The Beagle, Records of the Northern Territory Museum of Arts and Sciences, 1992 9(1):35-48

WARKALANIA, A NEW MEIOLANIID TURTLE FROM THE TERTIARY RIVERSLEIGH DEPOSITS OF QUEENSLAND, AUSTRALIA.

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ABSTRACT

Warkalania carinaminor sp. nov., is based on posterior skull elements from the (?) Oligocene - early Miocene Carl Creek Limestone, Pancake Site of Riversleigh Station, northwest Queensland. *Warkalania* is a meiolaniid cryptodire because it has the synapomorphies of the squamosal produced into posteriorly and posterolaterally directed processes and an extensive squamosal-quadratojugal contact beneath the cavum tympani. Within meiolaniids, *Warkalania* is unique in having the squamosal processes formed into low, horizontal ridges, small and roughly similar to each other in size, rather than having one or more of these scale areas extending prominently away from the skull, as in all other meiolaniids.

KEYWORDS: *Warkalania carinaminor* gen et sp. nov., new genus, new species, Meiolaniidae, horned turtle, Oligocene, Miocene, Carl Creek Limestone, Queensland.

INTRODUCTION

Turtles and other vertebrates were discovered in the Carl Creek Limestone at Riversleigh Station in northwestern Queensland by Tedford in 1968. Further work by teams led by M. Archer, S. Hand, and H. Godthelp resulted in the discovery of nearly 100 additional sites spanning in time the Oligocene to Pleistocene, and the recognition of a relatively rich turtle fauna (Gaffney *et al.* 1989). A review of the Riversleigh localities and an introduction to the growing literature on Riversleigh and its fossils can be found in Archer *et al.* (1989). The first turtles described from Riversleigh Tertiary sites were three genera of chelids based on fragmentary material (Gaffney *et al.* 1989). Meiolaniids in the Riversleigh Tertiary were first recognized by A. Ritchie (pers. comm.) on the basis of tail ring fragments (see below) in 1987. One of us (ESG) found more meiolaniid fragments in Riversleigh collections in 1989 but it was not until Neville Pledge's discovery of a partial skull, that diagnosable meiolaniid material was recovered from Riversleigh Tertiary deposits. This material represents a new genus of meiolaniid (Fig. 1) and is described here.

The reader should refer to Figures 5-7 and Gaffney (1983) for scale terminology of meiolaniid skulls. Descriptions of the skull of *Meiolania platyceps* Owen can be found in Gaffney (1983). Institutional prefixes to catalogue numbers are as follows: AMF, Australian Museum, Sydney; BMNH, British Museum of Natural History, London; QMF, Queensland Museum, Brisbane.

SYSTEMATICS

Order Testudines
Megaorder Cryptodira
Capaxorder Selmacryptodira
Hyperorder Daiocryptodira
Parvorder Eucryptodira
Suborder Meiolanoidea
Family Meiolaniidae

Type Genus. *Meiolania* Owen, 1886b.

Known Distribution. Pre-Oligocene ("Cretaceous or Eocene", Simpson 1938) of Argentina, Miocene to Pleistocene of Australia, Pleistocene (or younger) of Lord Howe Island, Walpole Island, and New Caledonia.

Previous work. Gaffney (1983) relates the long and complex history of work on the meiolaniids, beginning with Owen's (1881) identification of the first known meiolaniid as a giant horned lizard. Recent papers are Megirian (1989, 1992), Gaffney and McNamara (1990), and Gaffney (1992).

Revised Diagnosis. Eucryptodiran turtles with the squamosal and supraoccipital uniquely produced into posteriorly and posterolaterally directed processes, three scale areas (A,B,C in Gaffney, 1983) being most prominent; temporal emargination completely absent and related to extensive squamosal-supraoccipital contact and relatively small parietal; supraoccipital with large horizontal plate on skull roof; nasal bones unusually large; sinus formed from nasal and maxilla lateral to, and communicating with, apertura narium externa (determinable only in *Meiolania platyceps* and *Ninjemys oweni*); broad squamosal-quadratojugal contact ventral to completely enclosed incisura columellae auris which contains both stapes and eustachian tube; medial plate of pterygoid separated ventrally from basisphenoid to form intrapterygoid slit; palate concave ventrally with vomerine ridge on midline; well developed labial and lingual ridges 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 formula is (2((3((4))5))6))7))8); free cervical ribs present on cervicals 2-6; caudal vertebrae opisthocoelus with well developed haemal spines; plastron lacking axillary and inguinal buttresses; no mesoplastra present; plastron with fontanelles on midline; first thoracic of the carapace facing anteriorly, and first thoracic rib long and reaching plastron laterally; posterior peripherals scalloped; adults usually with cranial and shell sutures fused; carpal and tarsal formula 2-2-2-2-2.

It should be noted that most of these characters are known only in *Meiolania platyceps* (Gaffney, 1983, 1985).

Discussion. The higher phylogenetic relationships of meiolaniids and the higher classification of cryptodires is discussed in Gaffney (1983), Gaffney and Meylan (1988), Gaffney *et al.* (1991), and Gaffney (1992).

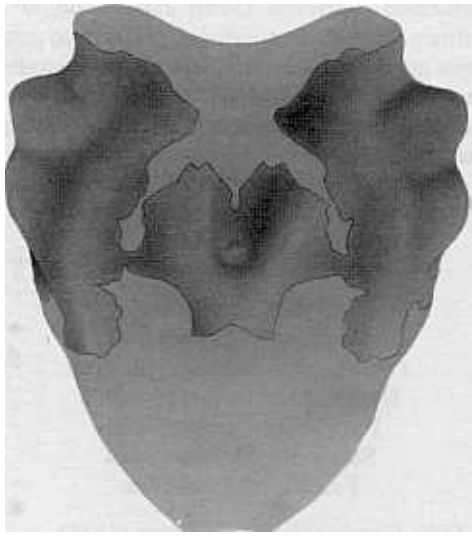

Fig 1. *Warkalania carinaminor* gen. et sp. nov. Dorsal view of skull based on QMF 22649, 22650, and 22651, partially restored by transferring side to side. See Figure 5 for scale labels.

Warkalania gen. nov.

Type Species. *Warkalania carinaminor* sp. nov.

Known Distribution. Mid Tertiary, northwest Queensland.

Diagnosis. Meiolaniid with B scale area (encompassing the largest horn in other meiolaniids), delimiting a low, horizontal ridge, not a recurved horn as in *Meiolania* nor a large lateral projection as in *Niolamia* (including *Crossochelys*) and *Ninjemys oweni*; A, B, and C scales formed into low, horizontal ridges, small and roughly similar in size to each other, in contrast to all other meiolaniids; A scale area not as protuberant as in *Niolamia* and *Ninjemys oweni* but more protuberant than in *Meiolania*; C scale area a low ridge, higher than in *Meiolania* but lower than in the other meiolaniids; X scale small, and D scales in midline contact as in *Ninjemys oweni* and *Meiolania*.

