in *Xinjiangchelys* and *Dracochelys.* The entoplastron of *Otwayemys* separates the epiplastra to a greater extent and the hyoplastra to a lesser extent than in *Xinjiangchelys.*

The dorsal surface of the disarticulated entoplastron, NMV P186048, shows two pairs of processes. The anterolateral pair is

TABLE 3
Comparison of Plastron in Some Primitive Eucryptodires

	Otwayemys	*Xinjiangchelys*	*Ordosemys*	*Dracochelys*	*Chelycara-pookus*
Epiplastra	wide	wide	narrow?	narrow	indet.
Extragular scales	small	large	large	large	indet.
Gular scutes extend onto entoplastron	yes	no	indet.	yes	indet.
Entoplastron	small and narrow	large and wide	indet.	very wide	indet.
Anterior processes on entoplastron	two	one	indet.	one	indet.
Strong posterolateral processes on entoplastron	present	absent	indet.	absent	indet.
Hypoplastron/hyoplastron fontanelle	present	absent	present	present	absent
Hypoplastron/xiphiplastron fontanelle	absent	absent	present	absent	absent
Bridge/peripherals fontanelle	absent	present	absent	present	absent?
Inframarginal scales small	yes	no	no	indet.	indet.
Inguinal buttress termination	peripheral 6	peripheral 8	peripheral 8	peripheral 8	indet.

short and can be contrasted to a single, midline projection seen in *Xinjiangchelys* and *Dracochelys*. The posterolateral pair is large and similar to those seen in *Chelydra* and lies in the dorsal part of the epiplastron/hyoplastron suture. The sinemydids and *Xinjiangchelys* have irregularly ovoid entoplastra without these processes.

The large midline, hyoplastron/hypoplastron fontanelle of *Otwayemys* does not occur in *Xinjiangchelys* but there is a small one in *Ordosemys* and *Dracochelys*. *Ordosemys* (but not *Xinjiangchelys* or *Dracochelys*) also has a hypoplastron/xiphiplastron fontanelle not found in *Otwayemys*. *Xinjiangchelys* and *Dracochelys* have bridge fontanelles that are absent in *Otwayemys* and *Ordosemys*. Fontanelles vary ontogenetically and intraspecifically in turtles, but in some species they are consistent enough to be systematically important. In these early eucryptodires a number of taxa, including meiolaniids, have fontanelles and they do seem to be useful at the alpha level of discrimination.

Primitively, eucryptodires have a full set of four inframarginal scales and this is the case in *Xinjiangchelys* and *Ordosemys*. *Otwayemys* appears to have lost one and reduced another. However, the inframarginals often do not form well-defined sulci and this region is known only from the right side of NMV P186116.

Mesoplastra are clearly absent in *Otwayemys*. The absence of mesoplastra coincides with the enclosure of the carotid artery, which defines the Eucryptodira of Gaffney and Meylan (1988) and Gaffney (1996).

The inguinal buttress of the hypoplastron in *Otwayemys* terminates on the sixth peripheral. In *Xinjiangchelys, Ordosemys,* and *Dracochelys* the buttress extends onto the seventh peripheral and contacts or nearly contacts the eighth peripheral.

SQUAMOSAL (fig. 12)

A right squamosal, NMV P201021, that can be attributed to *Otwayemys* on the basis of its similarity to sinemydids, plesiochelyids, and other primitive eucryptodires, is preserved in the Dinosaur Cove collections. Unfortunately, the squamosal is effectively unknown in *Ordosemys* and *Xinjiangchelys,* but *Sinemys* and *Plesiochelys* are available for comparison.

The squamosal in *Otwayemys* is well

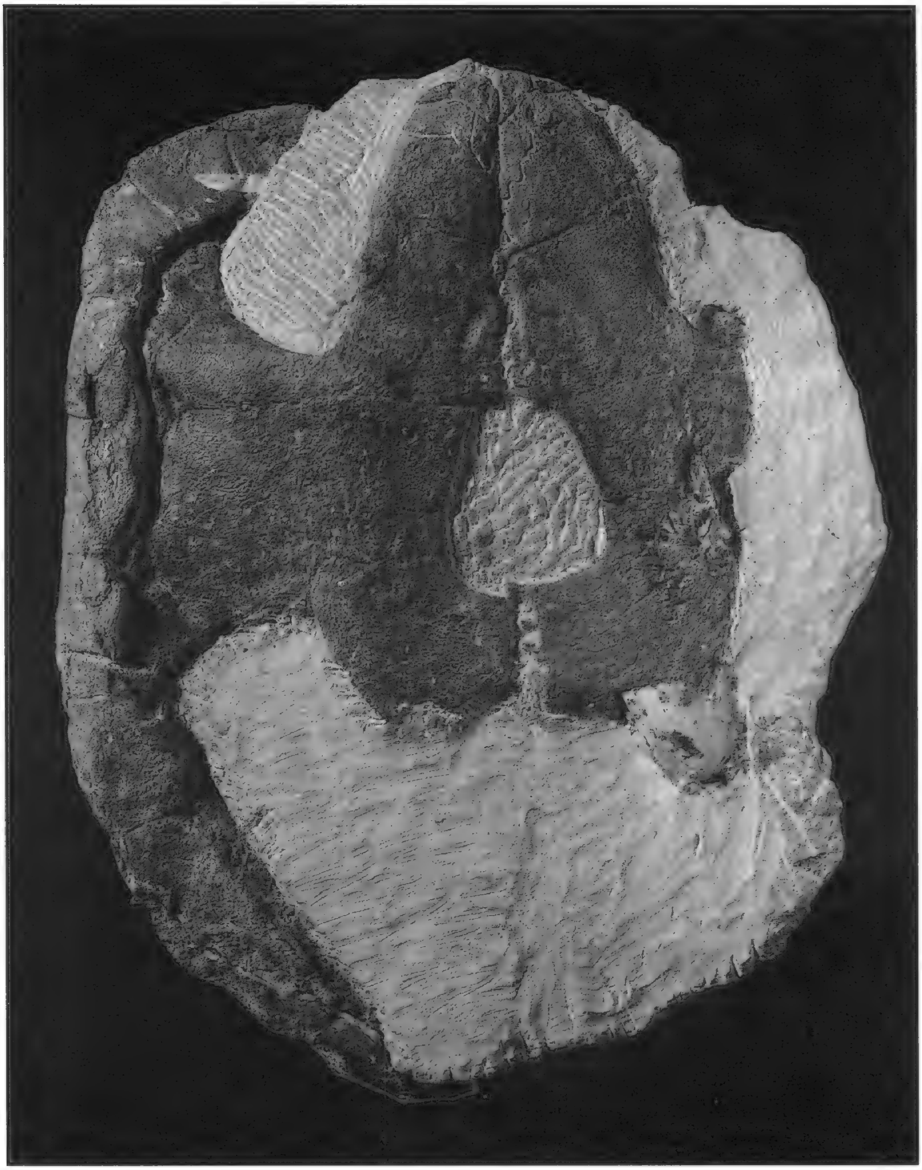

Fig. 10. *Otwayemys cunicularius.* NMV P186116, ventral view of shell.

enough preserved to see the cone-shaped antrum postoticum ventrally and the curved sheet of bone forming part of the skull roof dorsally. Almost all of the thin edges are broken or worn and definitive sutural edges are hard to determine. However, the extent of skull roof formed by the squamosal in *Otwayemys* is very similar to that seen in the baenids *Plesiobaena, Boremys,* and *Eubaena,* suggesting the limited degree of temporal emargination seen in these forms (Gaffney, 1979a; Brinkman and Nicholls, 1991).

