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Ninjemys, a New Name for "*Meiolania*" *oweni* (Woodward), a Horned Turtle from the Pleistocene of Queensland

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ABSTRACT

The new generic name, *Ninjemys,* is proposed for the meiolaniid species, *oweni* Woodward, 1888, formerly placed in the genus *Meiolania* Owen, 1886. *Ninjemys* is distinguished from all other meiolaniid genera by the unique possession of these characters: large squamosal horn directed laterally rather than posterolaterally as in *Niolamia* and *Meiolania,* nasal bones projecting anteriorly beyond rest of skull, medial accessory ridge on trituarating surface extending nearly to midline. *Ninjemys oweni* is known only from a skull and tail club from the Pleistocene of Queensland, Australia.

INTRODUCTION

The horned turtles or meiolaniids are an extinct group of Southern Hemisphere cryptodires known from the Eocene to the Pleistocene. Although they are characterized by some bizarre features, such as cranial horns and tail clubs, they are phylogenetically important because Gaffney (1983), Gaffney and Meylan (1988), and Gaffney et al. (1991) have argued that they are the sister group of the living cryptodires. The first meiolaniid to be described was found in Queensland in 1879 by G. F. Bennett, an Australian collector, and sent to noted paleontologist Richard Owen in the British Museum. Despite the fact that Bennett had correctly identified the unusual skull as a turtle (letter, Bennett to Owen in BMNH archives), Owen grouped the turtle skull elements with the vertebrae of a large varanid lizard (and later with the foot bones of a large marsupial, *Diprotodon*) and named

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it *Megalania prisca* (Owen, 1881). Owen identified the result as a giant horned lizard. The name *Megalania prisca* has been restricted to just the varanid vertebrae. In 1886, Owen described a new horned turtle from Lord Howe Island as *Meiolania platyceps,* but still thought it was a lizard. Huxley (1887) showed that the new Lord Howe form was a turtle and created the name *Ceratochelys* for it but this is clearly preoccupied by *Meiolania* Owen. Most of the current horned turtle nomenclature is based on Woodward's (1888) review. He formally separated the turtle material from Owen's original *Megalania prisca* and named a new species, *oweni,* for the chelonian elements in *Megalania prisca.* He placed this species and the Lord Howe species, *platyceps,* together in the same genus, *Meiolania* Owen. Gaffney (1983), Gaffney and Meylan (1988), and Megirian (1989) have argued that meiolaniid systematics has progressed to the point that the genus *Meiolania* should be restricted to those species with synapomorphies that clearly form a strictly monophyletic group. Although the species *oweni* may be the sister taxon to some or all of the species in *Meiolania* sensu stricto, these authors have adopted the usage, "*Meiolania*" *oweni,* to indicate the ambiguity of its relationship to species of *Meiolania* (fig. 4). With the recent description of new meiolaniid taxa (Megirian, 1989, and in prep; Gaffney et al., in press) and the further progress of a revision of all Meiolaniidae, the necessity and rationale for naming a new genus for *oweni* has become apparent.

In contrast to all other turtles, meiolaniids are characterized by a skull with many of the bones developed into processes or shelves extending posteriorly and laterally. These processes coincide with areas of bone covered in life by scales that in some cases were presumably so extended that they formed horns, in the case of *Meiolania,* very cowlike horns. I use the terms "scale area" and "horn core" interchangeably for these bony processes. Sutures are fused in most meiolaniid skulls, but the scale areas form a similar pattern among the known taxa and can be homologized with some degree of confidence. The scale areas thus provide a means of comparison unique to this family—even in the absence of sutures. The scale terminology used here is fully developed in Gaffney (1983).

An undescribed genus of meiolaniid from the Miocene of Riversleigh Station, Queensland is presented here (see skull 3 in fig. 4). A paper (Gaffney et al., in press) describing and naming this taxon has been accepted for publication. The taxon is referred to here as the "Riversleigh genus."