Etymology. *Warka*, Queensland aboriginal for turtle; *lania*, in reference to the usual endings for meiolaniids (*Lanius* is Latin for "butcher" but Owen (1886b) gave no indication of an etymology when he erected *Meiolania*).

Warkalania carinaminor sp. nov.

Type material. HOLOTYPE QMF 22649, a right squamosal (Fig. 2). This fragment includes the posterior margin of the cavum tympani, all of

scale C, most of scale K, and parts of scales B,H, and D. It is likely, but not definitely demonstrable, that QMF 22650-22653 and 22682 belong to the same individual.

Type locality. Pancake Site, Riversleigh Station, northwest Queensland, see Archer *et al.* (1989).

Horizon. "? late Oligocene to early Miocene" Archer *et al.* (1989:64).

Other material. Referred specimens, all from the type locality: QMF 22650, left squamosal with complete scale areas A,B, and C plus part of scale D (Fig. 3). A fragment of the posterior wall of the antrum postoticum is preserved internally; QMF 22651, central section of right and left parietals, bearing on its dorsal surface scale X and surrounding portions of scales G and D; QMF 22652, nearly complete right quadrate; QMF 22653, right exoccipital and basioccipital lacking ventral surface; QMF 22682, part of right supraoccipital containing semicircular canals, small portions of prootic and opisthotic; QMF 22654, left squamosal with scale areas B and C complete portions of scale areas A and K (Fig. 4).

Discussion. An important question to be dealt with in the proposal of *Warkalania* as a new genus of meiolaniid, is: do the seven skull fragments actually belong to one species or one specimen? It is apparent that at least two individuals are present because QMF 22650 and 22654 consist of the same bone elements. The remaining fragments, QMF 22649, 22650, 22651, 22652, 22653 and 22682, come very close to actual contact, show no overlap, and can be restored as a reasonable skull from one individual. However, the type specimen chosen, QMF 22649, has enough diagnostic characters so that it can stand alone as a new taxon of meiolaniid, even if the composite reconstruction is in error due to the mixing of more than one individual and more than one species. The holotype QMF 22649, shows the large squamosal, enclosed incisura columellae auris, and development of protuberances identifiable as B and C horns, diagnostic of Meiolaniidae. But the B and C horns of QMF 22649 differ significantly from all other meiolaniids. The C horn is cone shaped (or flat in *Meiolania*) in all other meiolaniids, but in *Warkalania* it is a horizontal ridge directed anteroposteriorly. The B scale of QMF 22649 is also a flattened ridge in strong contrast to the cow-like, recurved B horn core synapomorphic for *Meiolania*. The B horn cores of *Ninjemys oweni* and *Niolamia* are much larger, laterally directed spines, rather than the relatively low, horizontal ridge of *Warkalania*.

The other cranial fragments identified here as belonging to *Warkalania* allow the diagnosis to be extended to the X scale area, the A and D scales, and the posterior parts of the braincase.

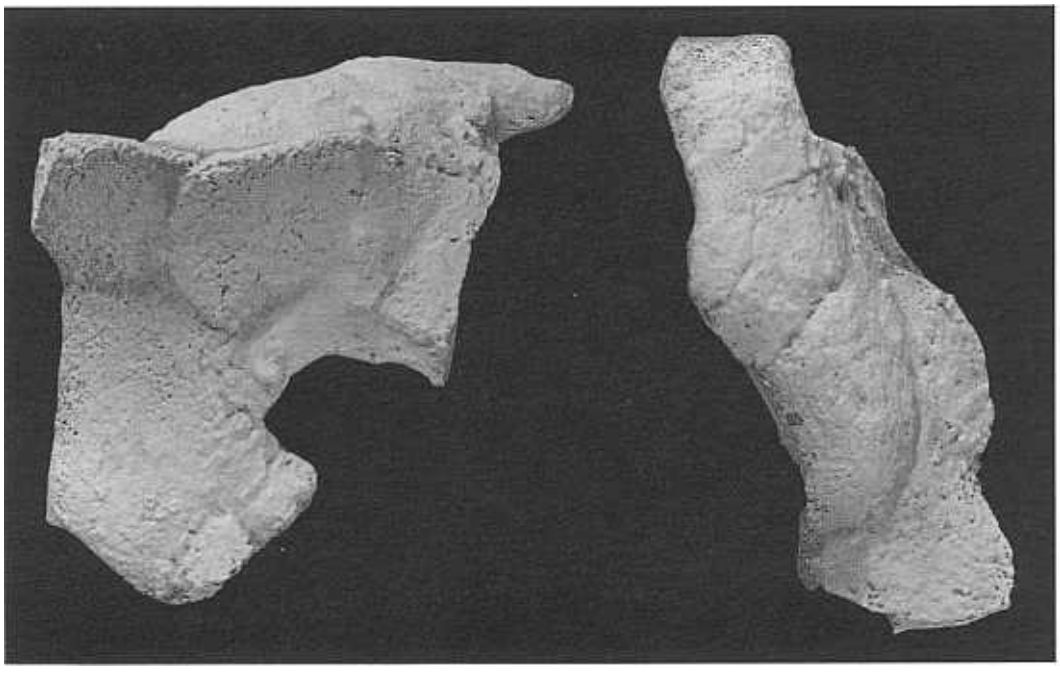

Fig 2. *Warkalania carinaminor* gen. et sp. nov. QMF 22649, type specimen, right squamosal. **Left**, lateral view; **Right**, dorsal view.

Diagnosis. Same as for genus.

Description. Because there are no bone sutures preserved in the *Warkalania* material, the description uses the scute areas as homologous entities that are hypothesized as suitable for comparisons. The scute terms and the order is from Gaffney (1983).