Sinemys gamera (Brinkman and Peng, 1993b) has a fairly extensive degree of emargination, much greater than that interpreted for *Otwayemys. Ordosemys* has the parietals and postorbitals preserved and the degree of emargination is distinctly less than that seen in *Sinemys,* but *Ordosemys* is probably more emarginate than *Otwayemys. Otwayemys* probably had a well-de-

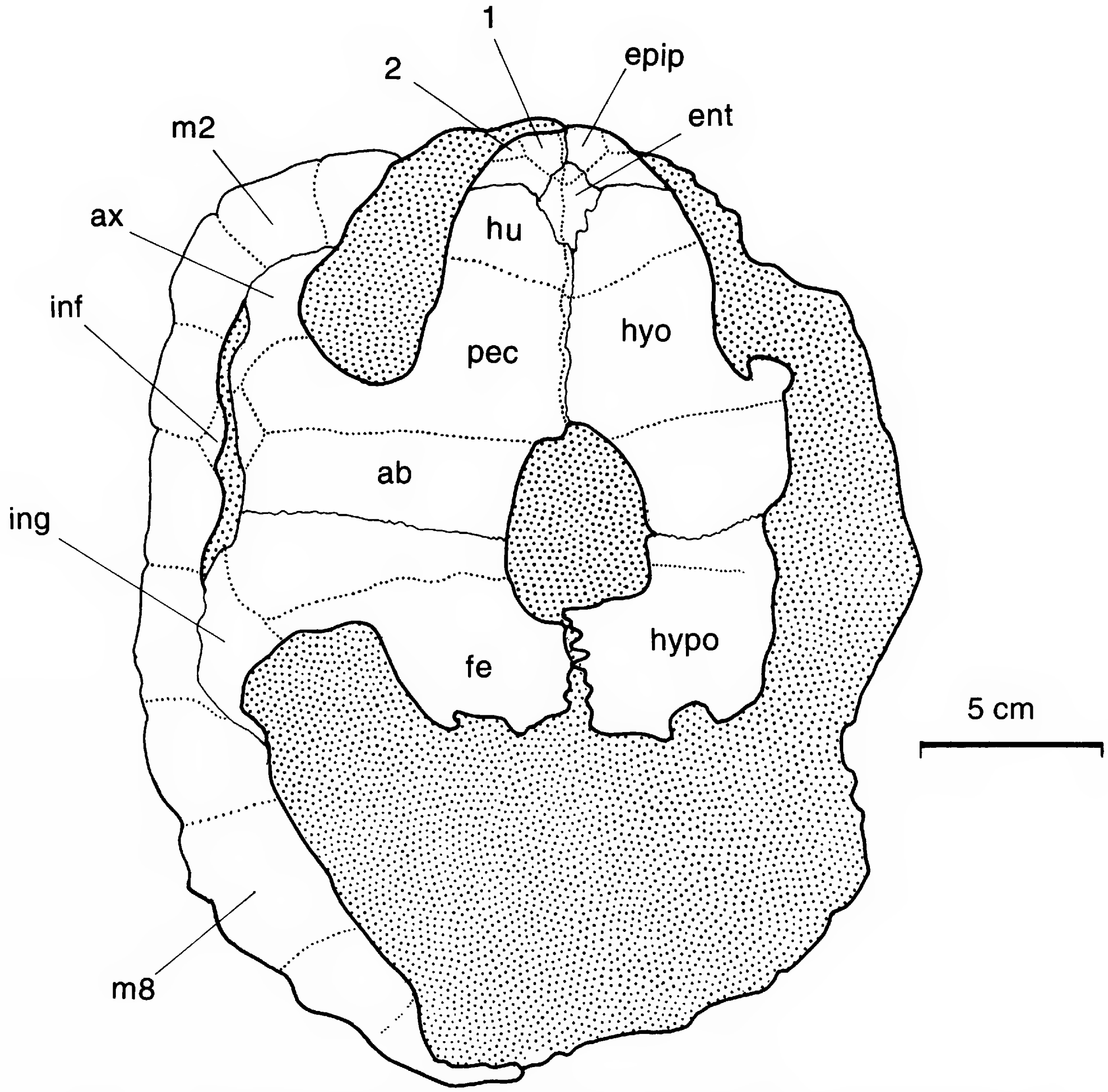

Fig. 11. *Otwayemys cunicularius.* NMV P186116, key to fig. 10. Abbreviations on page 2.

veloped postorbital-squamosal contact, but *Ordosemys* probably had very little or no postorbital contact.

MAXILLA (fig. 13)

A left maxilla, NMV P185952, preserved in the Dinosaur Cove material, can be attributed to *Otwayemys* on the basis of its close similarity to *Ordosemys.* The maxilla is missing some of the sutural edges but, as far as can be determined, it is nearly complete. For comparison, the figured *Ordosemys* maxilla in Brinkman and Peng (1993a: fig. 5) and the new *Ordosemys* skull, IVPP V12092, were available. There is no maxilla yet known for *Xinjiangchelys.*

In ventral view, *Otwayemys* and *Ordosemys* both have a relatively generalized turtle maxilla, with a simple triturating surface, a sharp tomial ridge, and a flat medial surface, much as is seen in plesiochelyids (Gaffney, 1976). In *Otwayemys* the posterior portion of the medial surface is more expanded than in *Ordosemys.*