Acknowledgments

This paper is the outgrowth of a larger project on meiolaniids extending back to 1976. All of the people acknowledged in Gaffney (1983) were equally important to this project. Particularly relevant to *Ninjemys oweni,* however, are A. Milner, C. Walker, and S. Chapman of the Natural History Museum, London (BMNH), staff. I thank them for assisting me in examining and cleaning this specimen, and for providing casts and photographs of it. I am grateful to F. Ippolito and E. Heck for the high quality of the figures. Drs. Peter Meylan and Howard Hutchison reviewed the paper and provided significant improvements.

SYSTEMATICS

ORDER TESTUDINES

MEGAORDER CRYPTODIRA

PARVORDER EUCRYPTODIRA

SUBORDER MEIOLANOIDEA

FAMILY MEIOLANIIDAE

Type Genus: *Meiolania* Owen, 1886.

Known Distribution: Eocene (possibly Cretaceous) of Argentina, Miocene to Pleistocene of Australia, Pleistocene (or younger) of Lord Howe Island, Walpole Island, and New Caledonia.

Previous Work: Gaffney (1983) related the long and complex history of work on meiolaniids. Other recent papers are those of Megirian (1989) and Gaffney and McNamara (1990). The suprafamilial relationships of meiolaniids are treated in Gaffney (1983) and the phylogeny and classification of cryptodires (including diagnoses of the higher taxa listed above) are in Gaffney and Meylan (1988) and Gaffney et al. (1991).

Revised Diagnosis: Eucryptodiran turtles with the squamosal and supraoccipital bones uniquely produced into posteriorly and pos-