The areas preserved in *Warkalania* only include the posterior parts of the skull. The overall proportions and size of the *Warkalania* specimens are roughly the same as *Meiolania platyceps* (Figs 5,6). In most *Meiolania platyceps* skulls the scute areas are delimited by raised ridges, while in *Ninjemys oweni* and *Niolamia* the scales

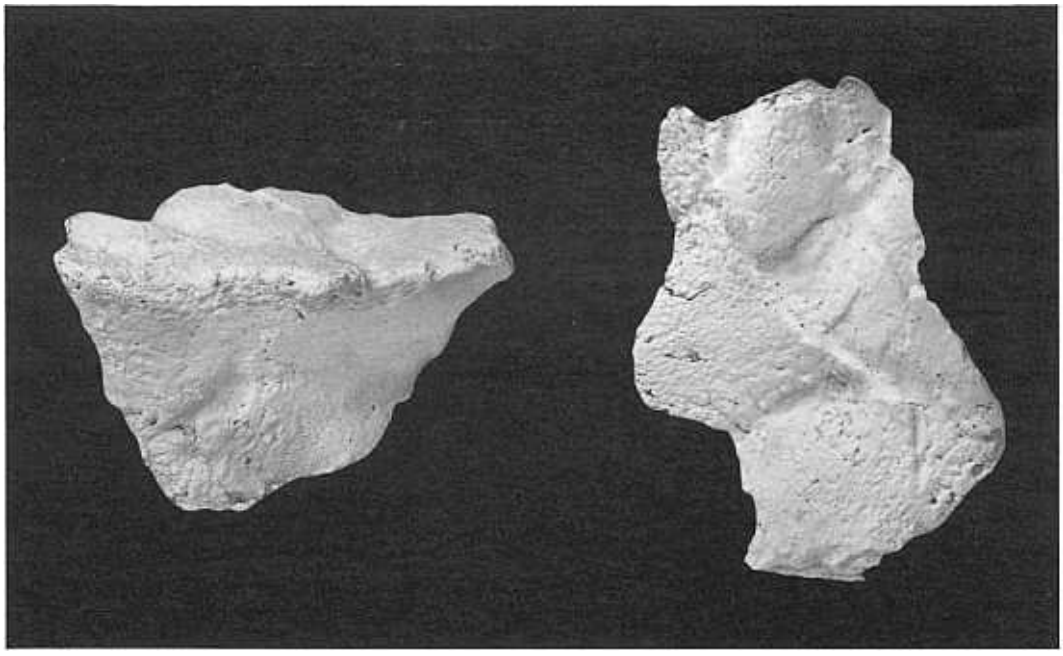

Fig 3. *Warkalania carinaminor* gen. et sp. nov. QMF 22650, left squamosal. **Left**, lateral view; **Right**, dorsal view.

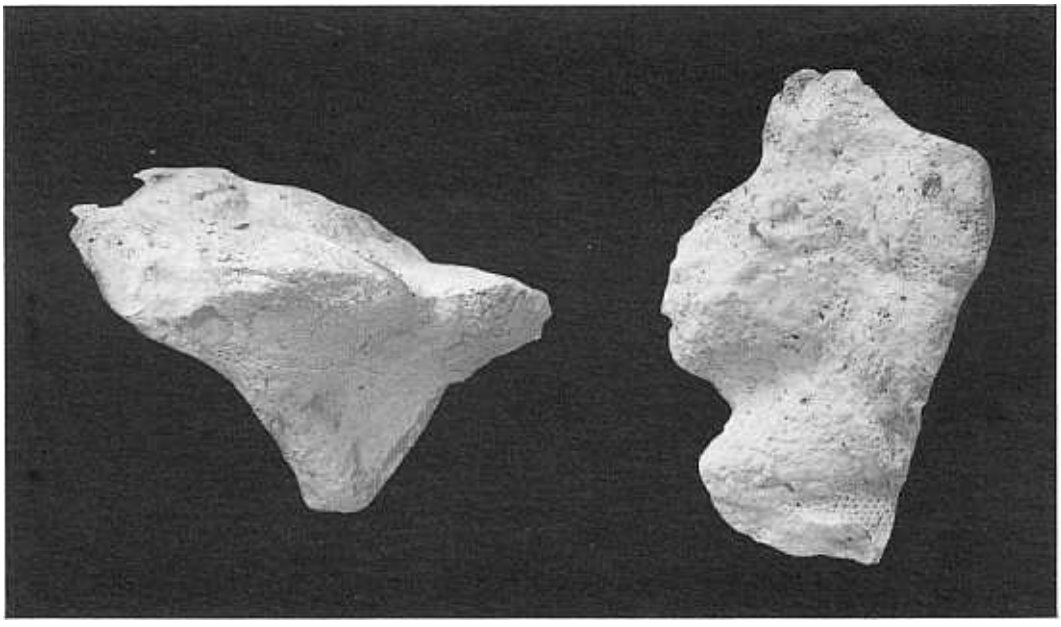

Fig. 4. *Warkalania carinaminor* gen. et sp. nov. QMF 22654, left squamosal. **Left**, lateral view; **Right**, dorsal view.

are bordered by shallow grooves. *Warkalania* has grooves rather than ridges and thus differs from *Meiolania platyceps*, and resembles *Ninjemys oweni* and *Niolamia* in this feature.

The midline area of the skull in *Warkalania* is preserved in QMF 22651, a fragment that consists of scale X and surrounding portions of scales G and D. It probably represents the anterior part of both parietals and the posterior part of both frontals. On its dorsal surface there is a clear, oblong scale area in the midline, scale X, with a small, cone-shaped projection just left of the midline. Although not as well defined as in most *Meiolania platyceps* specimens, scale X in *Warkalania* is similar in size and shape to the Lord Howe species. The small cone is also present in most *Meiolania*, but smaller. The dorsal surface is somewhat rugose in QMF 22651, and there are vague grooves that could be the sulci separating scales G and D from each other. However, if they are present, they are poorly differentiated from other surface irregularities.

In *Ninjemys oweni*, the X scale area is not well preserved, but it is smaller than in *Niolamia* and may be much as in *Meiolania platyceps*. The D scales of *Warkalania* and *Meiolania platyceps* meet in the midline. In *Niolamia* they are separated by a large X scale. In *Ninjemys oweni* the X scale margins are not clear but the X scale area is definitely not as large as in *Niolamia*, and the D scales probably do meet in the midline in *Ninjemys oweni*.

The ventral surface of QMF 22651 preserves the dorsalmost portion of the cavum cranii. Most of this region is formed by the parietal but a small part of the anterior extension of the supraoccipital is preserved on the midline. The area of the cavum cranii preserved includes the space usually filled in life by the cartilaginous remnant of the synotic tectum (Gaffney 1979). This area is preserved in a number of specimens of *Meiolania platyceps* and in *Ninjemys oweni* but not in *Niolamia*. Although this region is similar in all turtles, there are differences between *Ninjemys oweni* and *Meiolania platyceps*. Unfortunately, not enough is preserved in QMF 22651 to determine to which one it is most similar. The processus inferior parietalis is broken on both sides, but anterolaterally on the outside of each processus, is a concavity also seen in *Meiolania platyceps* but not in *Ninjemys oweni*. This concavity is apparently involved in the attachment area of the M. adductor mandibulae pseudotemporalis. The broken edge of the crista supraoccipitalis is preserved in QMF 22651. To the extent that it is preserved, it agrees with *Meiolania platyceps*.