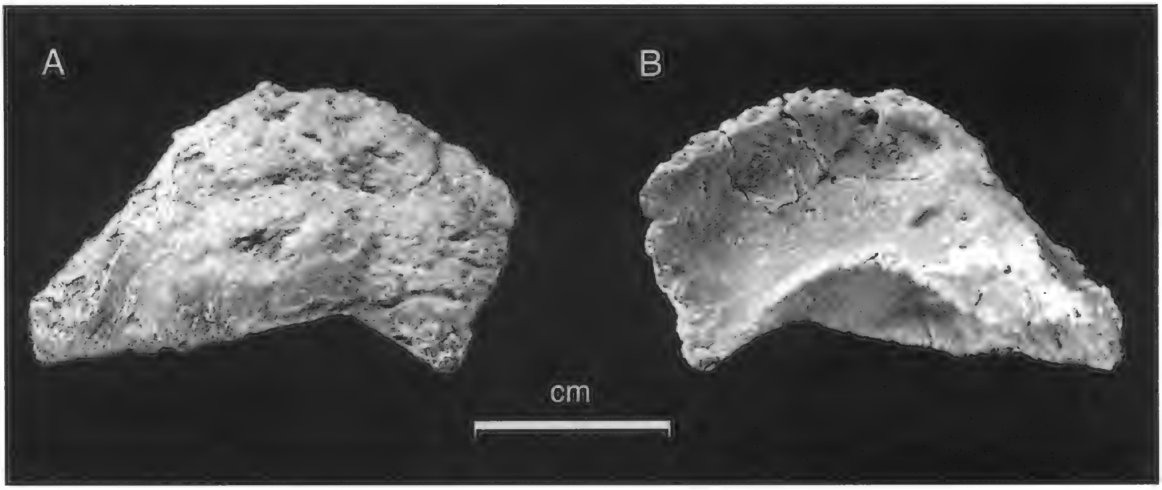

Fig. 12. *Otwayemys cunicularius.* NMV 201021, right squamosal. **A,** lateral view (anterior to right); **B,** medial view (anterior to left).

In lateral view the maxillae of *Otwayemys* and *Ordosemys* have a very similar profile. Dorsally, both taxa have unusually large orbits defined by a long, curved profile, concave upward. On the ventral margin, the edge of the tomial ridge also has a distinctive lateral profile in both. Both *Otwayemys* and *Ordosemys* have a shallow curved edge, convex ventrally, along the posterior margin of the tomial ridge. Anteriorly the curve is reversed and both have a concave margin. *Chelydra* and some other cryptodires also have a similar shape to the tomial edge. At the dorsal end of the anterior edge of the orbit is a sulcus in both *Otwayemys* and *Ordosemys* that marks the edge of the horny bill.

QUADRATE

A right quadrate, NMV P186108, is a Dinosaur Cove specimen attributable to *Otwayemys* on the basis of its close similarity to *Ordosemys* and other primitive eucryptodires. For comparison, complete quadrates are available in the new skull of *Ordosemys,* IVPP V12092, and plesiochelyids. The quadrates described for *Xinjiangchelys* (Kaznishkin et al., 1990; quadrate is probably the area labeled "op" in fig. 1b) are too ambiguously figured for close comparison.

The *Otwayemys* quadrate, NMV P186108, is largely complete but lacks the thin distal edges of the cavum tympani and most of the sutural surfaces are broken or damaged. The quadrate is clearly that of a cryptodire, with a typically developed processus trochlearis oticum (Gaffney, 1979a). In all its preserved features the quadrate of *Otwayemys* is very similar to that bone in *Ordosemys,* except that the *Otwayemys* quadrate is slightly larger.

In lateral view, both *Otwayemys* and *Ordosemys* have a cavum tympani relatively elongate, deep, and smoothly continuous between the antrum postoticum and the anterior part of the cavum tympani. The incisura columellae auris is similar in both. The incisura has a round opening for the stapes proximally and a narrow fissure extending posteroventrally. Thus, the incisura is restricted but open. This is in contrast to baenids and plesiochelyids that have a more open incisura columellae auris, and chelydrids that have a completely closed incisura.

Medially and ventrally the foramen stapedio-temprorale and the canalis stapedio-temporalis are preserved in NMV P186108. The aditus canalis stapedio-temporalis and the canalis cavernosus complete these medial structures, similar in position in most cryptodires (see Gaffney, 1979a: fig. 10). The area of the processus articularis is damaged but the size and extent of the jaw articulation can be determined, which is similar in *Ordosemys.*

LOWER JAWS (fig. 14)

Four lower jaws are present in the Dinosaur Cove collection. All consist only of the

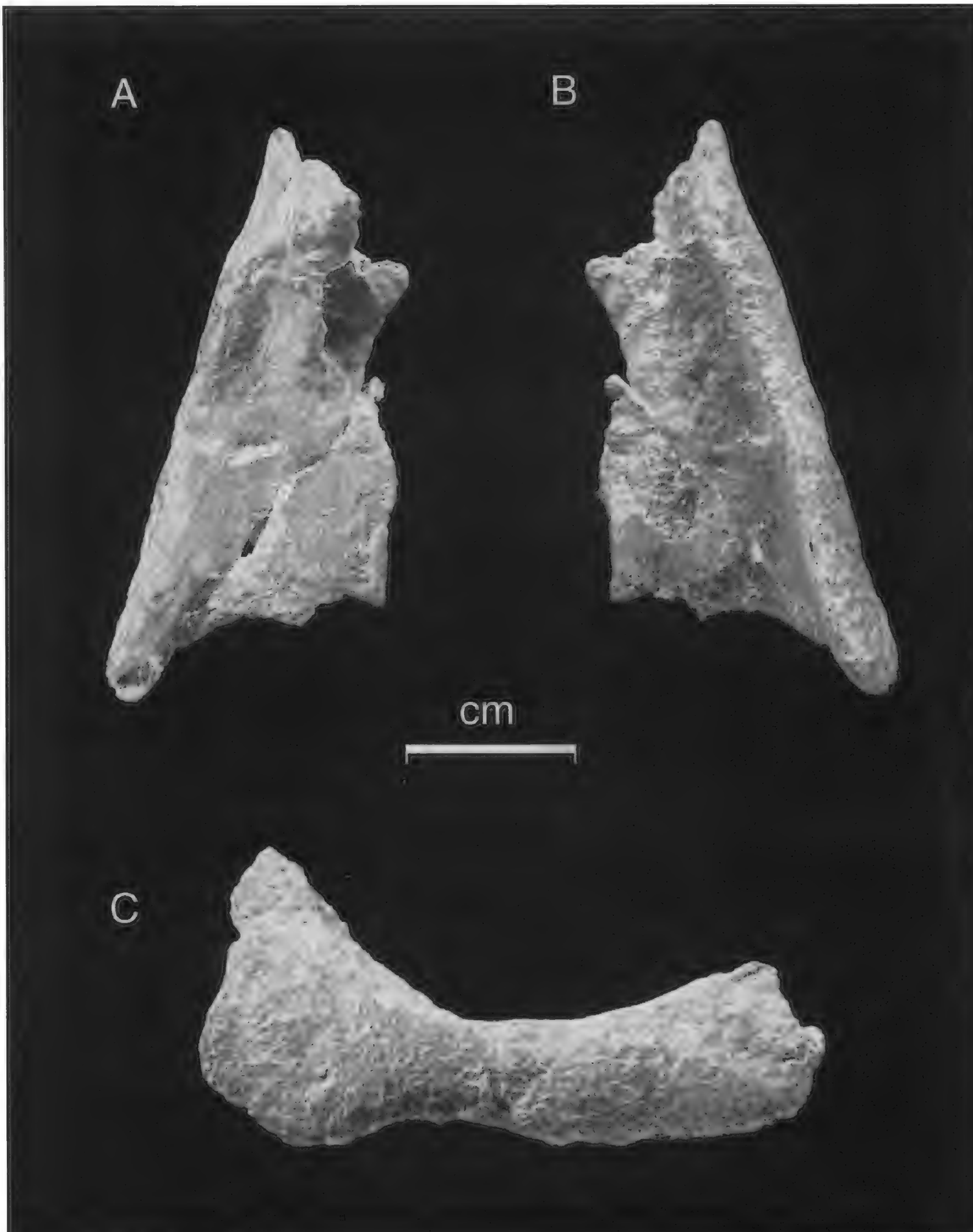

Fig. 13. *Otwayemys cunicularius.* NMV P185952, left maxilla. **A,** dorsal view; **B,** ventral view; **C,** lateral view (anterior to left).

dentary bone. Two, NMV P186223 and NMV P186109 (fig. 14), are right rami, the other two, NMV P186124 and NMV 186851, are both rami and symphysis.