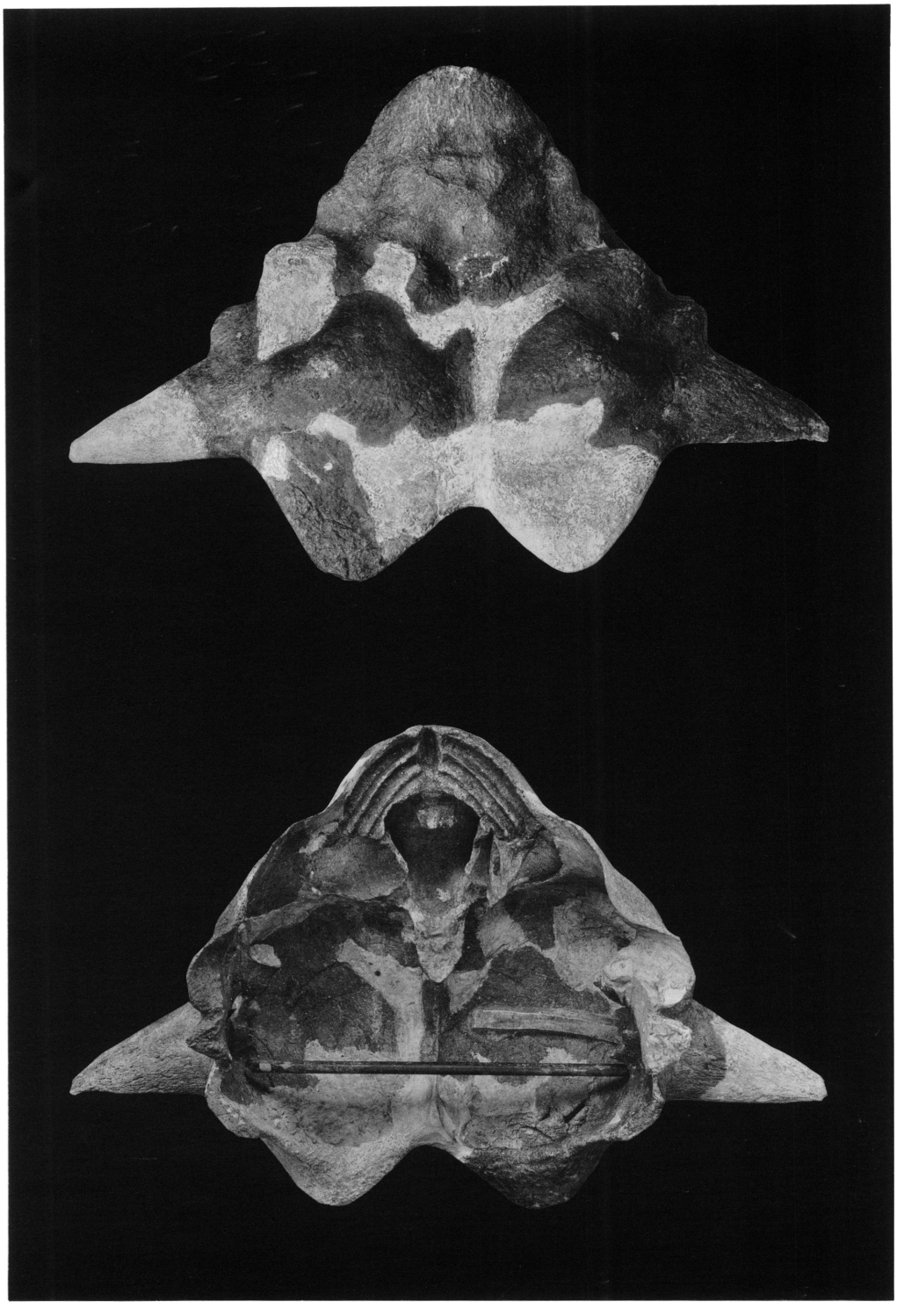

Fig. 1. Type specimen of *Ninjemys oweni,* new genus, BMNH R391. **Top,** dorsal view; **bottom,** ventral view. Light areas restored in plaster.