The fragment of cranial roof, QMF 22651, taken alone, could not be distinguished from *Meiolania platyceps*, except in the absence of raised scale edges. But even this feature varies in *Meiolania platyceps*; AMF 57984 also lacks raised scale edges.

Scute D is a large, paired scale covering much of the posterior portion of the skull, and consists mostly of parietal and squamosal. Parts of Scute D are preserved in QMF 22649, 22650, 22651 and 22654. Even when the fragments are combined, the D scale area is not completely preserved in *Warkalania*. The D scale area is best preserved on the left posterolateral portion of QMF 22651 and the left anteromedial portion of QMF 22650. The two areas do not have a good contact but, when restored using QMF 22652 and 22653 (braincase elements) for control of the skull width, only a small amount of bone appears to be missing between the two cranial roof sections. Posteriorly and laterally, the D scale lies against the A, B, and C scales, as in other meiolaniids. An anterior sulcus with scale H is not discernible in QMF 22649, which has enough bone preserved to expect the presence of the sulcus. It is likely, however, that poor preservation is the cause of the absence of the sulcus, rather than the actual absence of this sulcus. The posteromedial limits of the D scale are not preserved on any of the fragments. The region of the D scale is a distinctive convexity in both *Ninjemys oweni* and *Niolamia*. *Warkalania*, however, agrees with *Meiolania* in having the D scale area relatively low.

The three scale areas, A, B, and C, are the most useful skull regions within meiolaniids for taxonomic comparisons. Fortunately, nearly all of these scale areas are preserved in *Warkalania*. Scute C is a paired scale area on the posterolateral part of the skull, and is formed mostly by the squamosal bone. In QMF 22649, 22650, and 22654 are preserved significant parts of the C scale area. In these specimens the C scale forms a laterally projecting ridge that is roughly horizontal but with a slight anterodorsal trend. This ridge projects laterally to a lesser extent than either of the other scale areas, A and B. In QMF 22649 and 22650, the C scale has a more acute edge than in QMF 22654 but the entire scale area projects laterally to a greater extent in QMF 22654. In *Meiolania platyceps*, *Ninjemys oweni*, and *Niolamia* the C scale is more rounded and cone-shaped than in *Warkalania*. *Meiolania*

platyceps varies from nearly flat in AMF 43183 to a well developed cone in AMF 57984, but it is never a horizontal ridge as in *Warkalania*.

The B scale area is preserved completely in QMF 22650 and QMF 22654, and in QMF 22649 the anterior half is preserved. The B scale is larger and projects more than the A scale, and it is flattened in the same plane as the A scale. In QMF 22654 the B scale is thicker and has a blunter lateral edge than in QMF 22649 and 22650. The most striking differences in skull morphology of meiolaniids can be found in the shapes of scale B. In *Ninjemys oweni* and *Niolamia* the B scale areas are very large, laterally projecting processes that extend laterally beyond the rest of the skull. In *Meiolania platyceps* the B scale also forms a projection but in this case it is the cow-like horn core distinctive of this genus. *Warkalania*, with its relatively small B scale area, forms a projection that is much less extensive than in *Ninjemys oweni* or *Niolamia*. The B horn core of some individuals of *Meiolania platyceps* (e.g. AMF 43183, and AMF 18368) approaches the size of the B scale in *Warkalania*, but in none of the *Meiolania platyceps* specimens is the B scale as small as in *Warkalania*. *Meiolania platyceps* also has a B horn core that is conical, usually recurved, and not flattened in any plane. In both *Niolamia* and *Ninjemys oweni* the B horn is flattened in the horizontal plane as in *Warkalania* but not to the degree seen in *Warkalania*.

The A scale area lies at the back of the skull in meiolaniids and in *Meiolania platyceps* is formed mostly by the squamosal, with a smaller contribution from the supraoccipital. The A scale area in *Warkalania* is preserved in QMF 22650 and QMF 22654 but it is incomplete. Both specimens lack the posteromedial parts of the scale area that would allow the complete limits to be seen. We have restored the A scale area by assuming that the tympanic opening in *Warkalania* parallels the midline as in all other meiolaniids (and almost all other turtles) and filling in the missing

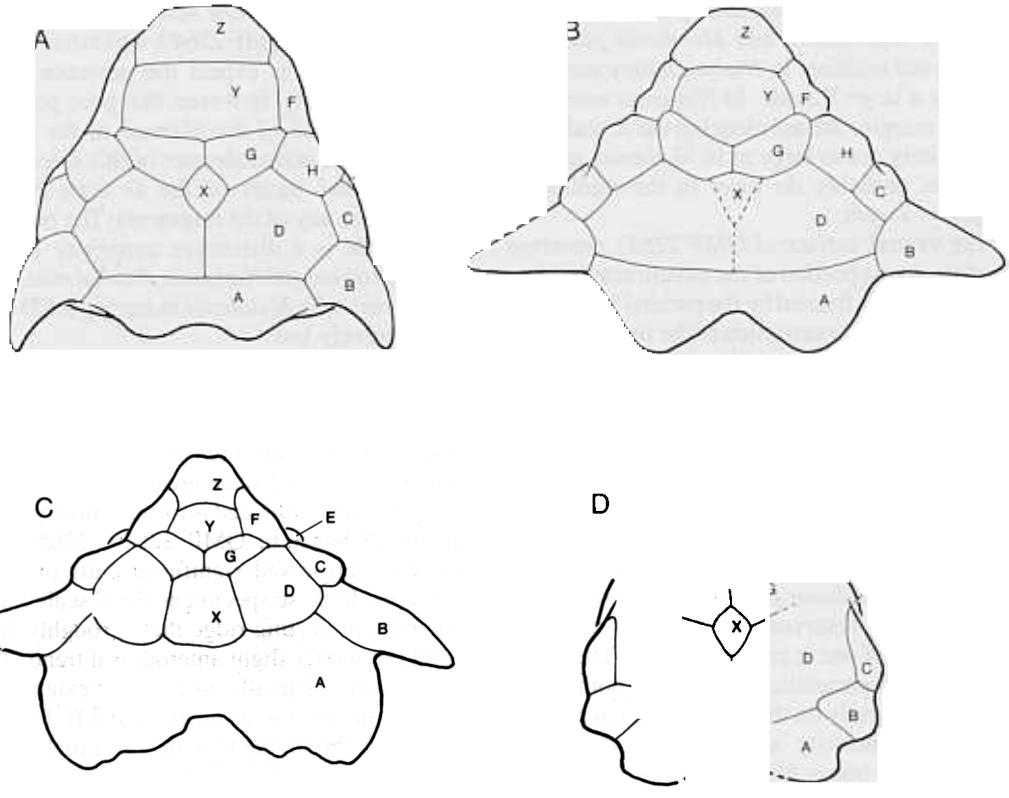

Fig 5. Meiolaniid skulls in dorsal view. **A**, *Meiolania platyceps* (after Gaffney 1983); **B**, *Ninjemys oweni*, (after Owen 1881, and BMNH R391); **C**, *Niolamia argentina* (after Woodward, 1901 and cast); **D**, *Warkalania carinaminor* gen. et sp. nov. outline from *Meiolania platyceps*. Scale terminology from Gaffney (1983).