These lower jaws offer the only strong evidence of more than one turtle taxon in the Dinosaur Cove collections. Three of the jaws, NMV P186223, NMV P186109, and NMV P186124, are relatively deep and robust in contrast to NMV P186851, which is

Fig. 14. *Otwayemys cunicularius.* NMV P186109, right lower jaw ramus. **A,** dorsal view; **B,** lateral view; **C,** medial view.

relatively shallow and gracile. NMV P186851 also has a slight symphyseal hook that appears to be absent in the other three jaws. However, it should be kept in mind that NMV P186851 is the smallest lower jaw of the four and that numerous changes in jaw morphology have been documented during growth in *Graptemys* and *Apalone* (Dalrymple, 1977). In any case, all four jaws are similar in having relatively narrow and simple triturating surfaces.

The primitive eucryptodire lower jaws available for comparison are limited to a probable set for *Dracochelys* (IVPP 4075) and plesiochelyids (Gaffney, 1976).

Assignment of the two larger lower jaws, NMV P186223 and NMV P186109 (fig. 14), to *Otwayemys* is supported by the close conformity between these dentaries and the right maxilla, NMV P185952 (fig. 13), when fitted together. These rami have relatively deep lateral profiles, much deeper than in *Dracochelys* and somewhat deeper than in *Plesiochelys*. The triturating surfaces are relatively narrow with a blunt, low tomial ridge and only a slight medial depression. There is no real groove as seen in plesiochelyids, and no lingual ridge. Anteriorly the triturating surface narrows toward the symphysis in contrast to the *Dracochelys* surface that is the same width along the entire jaw length. NMV P186124, consisting of both rami, is not as well-preserved as the two right rami or the other complete dentaries. There is no evidence of a sutured symphysis in any of the jaws.

Although these lower jaws help establish a diagnosis for *Otwayemys* and are clearly cryptodiran, they do not provide characters for a more precise determination of relationships.

Cervical 5

A cervical vertebra, NMV P186224, questionably identified as a fifth, is attributable to *Otwayemys* on the basis of its close similarity to cervical 5 in *Ordosemys*. The cervical lacks much of the anterior central surface and is distorted to some extent. Comparative material consists of cervicals for *Ordosemys, Xinjiangchelys, Dracochelys, Sinemys,* and plesiochelyids.

A biconcave cervical is another close similarity between *Ordosemys* and *Otwayemys*. The known cervicals of *Ordosemys* consist of three elements identified by Brinkman and Peng (1993a) as the fourth, fifth (?), and eighth. A complete neck is not yet known for *Ordosemys* but the condition of a biconcave anterior cervical and a biconvex posterior cervical is interpreted as primitive for the Sinemydidae in the analysis of Gaffney (1996). The sinemydids *Sinemys* (Brinkman and Peng, 1993b) and *Dracochelys* (IVPP 12091) are opisthocoelous for cervicals 2–7, and this is interpreted as synapomorphic for these taxa within the Sinemydidae.

NMV P186224 is more complete than the *Ordosemys* cervical 5 and is also compared here with the fourth cervical of *Ordosemys*. The neural spine in this cervical of *Otwayemys* is very low and continuous with the processes bearing the postzygapophyses, as in *Ordosemys* (cervicals 4 and 5), *Dracochelys, Sinemys,* plesiochelyids, and *Xinjiangchelys,* but in contrast to *Chelydra* (Williams, 1950) and the other living eucryptodires in which the zygapophyses are widely separated. The zygapophyses of *Otwayemys* are about as widely separated as in baenids (Hay, 1908; Brinkman and Nicholls, 1991) but not quite as wide as in cervical 4 of *Ordosemys* (cervical 5 being incomplete). The postzygapophyses of cervical 5 in *Otwayemys* are extended posteriorly slightly, as in *Ordosemys,* in strong contrast to those in *Chelydra.* This agrees with cervical 5 (?) of *Ordosemys* rather than the shorter extension in cervical 4 of *Ordosemys.* The prezygapophyses in *Otwayemys* are distorted but seem to be similar to those in cervical 4 of *Ordosemys* (they are lacking in cervical 5). The zygapophyses figured for *Xinjiangchelys,* Kaznyshkin et al. 1990, which is described with a complete neck, seem to have smaller articular areas than in *Otwayemys* and *Ordosemys* and are more elongate.

The central articulations in *Otwayemys* show a concave posterior articulation that is completely preserved and about one-third of a surface showing a concave anterior articulation, the rest of the area being lost. Nonetheless, the preserved bone surface is unequivocal and the centrum can only be interpreted as biconcave. Other than the central