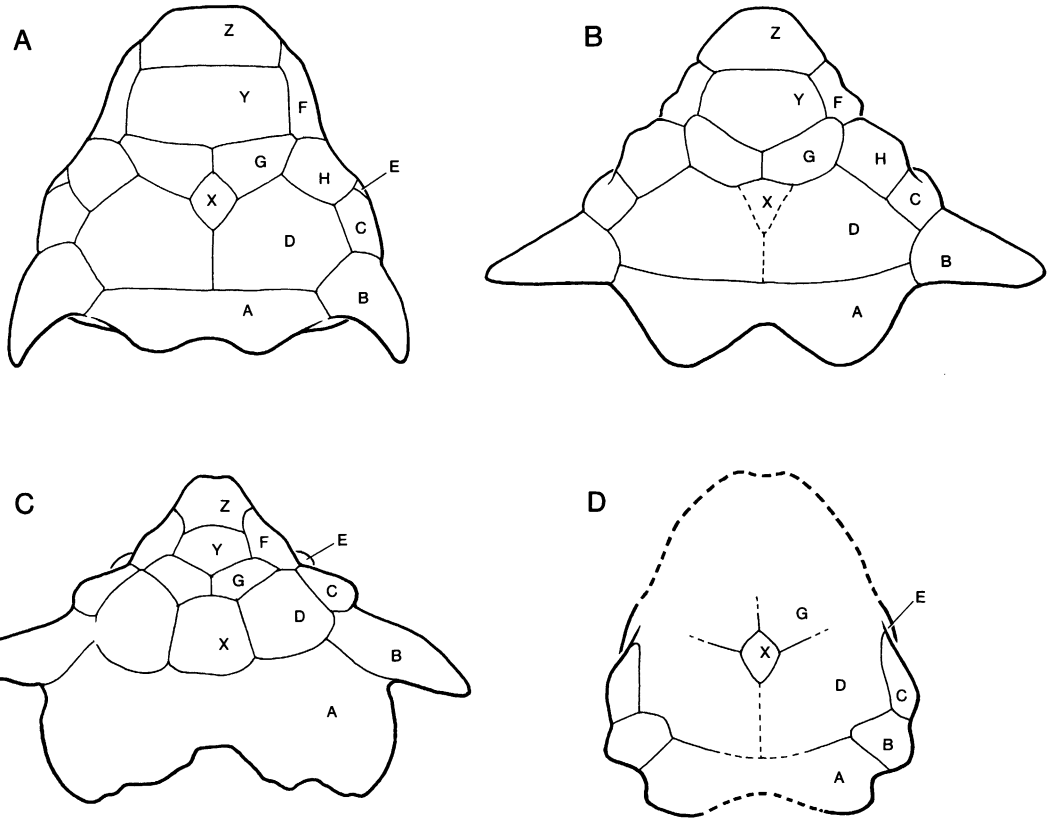

Fig. 2. Meiolaniid skulls in dorsal view. **A,** *Meiolania platyceps* (after Gaffney, 1983); **B,** *Ninjemys oweni,* new genus (after Owen, 1881, and BMNH R391); **C,** *Niolamia argentina* (after Woodward, 1901 and cast); **D,** undescribed genus and species (Gaffney et al., in press) from the Miocene of Riversleigh Station, Queensland; dashed outline from *Meiolania platyceps.* Scale terminology from Gaffney (1983).

terolaterally directed processes, three scale areas (A, B, C of Gaffney, 1983; also in fig. 2) being most prominent; temporal emargination completely absent and related to extensive squamosal-supraoccipital contact and relatively small parietal; supraoccipital with large horizontal portion on skull roof; nasal bones unusually large, rivaling their size in *Proganochelys*; sinus formed from nasal and maxilla lateral to and communicating with apertura narium externa as in no other turtle (determinable only in *Meiolania platyceps* and *Ninjemys oweni*); broad squamosal-quadratojugal contact ventral to completely enclosed incisura columellae auris of quadrate which contains both stapes and eustachian tube; medial plate of pterygoid separated ventrally from basisphenoid to form intrapterygoid slit as in no other turtle; palate concave ventrally with vomerine ridge on midline, most similar to some testudinids; well-developed labial ridge, triturating surfaces not greatly expanded; tail partially or completely surrounded by dermal ossifications; tail club formed by fusion of terminal caudal vertebrae and osteoderms (at least in *Ninjemys oweni* and *Meiolania platyceps*); cervical central articulation formula (2((3((4))5))6))7))8) as in most other eucryptodires; free cervical ribs present on cervicals 2–6 (in *Proganochelys* cervical ribs 2–5 are free); caudals opisthocoelus with well-developed hemal spines as in baenids and chelydrids, biconcave caudal absent; plastron lacking axillary and inguinal buttresses; mesoplastra absent as in other eucryptodires; plastron with irregular fontanelles on midline; carapace with first thoracic facing an-

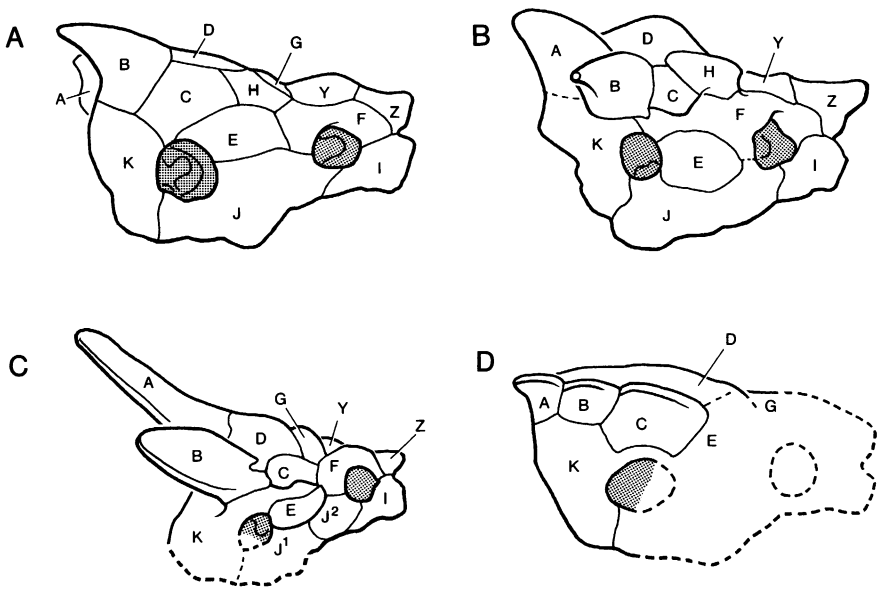

Fig. 3. Meiolaniid skulls, same as figure 2, but in right lateral view.

teriorly and first thoracic rib long and reaching plastron laterally as in baenids and pleurosternids; posterior peripherals scalloped; adults usually with cranial and shell sutures fused.