region as conservatively as possible. The A scale of *Warkalania* is very similar in size and shape to the B scale. In QMF 22650 it has an acute edge but in QMF 22654, the edge is blunter. The scale is flattened in a horizontal plane and extends posterolaterally from the main body of the skull. *Warkalania* has an A scale that is somewhat larger than in *Meiolania platyceps*, but it is much smaller than in *Ninjemys oweni* and *Niolamia*. In these latter taxa the A scale is the largest of the A, B, C series and forms a very prominent shelf at the back of the skull. In *Warkalania* the shelf still exists but it is relatively small, while in *Meiolania platyceps* the shelf is absent and the A scale is a flattened process smaller than the B scale horn core.

Portions of the ventral area of the squamosal, consisting mostly of the K scale area, are preserved in QMF 22649, 22650, and 22654. Of these, the most extensive and informative is QMF 22649. This specimen has the dorsal and ventral margins of the cavum tympani opening and a small part of the posterior edge. On the internal surface the attachment area of the processus articularis of the quadrate can be seen and, above it, the lateral wall of the antrum postoticum. The natural ventral margin of the squamosal is also preserved. It is clear from the specimens that *Warkalania* agrees with *Meiolania*, *Ninjemys oweni*, and *Niolamia* in having a completely closed incisura columellae auris with a considerable section of squamosal below and behind the tympanic opening. Neither *Niolamia* nor *Ninjemys oweni* have the entire limits of the squamosal preserved; only *Ninjemys oweni* and *Meiolania platyceps* have the internal features of the squamosal visible. In *Warkalania* the squamosal (K scale area) posteroventral to the tympanic opening is more extensive than in *Meiolania platyceps*. This appears to be a similarity to *Niolamia*, the extent of the squamosal in *Ninjemys oweni* being indeterminate. The K/J sulcus is preserved in QMF 22649 and it is more posterior to its position in *Meiolania platyceps*, but similar to the position in *Ninjemys oweni* in which the J scale extends more posteriorly than in *Meiolania platyceps*. The area is not preserved in *Niolamia*.

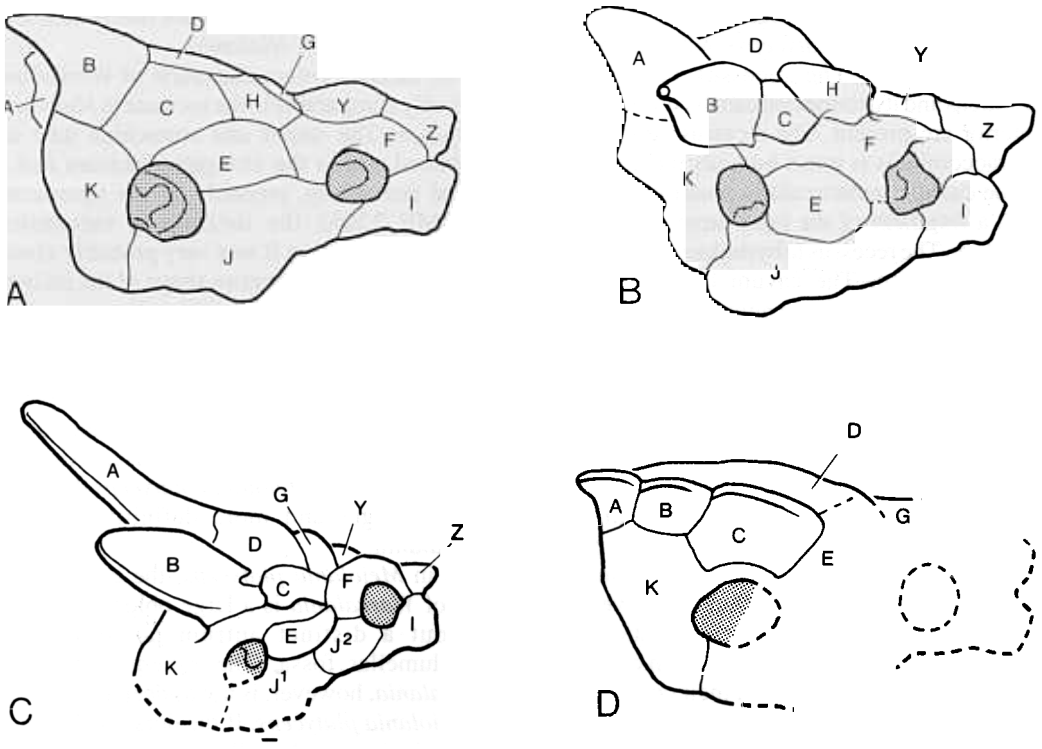

Fig 6. Meiolaniid skulls in right lateral view. Same as in Figure 2.

The three braincase fragments, QMF 22652, 22653, and 22682, all belong to the right side and probably are from the same individual. All three of these pieces very nearly come into contact when restored on the basis of *Meiolania platyceps* and are separated by relatively narrow areas of bone. Nonetheless, they do not have any contacts.

QMF 22682 is the part of the right supraoccipital that contains the semicircular canals, plus some small portions of the prootic and opisthotic. The fragment consists of the area of bone just anterior to the foramen magnum (the margin of that structure is not preserved) and posterior to the foramen nervi trigemini. The posterior margin of the foramen nervi trigemini is preserved. On the lateral surface of this piece of supraoccipital is the shallow groove that would lead to the foramen stapedio-temporale. Everything described so far is quite similar to *Meiolania platyceps* and does not vary a great deal from other generalized cryptodires.

The internal portion of QMF 22682 contains the dorsal impression of the canalis semicircularis horizontalis (see Gaffney 1979: Figs 49, 52, for terminology of the cavum labyrinthicum in turtles and Gaffney 1983: Figs 49-51, for the inner ear in *Meiolania platyceps*) with the ventral region missing. The recessus labyrinthicus prooticus and its connected canalis semicircularis anterior are present. The recessus labyrinthicus supraoccipitalis is intact but only the dorsal part of the canalis semicircularis posterior is present with a fragment of the bony strap defining this structure. The recessus labyrinthicus opisthoticus is missing also. The cavum labyrinthicum as preserved in *Warkalania* agrees with *Meiolania platyceps* except that the canals are smaller than in AMF 57984, presumably a function of the smaller skull in *Warkalania*.