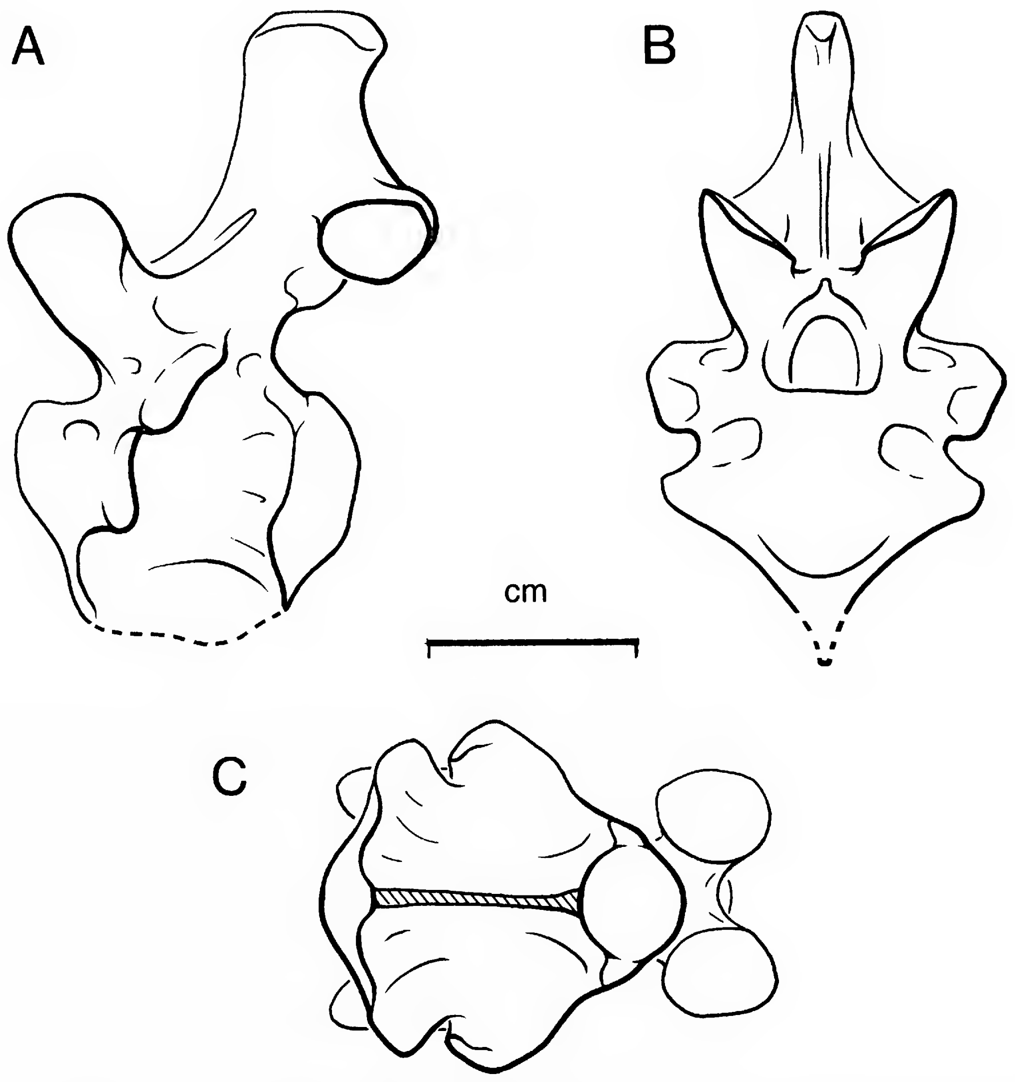

Fig. 15. *Otwayemys cunicularius.* NMV P187261, an eighth cervical vertebra. **A,** left lateral; **B,** anterior; **C,** ventral.

form, there is no similarity to the biconcave seventh cervical seen in chelids.

Cervical 8 (fig. 15)

An eighth cervical, NMV P187261, that can be attributed to *Otwayemys* on the basis of its close similarity to the eighth cervicals in *Ordosemys* and sinemydids, is preserved in the Dinosaur Cove collections. NMV P187261 (fig. 15) is well-preserved, with a small amount of breakage on the transverse processes and a crack through the centrum. Available comparative material includes eighth cervicals of *Ordosemys* (IVPP 9534-2, IVPP 9534-1, Brinkman and Peng, 1993a), *Dracochelys* (IVPP V12091), *Xinjiangchelys* (Kaznyshkin et al., 1990; Peng and Brinkman, 1993), and *Sinemys* (IVPP V9538-1).

The eighth cervical of *Otwayemys* is most similar to that bone in *Ordosemys* and *Dracochelys.* The biconvex central articulations, double transverse processes, pinched or keeled centrum, and high neural spine occur together only in the Sinemydidae (as defined in Gaffney, 1996) and *Otwayemys.*

The neural spine of *Otwayemys* is tall and columnar, taller than in the sinemydids. The greater length is mostly apparent in the ex-

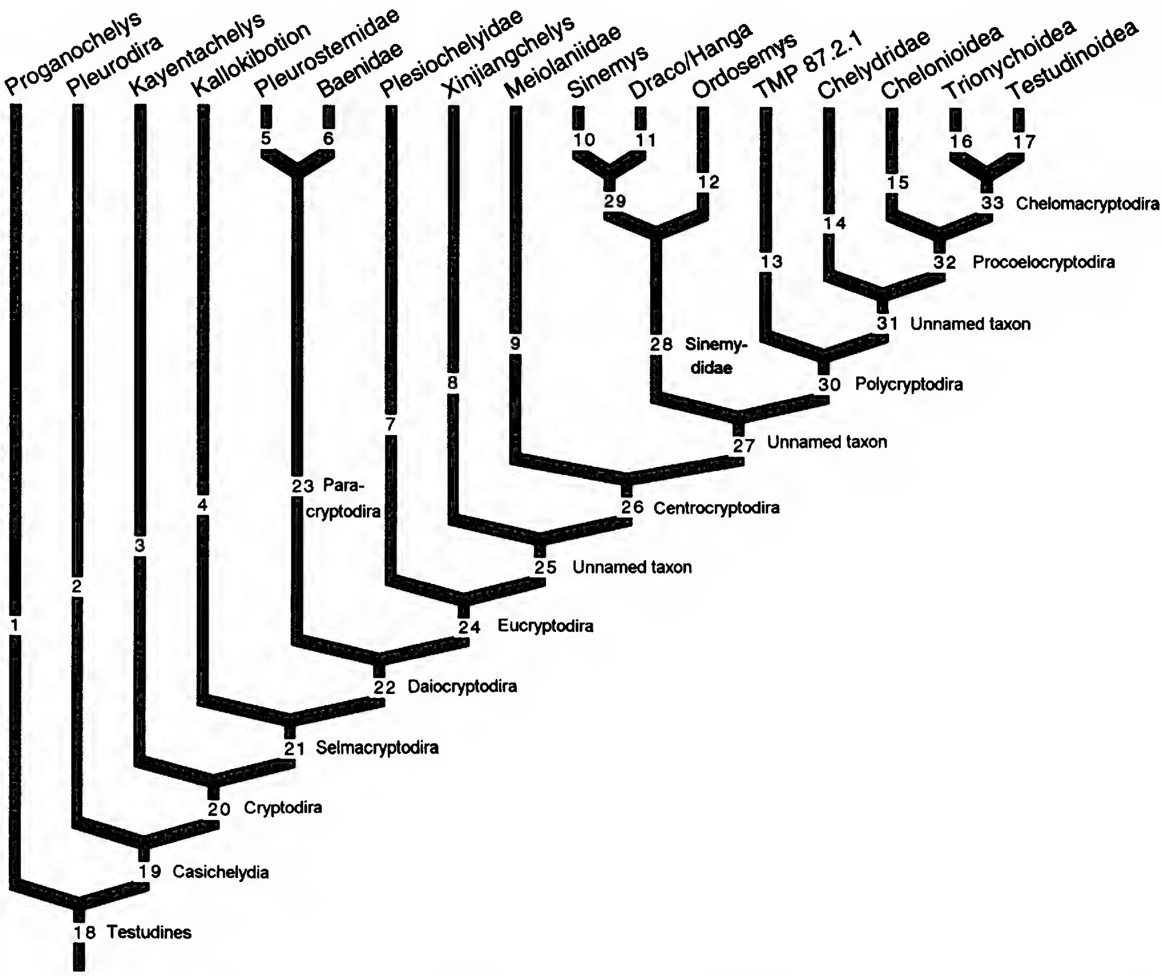

Fig. 16. Relationships of eucryptodires from Gaffney (1996). See that paper for character descriptions and diagnoses of taxa. This cladogram is 73 steps long, has a consistency index of 0.58, and a retention index of 0.80.