It should be noted that most of these characters are known only in *Meiolania platyceps,* the most completely preserved meiolaniid.

Ninjemys, new genus

Megalania Owen, 1881 (in errore).
Meiolania Owen, 1886 (in part).

TYPE SPECIES: *Meiolania oweni* (Woodward).

ETYMOLOGY: *Ninja,* in allusion to that totally rad, fearsome foursome epitomizing shelled success; *emys,* turtle.

KNOWN DISTRIBUTION: Pleistocene of southern Queensland, Australia.

DIAGNOSIS: A meiolaniid known only from skull and tail, characterized by unique possession of laterally projecting B horns and anterior extension of the nasals beyond rest of skull; A scale area large and forms posterior shelf as in *Niolamia* but A scale not significantly larger than B scale; D scales probably meet in midline, X scale small as in *Meiolania*; D scale area raised as in *Niolamia,* not flat as in *Meiolania*; Y scale relatively large as in *Meiolania*; apertura narium interna partially divided as in *Meiolania* but in contrast to *Niolamia*; well-developed second (more medial) accessory ridge on triturating surface of palate reaching nearly to midline in contrast to *Meiolania* in which it is lacking anteriorly and *Niolamia* in which it is absent; tail ring enclosed ventrally as in *Niolamia* but in contrast to *Meiolania*; tail club formed from two segments, rather than four as in *Meiolania.*

Ninjemys oweni (Woodward), new genus

TYPE SPECIMEN: BMNH (Natural History Museum, London, formerly British Museum [Natural History]) R391, a nearly complete skull (fig. 1) described and figured by Owen (1881: pls. 37, 38) as *Varanus* (*Megalania*) *priscus.* Owen's figures show the skull as originally discovered, without the plaster restorations made subsequently. However, with the kind assistance of the BMNH authorities and aided by the discovery in the Australian Museum of photographs showing the separate skull elements before assembly or reconstruction of any kind, it has been possible to fully determine the areas preserved versus those restored. Following this study, I can confirm not only the accuracy of Owen's orig-

inal figures but the accuracy of the restoration as well. Except in the depth of the sagittal division between the A horn cores, all of the restored areas in BMNH R391 are based on preserved bone from the opposite side. The widely distributed cast of the restored BMNH R391 is thus based on an accurate original.

LOCALITY: "King's Creek, part of Clifton Run . . ." (Owen, 1881: 1041), a branch of the Condamine River, eastern Darling Downs, Queensland. Collected in 1879 by Mr. G. F. Bennett, son of Dr. G. F. Bennett.

HORIZON: Pleistocene (Bartholomai, 1976).

REFERRED SPECIMENS: BMNH R392 is a tail club and single tail ring, also collected by Mr. G. F. Bennett at or near the same spot as the skull, but a year later, 1880. Described and figured by Owen (1882: pls. 64, 65, figs. 1–4) as *Megalania prisca.* The inference that the tail club and ring belong to the same individual as the type skull has neither been supported nor challenged in the intervening century. However, the discovery of another genus of large meiolaniid in the Pleistocene of Queensland (Gaffney and McNamara, 1990) does, for the first time, present the possibility that the tail club could belong to another genus of meiolaniid. Nonetheless, because the tail club and skull were found close together, I will continue to interpret them as belonging to the same species.

DIAGNOSIS: Same as for genus.