QMF 22682 has two grooves preserved in the region of the dorsal edge of the hiatus acusticus. This opening is usually nearly closed in *Meiolania platyceps* and the edges are broken in QMF 22682. The grooves do not appear to be part of the fossa acustico-facialis but rather may be interpreted as the foramen aquaducti vestibuli and one of the foramen nervi acustici. Both grooves lead directly from the cavum cranii into the cavum labyrinthicum and their contents cannot be definitely determined. QMF 22652 is a right quadrate separated from the more medial part of the otic chamber at roughly the position of the quadrate-opisthotic/pterygoid suture, exposing the canalis stapedio-temporalis and the canalis cavernosus. Laterally it preserves much of the cavum tympani and the incisura columellae auris. Although no sutures are present, the posterior part of the processus paroccipitalis of the opisthotic is preserved.

The medial surface of QMF 22652 shows the canalis stapedio-temporalis and the aditus canalis stapedio-temporalis (see Gaffney 1979: Fig 10) but not the foramen stapedio-temporale itself. The foramen would lie in the area broken off. The supraoccipital fragment, QMF 22682, has the more medial groove leading to the foramen which would lie in the missing contact area between pieces QMF 22682 and QMF 22652. The canalis cavernosus lies below the aditus canalis stapedio-temporalis and its posterior length is preserved in QMF 22652. The anterior part of the canalis and the foramen cavernosum are not preserved. These structures on the medial surface of the quadrate in *Warkalania* agree closely with *Meiolania platyceps*.

The anterior surface of the quadrate, probably with some of the prootic attached, bears the processus trochlearis oticum. The processus in *Warkalania* is slightly thicker than in *Meiolania platyceps*. The processus is not determinable in *Ninjemys oweni* or *Niolamia*.

The incisura columellae auris of *Warkalania* is closely comparable to the incisura in *Meiolania platyceps*. The stapes and eustachian tube are contained within the elongated incisura that is closed posteriorly, probably by the squamosal. In QMF 22652 the incisura is incomplete posteroventrally but it was very probably closed as in *Meiolania*. The entire shape of the incisura is preserved only in *Meiolania platyceps* where there is some variability. The incisura of *Warkalania* is nearly identical to *Meiolania platyceps* except for the degree of development of the lobe of bone supporting the stapes about midway along the length of the incisura (Gaffney 1983: Fig. 45). In *Meiolania platyceps* this bony lobe is larger and more definitive than in *Warkalania*.

As in *Meiolania platyceps*, the cavum tympani of *Warkalania* is a large oblong spheroid, without a distinct antrum postoticum or precolumellar fossa. The cavum tympani in *Warkalania*, however, is not as deep medially as in *Meiolania platyceps*. If the dorsomedial limit of the incisura columellae auris is used as a landmark when comparing both taxa, it is particularly apparent that the cavum extends medi-

ally to a greater degree in *Meiolania platyceps* than in *Warkalania*. Unfortunately, this area is not well enough preserved in other meiolaniid taxa for rigorous comparisons.

QMF 22653 consists of most of the basioccipital plus the right exoccipital. As in all the other *Warkalania* fragments, sutures are not distinguishable. The condylus basioccipitalis of *Warkalania* is similar in shape and proportions to *Meiolania platyceps*, the neck is relatively short and stout in both taxa, in contrast to most other turtles. The articular surface of the condylus is slightly concave in *Meiolania platyceps* and slightly convex in *Warkalania*. The degree to which the condylus occipitalis is made up of basioccipital versus exoccipitals is not determinable in *Warkalania*. The ventral surface of the basioccipital is broken off.

The foramen magnum of *Warkalania* slopes anterodorsally as in *Meiolania platyceps*, a relatively unusual chelonian condition but indeterminate in the other meiolaniids. There are two pairs of foramina nervi hypoglossi, one pair penetrating each exoccipital. In some *Meiolania platyceps* a very small, third foramen nervi hypoglossi is present (Gaffney 1983) but most specimens have two prominent foramina on each side as in *Warkalania*. The area of the exoccipital between the foramen magnum and the medial edge of the foramen jugulare posterius contains the two hypoglossal foramina, and in *Warkalania* this forms a relatively flat surface roughly parallel to a transverse plane. Both posterior foramina nervi hypoglossi open at an acute angle to this surface. In *Meiolania platyceps* this area between foramen magnum and foramen jugulare posterius is more curved, so that the more posterior of the foramina nervi hypoglossi opens at nearly right angles to the bone surface. In the absence of the rest of the cavum acustico-jugulare and fenestra postotica in *Warkalania*, and the absence of comparable regions in the other meiolaniids, the significance of this difference cannot as yet be determined.

In QMF 22653 the anterior and posterior openings of the foramina nervi hypoglossi can be seen on the right side, and on the left side some of the internal parts of the canals for these nerves can be seen in the broken surface. The anterior and lateral margins of QMF 22653 are mostly broken edges but the posterior margin of the foramen jugulare anterius and the posterior wall of the recessus scalae tympani (*fide* Gaffney, 1979) are identifiable.

Etymology. *Carina*, ridge, and *minor*, small, in reference to this species having scale areas A,B, and C as small ridges, a condition unique among meiolaniids.

Relationships of *Warkalania*. *Warkalania* is clearly a meiolaniid. It possesses two of the three synapomorphies proposed for the family by Gaffney (1983) and Gaffney and Meylan (1988):

1. Squamosal and supraoccipital produced into large posteriorly and posterolaterally directed processes that extend clear of skull.
2. Broad squamosal-quadratojugal contact ventral to quadrate.

The third character, the intrapterygoid slit, is indeterminate in *Warkalania*.

Relationships within the Meiolaniidae have only been briefly referred to by Gaffney and Meylan (1988:181 and Figs 5,8). They grouped *Ninjemys oweni* (now named *Ninjemys owni*, Gaffney 1992) and *Meiolania platyceps* as the sister group to *Niolamia* on the basis of A scute area relatively small in comparison to the A scute area in *Niolamia*. However, the squamosal-supraoccipital scale characters cannot be readily polarized by reference to a cryptodiran outgroup because the very presence of these elements is a meiolaniid synapomorphy unique to this group. The entire polarizing of the scales in meiolaniids rests on the argument that *Niolamia* is the sister group of all other meiolaniids. This argument is based on a character that can be polarized by outgroup comparison, the structure of the intrapterygoid slit. Gaffney (1983:431-435, Fig. 60) argued that "*Crossochelys*" (Simpson 1938, congeneric with *Niolamia*) has an intrapterygoid slit that is primitive with respect to the intrapterygoid slit of *Meiolania platyceps*. This is only one character, but, at present, it is the only character with any degree of complexity that can be used to resolve the polarity problem within the meiolaniids. It is then possible to hypothesize *Niolamia* as the sister taxon to other meiolaniids and to use this hypothesis to resolve the various squamosal scale characters. In addition to the inherent weaknesses of this character, it should be noted that the intrapterygoid slit character is determinable only in *Niolamia* (="*Crossochelys*") and *Meiolania platyceps*, the region is absent in *Ninjemys oweni*, *Warkalania*, and other presumed species of *Meiolania*. Nonetheless, it seems reasonable to adopt the idea of *Niolamia* as the sister taxon to all other meiolaniids (Fig. 7) as a working hypothesis and accept the limitations.