TABLE 4
Comparison of Eighth Cervical Vertebra in Some Primitive Eucryptodires

	Otwayemys	*Xinjiangchelys*	*Ordosemys*	*Dracochelys*	*Chelycara-pookus*
Biconvex	yes	no	yes	yes	indet.
Neural spine	very high	high	high	high	indet.
Postzygapophyses	angled	flat	flat	flat	indet.
Transverse processes	double	intermediate	double	double	indet.
Pinched centrum	yes	yes	yes	yes	indet.
Ventral keel	probably no	yes	yes	yes	indet.

tension dorsal to the postzygapophyses. The neural spine is also more slender than in the other taxa. As in the sinemydids, there appears to be an articulation between the eighth cervical neural spine and the carapace as described in *Ordosemys* (Brinkman and Peng, 1993a: fig. 3).

The postzygapophyses in *Otwayemys* and the sinemydids are an outgrowth of the neural spine. This is more extreme in *Otwayemys* owing to the relative elongation of the neural spine. The postzygapophyses are closer together in *Otwayemys* than in *Ordosemys,* and more like those of *Xingjiangchelys* and *Dracochelys.*

The prezygapophyses are not complete in *Ordosemys,* but the ones in *Dracochelys* are very similar to those in *Otwayemys.* The articular facets of the zygapophyses in *Otwayemys* are at an angle to the horizontal rather than horizontal as in *Ordosemys* and *Dracochelys.* They are also angled in baenids and this may be the primitive condition.

The biconvex central articulation is a synapomorphy for the Sinemydidae according to Gaffney (1996). Although this also occurs in chelids and testudinoids, the most parsimonious interpretation of this character is that it has arisen independently in these groups (Gaffney, 1996; see also Brinkman and Peng 1993a, 1993b). The central articulations are distinctly oval in *Otwayemys* in contrast to the more circular ones of *Dracochelys* and *Ordosemys. Xinjiangchelys* and plesiochelyids lack formed central articulations. Meiolaniids, chelydrids, and primitive members of the living eucryptodire groups have a procoelous eighth cervical, which is interpreted as the primitive conditon for the Eucryptodira with formed centra (Gaffney, 1996).

Double transverse processes were described by Brinkman and Peng (1993a) in *Ordosemys,* which were subsequently found in *Dracochelys. Otwayemys* has double transverse processes preserved on both sides that are very similar to those in *Ordosemys* and *Dracochelys.* Although baenids and plesiochelyids have single transverse processes, the double condition is interpreted as the retention of the primitive cryptodiran condition, and strongly suggests the presence of cervical ribs.

The centrum of primitive cryptodiran cervicals usually is narrower or pinched in its main body between the articulations. This is seen in baenids as well as *Otwayemys* and sinemydids. In sinemydids and *Xinjiangchelys* there is a variably developed keel, which seems to be present but lower in *Otwayemys,* but the margin is not a finished edge.

Caudal Vertebrae

One anterior caudal, NMV P197768, and one posterior caudal, NMV P186024, are preserved in the Dinosaur Cove collections and can be attributed to *Otwayemys* on the grounds that they are primitive cryptodires. NMV P197768 is well-preserved and nearly complete, while NMV P186024 is damaged on the central articulations and zygapophyses but has its neural spine and a transverse process. Comparative material was figured for *Ordosemys* by Brinkman and Peng (1993a) and *Sinemys* by Brinkman and Peng (1993b). Gaffney (1985) reviewed the literature and described the caudal vertebrae of *Meiolania.*

NMV P197768 is very similar to the *Meiolania platyceps* caudal 7 figured by Gaffney (1985: fig 15c). The anterior caudals of all primitive cryptodires with formed centra, e.g., chelydrids (Gaffney, 1990: fig. 130c) and baenids (Brinkman and Nicholls, 1991), are all similar and vary only slightly. The principal significance is that the Procoelocryptodira (Gaffney and Meylan, 1988), consisting of chelonioids, trionychoids, and testudinoids, have procoelous caudals rather than the opisthocoelous condition seen in *Otwayemys,* sinemydids, baenids, and meiolaniids.

The more posterior caudal, NMV P186024, is comparable to the more posterior caudals of such cryptodires as meiolaniids and chelydrids.

RELATIONSHIPS OF *OTWAYEMYS*

Determination of the relationships of *Otwayemys* is hampered by the absence of a good skull and by the incomplete understanding of many known, but incompletely described, primitive eucryptodires. A good starting place for examining the relationships of *Otwayemys* is the analysis of meiolaniid relationships in Gaffney (1996). This analysis was

TABLE 5

Cryptodira Data Set (Gaffney, 1996) with *Otwayemys* Added

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Proganochelys	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleurodira	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Kayentachelys	0	0	1	1	0	0	1	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	1	0	0	0	0
Kallokibotion	0	0	1	1	0	1	1	1	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	1	0	1	0	0
Pleurosternidae	0	0	1	1	0	1	1	1	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	1	0	1	0	0
Baenidae	0	0	1	1	0	1	1	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0
Plesiochelyidae	0	1	1	1	0	1	1	1	1	1	0&1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	?	0	0	0	0	0	1	0	1	1	1	0	0
Xinjiangchelys	?	?	?	?	?	?	?	1	1	1	0	0	0	0	?	?	1	?	?	0	1	0	0	0	0	0	0	0	?	?	?	1	0	1	1	1	1	1	0	0
Meiolaniidae	0	0	1	1	0	1	1	1	1	1	0	1	?	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0
Otwayemys	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	?	1	2	0	0	0	?	0	0	0	0	1	1	1	1	1	0	0
Sinemys	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	0	0	2	2	0	1	?	1	1	0	0	0	1	1	1	1	1	1	1
Draco/Hanga	?	1	1	1	1	1	1	1	1	1	0	0	?	0	?	1	1	1	?	1	0	0	?	2	2	0	0	0	?	?	?	0	0	1	1	1	1	1	1	1
Ordosemys	0	0	1	1	0	1	1	1	1	1	0	0	0	0	?	1	1	1	0	1	1	0	0	1	2	0	0	0	1	1	0	0	0	1	1	1	0	1	?	?
TMP 87.2.1	0	1	1	1	0	1	1	1	1	1	1	1	?	0	?	1	1	1	0	1	1	1	1	1	1	0	1	0	1	1	0	1	0	1	1	1	1	1	1	1
Chelydridae	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1
Chelonioidea	0	1	1	1	0	1	1	1	1	1	1	1	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
Trionychoidea	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	0	0
Testudinoidea	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	2	1	1	1	0	1	1	1	1	1	0	1	1	1	0	1

TABLE 6
Characters Used in Table 5 (from Gaffney, 1996)