OTHER SPECIMENS POSSIBLY REFERABLE TO NINJEMYS: There are three other specimens of very large meiolaniids, two from southern Queensland and one from New South Wales, all described in Gaffney (1981). The Queensland specimens, peripheral bones and a caudal vertebra, could belong to either the large mainland *Meiolania* sp. from Wyandotte or *Ninjemys oweni* or a third, yet unknown, meiolaniid taxon. The New South Wales specimen, identified by Etheridge (1893) as the large bosses on a tail club similar to *Ninjemys oweni,* was substantiated by Gaffney (1981) who went so far as to identify the material as *Meiolania oweni.* Presumably the Wyandotte meiolaniid had a very large tail club so this identification should be downgraded to meiolaniid, cf. *Ninjemys oweni.* The caudal vertebra may be Pliocene but other than possible range extensions, these fragments do not significantly contribute to our understanding of *Ninjemys oweni.*

DISCUSSION: The type skull of *Ninjemys oweni* (fig. 1) was described and figured in Owen (1881) and the tail club in Owen (1882). The descriptive text of these papers suffers primarily from the comparisons of the material with lizards and dinosaurs rather than turtles. With this qualification, however, the information in the text is largely accurate and certainly sufficient for the purposes of nomenclature. Although the material in Gaffney (1983) is primarily a description of *Meiolania platyceps,* extensive comparisons are also made with "*Meiolania*" *oweni* (= *Ninjemys oweni*) and *Niolamia argentina.* The reader is also referred to Woodward (1901) for description and figures of *Niolamia* and to Simpson (1938) for description and figures of *Crossochelys,* here interpreted as a synonym of *Niolamia.*

The argument that the meiolaniid species *oweni* requires its own genus is primarily based on the idea that the genus *Meiolania* should be restricted to species that clearly form a monophyletic group; and to include *oweni* in *Meiolania* would result in a paraphyletic group. Another alternative would be to extend the genus *Meiolania* to include all of Group II in figure 4. However, as long as the named taxa are arguably monophyletic, the level of taxonomic category used has no objective restrictions (other than the code of Zoological Nomenclature). In this case it seems convenient and useful to legitimize current usage and restrict *Meiolania* to Group IV. Although the many specimens of *Meiolania platyceps* (type species of the genus) found on Lord Howe Island (Gaffney, 1983) show a remarkable degree of variation in horn development, they all have a posterolaterally directed B horn (fig. 2) that is circular in cross section and distinctly recurved. They also have the A, B, and C scale areas distinct and not on a continuous shelf as in the other meiolaniids (fig. 3). The discovery of recurved horn cores in localities far removed from Lord Howe Island (fig. 4) suggests that, even though the material is very fragmentary, a number of species with recurved horns, i.e., *Meiolania* sensu stricto, flourished in the Australo-Pacific region. New Caledonia

TABLE 1
Comparison of Meiolaniid Genera

Character	*Ninjemys*	*Meiolania*	*Niolamia*	Riversleigh genus
Nasal bones project anteriorly beyond rest of skull	yes	no	no	no
B scale projects laterally rather than posterolaterally	yes	no	no	no
B scale posterolaterally recurved	no	yes	no	no
D scales meet in midline, X scale small	yes	yes	no	yes
D scale low	no	yes	no	yes
A, B, and C scales form a continuous shelf	yes	no	yes	no
A scale large and forms large shelf	yes	no	yes	no
A scale significantly larger than B scale	no	no	yes	no
Y and Z scale relatively large	yes	yes	no	indet
Tail club segments	two	four	indet	indet
Tail rings enclosed ventrally	yes	no	yes	indet
Apertura narium interna divided	partially	yes	no	indet
Second accessory ridge on maxillary triturating surface present	yes	yes	no	indet
C scale cone-shaped or flat	yes	yes	no	no
C scale a horizontal ridge	no	no	no	yes
B scale round in cross section	no	yes	no	no
Second accessory ridge on maxilla extends nearly to midline	yes	no	no	indet
X scale partially separates G scales	yes	yes	no	yes

(Gaffney et al., 1984), Walpole Island (Anderson, 1925), northern Queensland (Gaffney and McNamara, 1990), and the Northern Territory (Megirian, 1989, soon to be named on the basis of more complete specimens) have all yielded recurved horn cores and fragmentary associated material. The first three are Pleistocene; the fourth is Miocene. Although none of these except the Northern Territory specimens can be diagnosed satisfactorily (although the horn cores can be differentiated statistically), it is unlikely that they all belong to the same species as *Meiolania platyceps*. Therefore, it would be appropriate to reflect this situation by restricting the genus *Meiolania* to those taxa having the indicated synapomorphies (Group IV, fig. 4).