The genus *Meiolania* can be restricted to just those taxa with cylindrical, recurved, cow-like B horns, following Gaffney (1983) and Megirian (1989, 1992). The species *oweni* named by Woodward (1901) and placed in *Meiolania* by him should be removed to its own genus, *Ninjemys* , characterized by small, cone shaped C scales, laterally projecting B horns, and A scales intermediate in size between *Niolamia* and *Meiolania* (see also Table 1). Given these taxa and *Niolamia* being a senior synonym of *Crossochelys*, there are three generic level taxa of meiolaniids to compare with *Warkalania* (Table 1).

The small size of the B scales is unique to *Warkalania* but the small size of the A scales may be interpreted as a synapomorphy in common with *Meiolania* and not found in *Ninjemys oweni* and *Niolamia*. The absence of a laterally projecting B scale, found in *Ninjemys oweni* and *Niolamia*, and presumably a primitive meiolaniid feature, could also be argued as a synapomorphy uniting *Meiolania* and *Warkalania*. However, the B scales of *Meiolania* and *Warkalania* are very different from each other. A better character is the low D scale of *Warkalania* and *Meiolania*, produced into a raised tubercle in *Ninjemys oweni* and *Niolamia*. This analysis of the few characters available at present is reflected in the cladogram in Figure 7.

Other meiolaniid specimens from Riversleigh sites. *Skull fragment.* QMF 22655 appears to be the left A scale area of a species very similar to *Meiolania platyceps*. The specimen is unfortunately very limited in useful features, and a break in the middle of the scale area makes other interpretations possible. As preserved, the fragment is a triangular piece of bone with the apex divided by breakage. It looks as if the broken area was originally filled with bone forming a single, large projection. However, the presence in the Miocene of northern Australia of at least two meiolaniid taxa makes a less likely alternative possible, namely that this is a B plus C scale area with the gutter between the two represented by the broken area. However, on the dorsal surface there is no sign of a trough or depression as in *Warkalania*, and, most importantly, on the internal surface there is one continuous sheet of finished bone with no indications of a depression for each scale area as in *Warkalania*. QMF 22655 does differ from *Meiolania platyceps* in having more acute posterior edges, which are rounded in *Meiolania platyceps*. The A horn of the Bullock Creek *Meiolania* s *brevicollis* (Megirian 1989, 1992) is lower than in either *Meiolania platyceps* or QMF 22655 and does not have acute edges either. At present, however, the best interpretation of this specimen is that of *Meiolania* in the strict sense, species indet.

Lower jaws. A lower jaw of a meiolaniid from Riversleigh is QMF 22656 (Camel Sputum Site). The specimen consists of most of the fused dentaries, the right side being more broken posteriorly. The jaws are very deep, much deeper than any chelid, but relatively narrow. In addition to *Meiolania platyceps* (Gaffney, 1983), partial lower jaws are known for *Niolamia* (Woodward 1901) and for an unnamed meiolaniid known from very fragmentary material from Gulgong, NSW (Mining Museum of Sydney 13898). All the jaws are relatively deep, have fused mandibular symphyses, and parallel labial and lingual ridges separated by a trough. In *Niolamia* and the Gulgong fragment, the ridges are low and the trough shallow (probably exaggerated by breakage) and there is no symphyseal or median cusp. In *Meiolania platyceps* and QMF 22656, the ridges are sharp and well defined and a median cusp is present (Gaffney 1983:449). The lingual (inner) ridge is distinctly higher than the labial (outer) ridge in *Meiolania*

Table 1. Comparison of the cranial morphology meiolaniid genera.

	Warkalania	*Meiolania*	*Ninjemys oweni*	*Niolamia*
D scales meet in midline	yes	yes	probably	no
X scale large	no	no	intermediate	yes
D scale	low	low	high	high
A, B, and C scales forming a continuous shelf	yes	no	yes	yes
C scale cone-shaped	no	yes (when present)	yes	yes
C scale a horizontal ridge	yes	no	no	no
B scale projecting laterally	no	no	yes	yes
B scale flattened	yes	no	yes	yes
A scale very large and forming shelf at back of skull	no	no	yes	yes
Y scale relatively large	indet	yes	yes	no

platyceps and QMF 22656 in contrast to the ridges being even in *Niolamia* and the Gulgong fragment. The Riversleigh jaws, however, do differ significantly from *Meiolania platyceps*. The lingual ridge in *Meiolania platyceps* is accompanied by an equally well developed accessory ridge, absent in QMF 22656. This accessory ridge (Gaffney 1983:Fig 62) is matched by an accessory ridge in the skull (Gaffney 1983: Fig. 32), also present in *Ninjemys oweni* and the Bullock Creek *Meiolania* s *brevicollis* (both of which lack lower jaws but presumably would have accessory ridges on them). It is unlikely that QMF 22656 belongs to the genus *Meiolania*. It is possible that it belongs to *Warkalania*, although there is no real evidence for this.

Caudal vertebra. QMF 22657 (Camel Sputum Site) is a caudal vertebra split horizontally through the centrum with the lower part lost. The preserved section, consisting of neural spine, zygapophyses, and dorsal part of the centrum, is very similar to described caudals of *Meiolania platyceps*. QMF 22657 is similar to AMF 18715, figured in Gaffney (1985: Fig. 15C). The neural spine is a bit shorter and more like AMF 57984 (Gaffney 1985: Fig. 15B) which is a more anterior caudal vertebra.