1. Nasals
   0: present
   1: absent
2. Prefrontals meet
   0: not on midline
   1: on midline
3. Prefrontal-Vomer contact
   0: no
   1: yes
4. Processus pterygoideus externus
   0: no flange
   1: with vertical flange
5. Foramen palatinum posterius
   0: small or moderate
   1: very large
6. Interpterygoid vacuity
   0: open
   1: closed
7. Processus trochlearis oticum
   0: absent
   1: present
8. Middle ear with
   0: nothing
   1: pterygoid floor
9. Canalis caroticus internus
   0: not formed by pterygoid
   1: partially or entirely by pterygoid
10. Canalis caroticus internus
    0: formed partially by pterygoid
    1: formed entirely by pterygoid
11. Split between palatine artery and internal carotid artery
    0: outside skull
    1: embedded in bone
12. Floor of canalis caroticus internus
    0: thin or absent
    1: thick
13. Palatine vs carotid
    0: palatine equal to or greater than carotid
    1: palatine less than carotid
14. Foramen posterius canalis carotici interni formed by
    0: BS or PT
    1: BS and PT as in baenids
15. Fenestra perilymphatica
    0: large (normal)
    1: small
16. Blind pits on BS
    0: no
    1: yes

TABLE 6—*(Continued)*

17. Posterior temporal emargination
    0: not developed
    1: at least partially developed
18. PA-SQ contact
    0: present
    1: absent
19. PO-SQ contact
    0: present
    1: absent
20. Vertebral articulations
    0: platycoelous or amphicoelous
    1: formed: concavo-convex
21. Transverse process of cervicals
    0: on middle of centrum
    1: on anterior of centrum
22. Posterior cervicals with
    0: no ventral process
    1: ventral process
23. Cervical ribs
    0: present
    1: absent
24. Cervical 4
    0: amphicoelous
    1: biconvex
    2: opisthocoelous
25. Cervical 8
    0: amphicoelous
    1: procoelous
    2: biconvex
    3: opisthocoelous
26. Double art between cervicals 7 and 8
    0: no
    1: yes
27. Transverse processes on cervicals
    0: double
    1: single
28. Spine on cervical 8
    0: high
    1: low
29. Biconcave caudal
    0: absent
    1: present
30. Caudal centra
    0: amphicoelous or opisthocoelous
    1: procoelous
31. Chevrons
    0: well developed
    1: small or absent
32. First thoracic rib
    0: extends to peripherals
    1: fails to reach peripherals

TABLE 6—*(Continued)*

33. First thoracic centrum
    0: faces anteriorly
    1: faces strongly anteroventrally
34. Mesoplastra
    0: present
    1: absent
35. Ligamentous carapace-plastron attachment
    0: no, sutured
    1: yes
36. Supramarginal scales
    0: present
    1: absent
37. Dorsal process on epiplastron
    0: present
    1: absent
38. Entoplastron separating epiplastron
    0: yes
    1: no, epiplastra broadly contact
39. Epiplastron
    0: broad
    1: narrow
40. Gular (extragular) scales
    0: present, full set
    1: absent, one set

an outgrowth of work by D. Brinkman, E. Gaffney, H. Hutchison, and P. Meylan. The limitations of the Gaffney (1996) analysis are that it is focused on meiolaniids and emphasizes characters relevant to that group, and it excludes many named "sinemydid/macrobaenid" taxa because of missing data. Obviously, we are at an early stage of understanding the primitive eucryptodires, and the addition of better-known taxa and the discovery of more characters is likely to alter present conclusions.

Gaffney (1996) obtained a single cladogram (here reproduced as fig. 16) that fully resolved the taxa, but it was only weakly supported with a consistency index of 0.58 and only two steps from cryptodire chaos. Of the 40 characters in the Gaffney (1996) data set, *Otwayemys* can be determined for only 20 of them. The addition of *Otwayemys* (tables 5 and 6) with its 50% missing data produces 12 equally parsimonious cladograms with each cladogram having a length of 74 steps, a retention index of 0.80, and a consistency index of 0.58. The original cladogram was 73 steps long and had an RI of 0.80 and a CI of 0.58. The strict consensus tree of the 12 cladograms containing *Otway-*

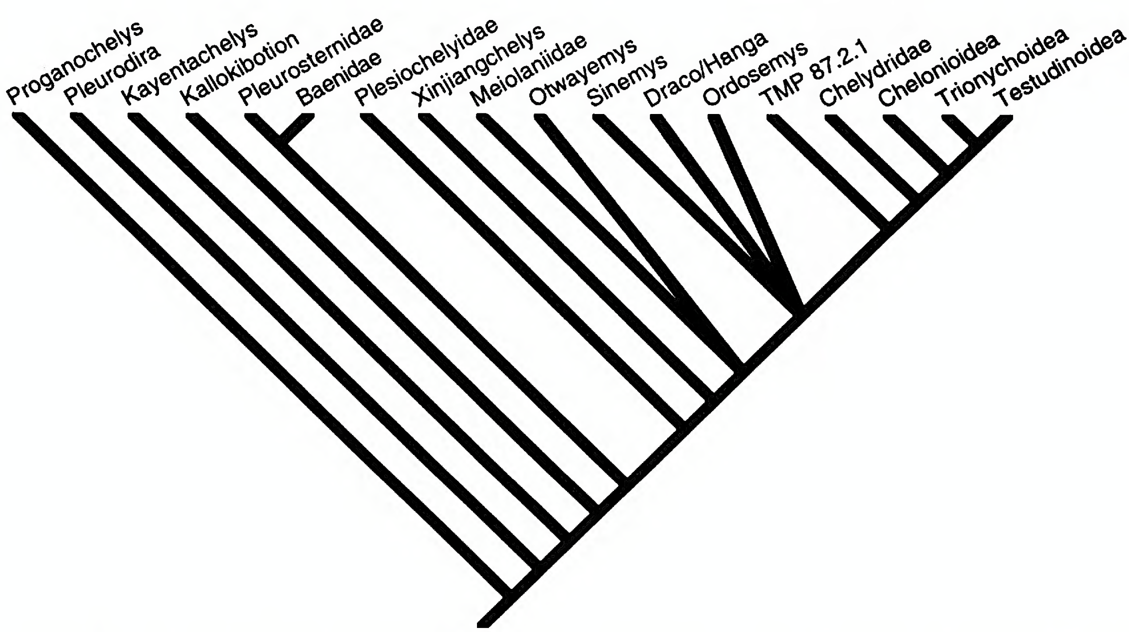

Fig. 17. Consensus cladogram of 12 equally parsimonious cladograms generated by the addition of *Otwayemys* (with 50% of its characters missing) to the data matrix of Gaffney (1996). The 12 cladograms are 74 steps long, have a consistency index of 0.58, and a retention index of 0.80.