Furthermore, in terms of phenetic resemblance, *oweni* is clearly more similar to the South American *Niolamia argentina* than to *Meiolania platyceps* (figs. 2, 3). The union of *oweni* and *platyceps* was the result of geographic convenience and the absence of a systematic review of the whole group (see Gaffney, 1983, for literature).

Although *Ninjemys oweni* is described in the literature, some discussion of the autapomorphies defining the species is appropriate (table 1). The nasal bones in *Ninjemys* (fig. 3) form an anteriorly projecting overhang that extends farther forward than the premaxillae, a condition that I have been unable to find in any other turtle. Kinosternids have the prefrontals overhanging the nasal opening and most testudinoids have the upper and lower margins of the apertura narium externa at about the same place. All of these groups, however, have no nasals and the apertura margin is formed by the prefrontals.

The triturating surface of the maxilla bears two accessory ridges in *Meiolania* and *Ninjemys* (described in Gaffney, 1983). They lie between a high labial ridge and a lingual margin that has no ridge. *Ninjemys* (Owen, 1881: pl. 38, fig. 3) has the more medial of these ridges distinctly formed and extending anteriorly to connect with a low parasagittal ridge just lateral to the midline. In *Meiolania platyceps* (Gaffney, 1983: figs. 30, 32, 42, 44) this more medial accessory ridge is barely developed, being distinct posteriorly but disappearing anteriorly. Although this triturat-