Tail Rings. Three meiolaniid tail ring pieces have been recovered from Riversleigh sites. Despite the relatively large number of specimens of meiolaniids found on Lord Howe Island, an articulated caudal series of vertebrae or dermal ossifications is still unknown for any meiolaniid. It is possible to determine roughly relative positions of tail rings and to categorize serial differentiation (Gaffney, 1985:26). Using criteria de-

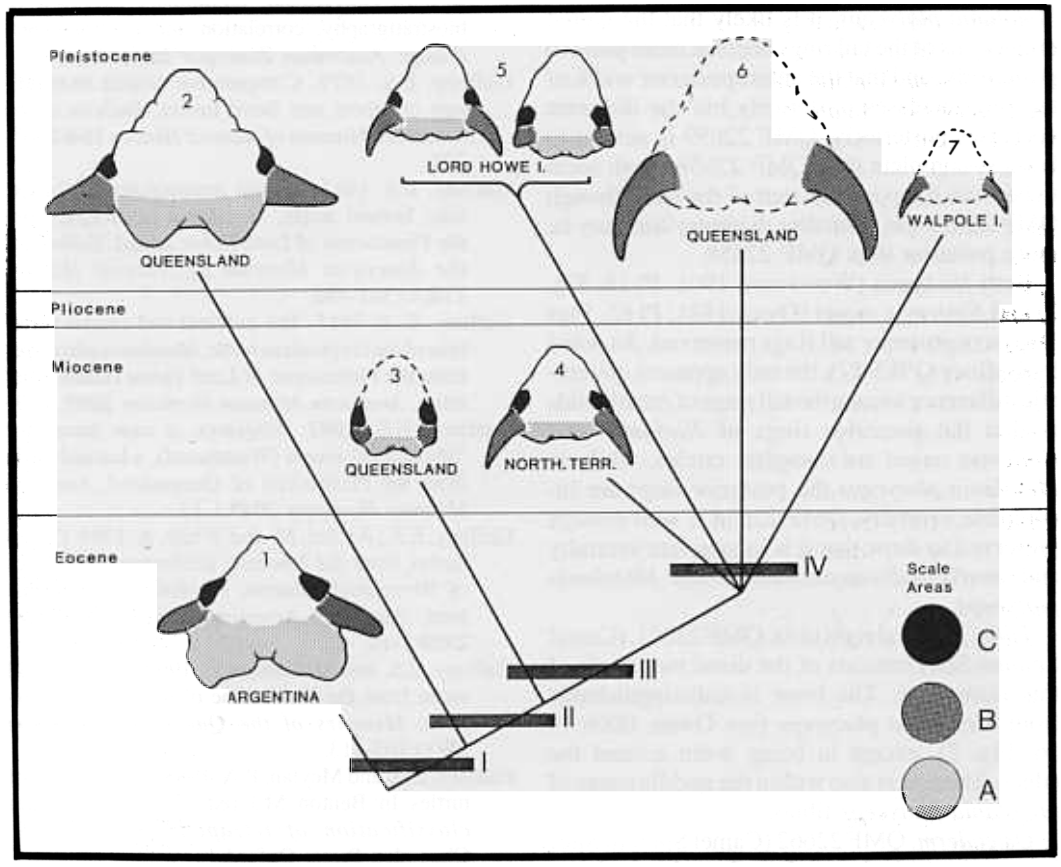

Fig 7. Cladogram of meiolaniid turtles showing skulls in dorsal view with three scale areas (A,B,C) indicated for comparison. Temporal range not to scale. Synapomorphies for the following groups: **I**, Meiolaniidae, see diagnosis; **II**, D scales meet in midline, X scale small; A scale equal to or smaller than B scale; apertura narium externa divided; Y scale relatively large; two accessory ridges on triturating surfaces; **III**, D scale low, A scale relatively small and not forming shelf at back of skull; **IV**, 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*; (**3**) *Warkalania carinaminor* gen. et sp. nov.; (**4**) *Meiolania brevicollis*; (**5**) *Meiolania platyceps*, showing two extremes of horn variations; (**6**) *Meiolania* sp., Wyandotte; (**7**) *Meiolania mackayi*.

veloped from *Meiolania platyceps*, the most anterior tail ring is QMF 22660 (Camel Sputum Site), with more posterior rings being QMF 22658 (Ringtail Site), and QMF 22659 (Sticky Beak Site). The anterior ring, QMF 22660, has two projections, probably the two on the right side, and is similar to the fragment figured by Owen (1888: Pl. 36, Figs 7-9). The projections in QMF 22660 are more acute than in the figured specimen, but this is probably due to the Riversleigh specimen being from a more posterior position.

A more posterior tail ring is QMF 22658 (the specimen originally identified by A. Ritchie), which is the only Riversleigh tail ring to be essentially complete. It is similar to AMF 50635, figured in Gaffney (1985: Fig. 21), but the projections are lower in QMF 22658. Again, however, this is probably due to QMF 22658 being more anterior than AMF 50635. In *Meiolania platyceps*, it is likely that the paired projections of the tail rings become more pointed posteriorly, and that the anteroposterior width of the ring increases posteriorly but the diameter decreases posteriorly. QMF 22659 is similar to but less complete than QMF 22658. Both seem to be from the posterior part of the tail although QMF 22659 has a smaller diameter and may be more posterior than QMF 22658.

Both *Niolamia* (Woodward 1901: Pl 18, Fig. 2) and *Ninjemys oweni* (Owen 1881: Pl 65, Figs 1-4) have posterior tail rings preserved. As noted by Gaffney (1985:27), the only apparent systematic difference among the tail rings of meiolaniids is that the posterior rings of *Niolamia* and *Ninjemys oweni* are complete circles, while in *Meiolania platyceps* the posterior rings are incomplete ventrally. QMF 22658 is well enough preserved to show that it is incomplete ventrally and nearly indistinguishable from *Meiolania platyceps*.

Tibia. A partial right tibia, QMF 22661, (Camel Sputum Site) consists of the distal two thirds of this limb bone. The bone is indistinguishable from *Meiolania platyceps* (see Owen 1888: Pl 36, Fig. 2), except in being worn around the edges. The size is also within the middle range of *Meiolania platyceps* tibias.

Osteoderm. QMF 22662 (Camel Sputum Site) is an asymmetrical, tear-drop shaped osteoderm, typical of meiolaniids and nearly identical to ones found on Lord Howe Island belonging to *Meiolania platyceps*. A figure of a *Meiolania platyceps* osteoderm that is very similar to this Riversleigh specimen can be found in Owen (1888: Pl. 36, Fig. 10).

ACKNOWLEDGEMENTS

We would like to thank Neville Pledge of the South Australia Museum for collecting the type specimen of *Warkalania* and bringing it to our attention. One of us (ESG) is very grateful to the following individuals and institutions for making their specimens of meiolaniids available: R. Jones, A. Ritchie, Australian Museum, Sydney; J. Picket, Mining and Geological Museum, Sydney; A. Milner, C. Walker, S. Chapman, British Museum (Natural History), London; D. Megirian, Northern Territory Museum, Darwin.

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Accepted 23 April, 1992