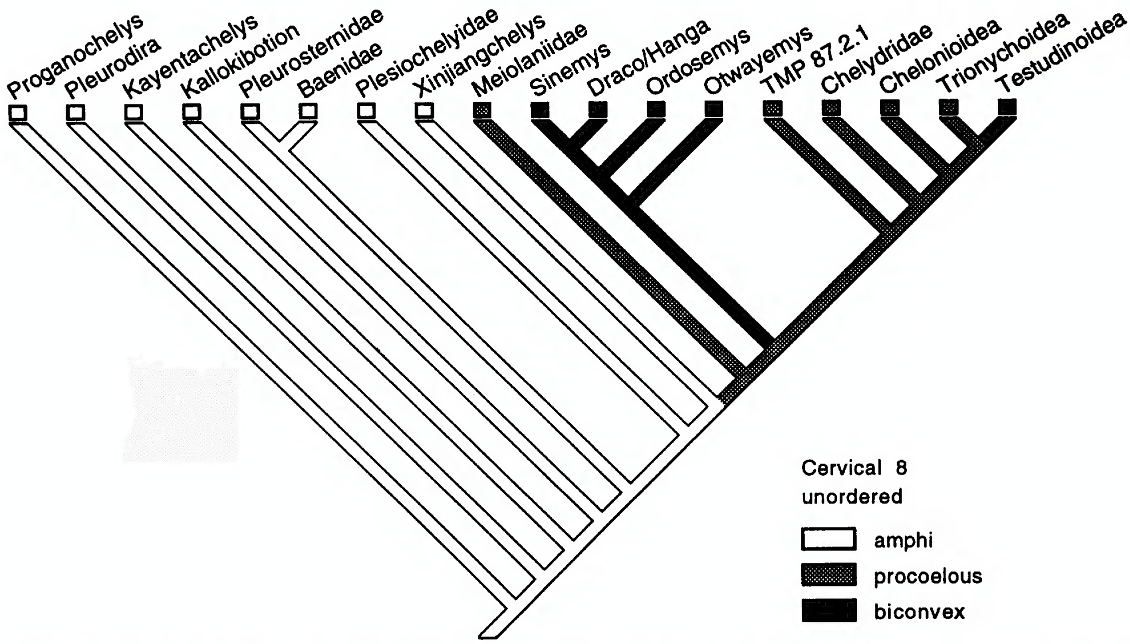

Fig. 18. Cladogram showing a monophyletic Sinemydidae including *Otwayemys* and the distribution of biconvex eighth cervicals. This cladogram is 77 steps long in contrast to the 74-step consensus cladogram, which is the shortest resolution of this character set.

emys (fig. 17) differs from the Gaffney (1996) cladogram in a number of areas. Despite the many similarities between *Otwayemys* and *Ordosemys*, *Otwayemys* is combined with Meiolaniidae and taxon 27 of Gaffney (1996) in an unresolved trichotomy. This places *Otwayemys* with the Centrocryptodira of previous authors (Gaffney and Meylan, 1988; Gaffney et al., 1991; Gaffney, 1996) and is tested by formed cervical central articulations (character 20) and the fourth cervical biconvex (character 24). The last character is absent in *Sinemys* and *Dracochelys*, which have opisthocoelous fourth cervicals, probably a derivative of the biconvex condition. Placing *Otwayemys* within the Centrocryptodira is well-supported.

The group consisting of Sinemydidae plus Polycryptodira, taxon 27 in Gaffney (1996), has six characters uniting it. Three of these, paired pits on basiphenoid (character 16), parietal separated from squamosal (character 18), and biconcave caudal (character 29) are not determinable in *Otwayemys*. These missing characters are important because there are contradictions in placing *Otwayemys* either within the Sinemydidae or even within taxon 27. The three other synapomorphies of taxon 27 presented by Gaffney (1996) are the presence of at least some procoelous caudals (character 30), narrow epiplastron (character 39), and only one set of anterior plastral scales (character 40). *Otwayemys* clearly has the primitive condition for these three characters. However, *Otwayemys* also has the biconvex eighth cervical that is very similar in all other features to the eighth cervical in *Ordosemys*. The biconvex eighth cervical occurs in *Ordosemys*, *Dracochelys*, and *Sinemys* and was argued by Gaffney (1996) to be a synapomorphy of the Sinemydidae as restricted in that paper. The biconvex eighth cervical is known for all the relevant taxa but the narrow epiplastron and plastral scale arrangement are not known for *Ordosemys*, although the preserved plastral morphology suggests that it would have a narrow epiplastron. Determination of this character and characters 16, 18, and 29 (tables 5 and 6) in *Otwayemys* could fully resolve this conflict or could make it worse. In any case, finding the missing characters could seriously alter the conclusions presented here.

Given the characters as currently known, however, we can examine the 12 alternative cladograms and compare their implications. In some of the trees *Otwayemys* is the sister taxon to Meiolaniidae. Because of the very interesting geographic possibilities of this alternative (Gaffney, 1996), it has been examined in some detail. Unfortunately, we could find no unique synapomorphies common to these taxa. The general lack of cranial data for *Otwayemys* frustrates further exploration of this alternative. Nonetheless, it is interesting that a primitive eucryptodire was present in Australia in the Early Cretaceous that could be a sister taxon to the Meiolaniidae. This alternative would require the independent evolution of the procoelous eighth cervical in meiolaniids or its loss in *Otwayemys*. An alternative requiring the same parallelism would have *Otwayemys* as the sister group to Sinemydidae plus Polycryptodira (or to a paraphyletic Sinemydidae with successive sister taxa to Polycryptodira). In this case also the biconvex eighth cervical would be primitive at the level of taxon 27 and would be the primitive condition for the procoelous eighth cervical of Polycryptodira. Both alternatives require the procoelous eighth cervical of the meiolaniids to be evolved independently.

A monophyletic Sinemydidae consisting of *Ordosemys, Dracochelys,* and *Sinemys* does appear in three of the alternative cladograms but *Otwayemys* is not united with them. The most plausible cladogram (fig. 18), with *Otwayemys* united in a monophyletic Sinemydidae with *Ordosemys* as the sister group to *Sinemys* plus *Dracochelys,* requires 77 steps in contrast to the 12 shortest trees of 74 steps. However, this cladogram has the advantage of resolving the procoelous eighth cervical as primitive for Centrocryptodira, an alternative favored by one of us (ESG). Homoplasy here consists of independent evolution of the narrow epiplastron (39) and loss of gular scales (40). But the reversal of this character is required even in the shortest cladograms because the Chelomacryptodira have broad epiplastra in their primitive conditions (see Gaffney, 1996, for discussion). Considering the numerous contradictions present in the shortest set of trees and the many missing characters for *Otwayemys,* this longer alternative should not be discarded.

Otwayemys is clearly within the Centrocryptodira, and it has the biconvex eighth cervical of Sinemydidae. However, it lacks the plastral and caudal synapomorphies of taxon 27, which consists of Sinemydidae plus Polycryptodira. The most parsimonious resolution of *Otwayemys* at present is an unresolved trichotomy with Meiolaniidae and taxon 27.

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