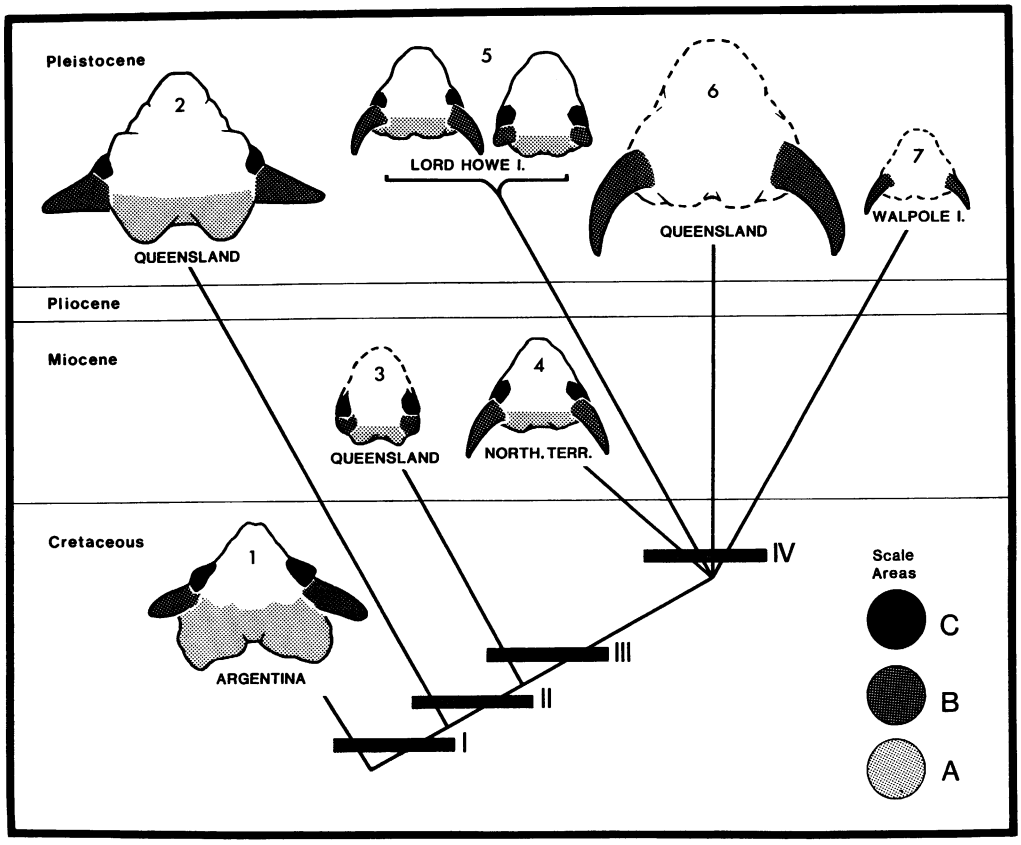

Fig. 4. Cladogram of meiolaniid turtles showing skulls in dorsal view with three scale areas (A, B, C) indicated for comparison. Temporal range incomplete and not to scale. Synapomorphies for the following groups: **I.** Meiolaniidae, see diagnosis. **II.** D scales meet in midline, X scale small, A scale equal to or smaller than B scale, apertura narium externa divided, Y scale relatively large, two accessory ridges on triturating surfaces, apertura narium externa at least partially divided. **III.** D scale low, A scale relatively small and not forming shelf at back of skull. **IV.** The genus *Meiolania*; B scale forming recurved horn; A, B, and C scales do not form continuous shelf.

The taxa illustrated are: **(1)** *Niolamia argentina,* **(2)** *Ninjemys oweni* new genus, **(3)** undescribed Riversleigh genus, **(4)** *Meiolania,* undescribed species from Bullock Creek, Northern Territory, **(5)** *Meiolania platyceps,* showing two extremes of horn variations, **(6)** *Meiolania* sp., Wyandotte, **(7)** *Meiolania mackayi.*

ing surface morphology in meiolaniids is not exactly paralleled in other turtles, many testudinoids have two accessory ridges and some testudinids closely approach the meiolaniid condition (e.g., *Hesperotestudo in* Hay, 1908: figs. 567, 580; pl. 66, fig. 3; pl. 80, fig. 3).

The scale areas, particularly the A, B, and C scales, provide the most important autapomorphies for *Ninjemys.* The morphology of these scale areas is not duplicated in any other meiolaniid (or any other turtle). Uniquely, in *Ninjemys* the B horn core (fig. 2) projects primarily in a lateral direction, although there is a posterior component. The orientation of the B horn core in *Ninjemys* differs noticeably from that in *Niolamia,* but it is very different from the B horn core of *Meiolania.* In the Riversleigh genus the B scale area is a low ridge and not projected into a horn core.

Ninjemys resembles *Niolamia* in the relatively large A scale area which in *Meiolania* and the Riversleigh genus is significantly smaller. This portion of the skull, made up of squamosal and supraoccipital, is a large, overhanging shelf in *Niolamia* and *Ninjemys,* but in *Meiolania* it is a small posterior ridge, nearly flat in some individuals.

The development of a theory of relationships for the meiolaniids must rely mostly on features of the scale areas, but polarizing these characters is difficult. Because of this unique morphology, there is no outgroup to provide comparisons. However, Gaffney (see 1983 paper for further discussion) and Gaffney and Meylan (1988) have argued that the more primitive condition of the intrapterygoid slit (Gaffney, 1983: fig. 60) in *Niolamia* suggests that it may be the sister group to all other meiolaniids. There are other characters that occur in Group II of fig. 4 that support this contention. The sister group of all turtles, *Proganochelys,* has divided nares but the series of outgroups (Gaffney and Meylan, 1988) to the Eucryptodira show that undivided nares are primitive for that taxon. The divided nares occurring in *Ninjemys* and *Meiolania* can be interpreted as derived. Although accessory triturating ridges occur throughout the turtle empire, the primitive condition for Eucryptodira is probably a smooth surface with only one or no accessory ridges. The accessory ridges found in *Ninjemys* and *Meiolania* are absent in *Niolamia* and can be considered synapomorphies for Group II. The snout and covering scale areas Y and Z in *Ninjemys* and *Meiolania* are broad in comparison to those of *Niolamia.* Although this feature is somewhat difficult to compare with the snout in other turtles because the interorbital region in all meiolaniids is broader than in most other cryptodires, if a narrow snout is considered primitive for Eucryptodira, then the even broader snout of *Ninjemys* and *Meiolania* could be interpreted as a synapomorphy for Group II also.

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