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THE POSTCRANIAL MORPHOLOGY OF *MEIOLANIA PLATYCEPS* AND A REVIEW OF THE MEIOLANIIDAE

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ABSTRACT

A series of partial shells and disarticulated shell elements is the basis for a nearly complete restoration of the carapace and plastron of *Meiolania platyceps* from the Pleistocene of Lord Howe Island, New South Wales. The carapace is broadly domed, with C-shaped bridge peripherals, but is not as arched as in living testudinids. A small cervical scale lies on a protuberant nuchal bone that has two midline articulation facets on its ventral surface for the 7th and 8th cervical vertebrae. The bones of the shell are usually fused with sutures present in a small number of disarticulated specimens. The shell bones tend to be thin in the central areas with the peripherals and other marginal areas thicker. The bone surface is coarsely textured with irregular grooves, pits, and foramina. The scale sulci are usually poorly defined, shallow troughs. In most specimens the posterior margin is strongly serrated with no caudal notch. There are 8 costals and 11 peripherals, but the number of neurals and the presence of a pygal and suprapygals are unknown. The first thoracic centrum faces directly anteriorly and the first thoracic rib reaches the axillary buttress on the third peripheral.

In the plastron the epiplastra meet on the midline and bear a short median process, apparently not homologous to that in *Proganochelys* and *Kayentachelys,* that bifurcates dorsally and articulates with the scapula. The epiplastra are relatively broad and bear two pairs of scales, about equal in size, with moderate anterior projections. No other plastral scale sulci are determinable. The entoplastron is a large, ovoid bone with a long posterior median process that separates the hyoplastra for much of their length on the dorsal surface. The axillary and inguinal buttresses do not extend onto the costals, and contact peripherals 3 and 8, respectively. The hyoplastron and hypoplastron send digitate processes to the peripherals producing a thin, partially ligamentous contact with numerous fontanelles. Mesoplastra are absent. A large, irregular, median fontanelle is present at the junction of hyoplastra and hypoplastra. The posterior plastral lobe tapers strongly in contrast to the squared off end of the anterior lobe. Small articulation facets are present on the xiphiplastra for the pubis.

The available shell material of *Meiolania platyceps* shows a great range of variation. Most shells have an extensive peripheral overhang but some specimens have almost no overhang. The shell sulci are usually broad and indistinct but in some specimens they are finely incised with raised edges.

The limbs and girdles are completely known in *Meiolania platyceps* and are represented by both articulated and disarticulated specimens. The shoulder girdle is a stout element with a wide scapular-acromion angle and without a glenoid neck. The coracoid is wide and flat, flaring medially. The pelvis has large but widely separated thyroid fenestrae and a small epipubic process. The ilium flares slightly dorsally. There are two sacral ribs and, usually, the rib of the first caudal is fused to the second sacral.

The humerus in *Meiolania* is expanded distally and proximally which contrasts to the narrower condition in nearly all cryptodires, but is similar to *Proganochelys.* The articular and surface morphology, however, is more similar to baenids and other primitive cryptodires. The ulna, radius, tibia, fibula, and femur of *Meiolania* are similar to those bones in *Proganochelys* and primitive cryptodires, except that in *Meiolania* they are generally stockier and more robust, with wider ends.

The carpus of *Meiolania* has seven carpal bones: ulnare, intermedium, medial centrale, and four distal carpals. The manus formula is 2-2-2-2-2 with broad, flat unguals. The tarsus of *Meiolania* has an astragalocalcaneum showing no sign of sutures or fusion. Two distal tarsals are definitely known, but four were probably present. The pedal formula of *Meiolania* is 2-2-2-2-0.

A revision of the family Meiolaniidae recognizes four genera: *Niolamia* (Eocene, Argentina), *Ninjemys* (Pleistocene, Queensland), *Warkalania* (Miocene, Queensland), and *Meiolania* (Miocene to Pleistocene, Northern Territory, Queensland, Lord Howe Island, New Caledonia). A PAUP analysis of 22 characters results in one cladogram: (*Niolamia* (*Ninjemys* (*Warkalania, Meiolania*))).

The relationships of meiolaniids are analyzed using 17 taxa and 40 characters. Within the eucryptodires the shortest cladogram in a PAUP analysis is as follows: (Plesiochelyidae (*Xinjiangchelys* (Meiolaniidae (((*Sinemys, Dracochelys*) *Ordosemys*) (Chelydridae (Chelonioidea (Trionychoidea, Testudinoidea))))))). The data matrix consists of 19 cranial characters, 12 vertebral characters, and 9 shell characters. The cervical vertebrae prove to be particularly significant in resolving the extinct eucryptodires. In this analysis the biconcave caudal, ligamentous bridge attachment, and narrow epiplastra are seen to originate within the extinct eucryptodires. The family level name Sinemydidae is expanded to include *Sinemys, Dracochelys,* and *Ordosemys.*

INTRODUCTION

The meiolaniids are a group of extinct, Southern Hemisphere turtles with a bizarre appearance, sporting cranial horns and frills and a tail club. Some species were very large, with lengths probably in excess of 3 m. The relationships of the meiolaniids have been controversial since the days of Richard Owen (1881), who first described them as giant horned lizards. Phylogenetic work on meiolaniids has been hampered by incomplete and misinterpreted material. As an example, even though meiolaniids have been known for over 100 years, this paper provides the first description of a meiolaniid carapace.

The present paper is the last in a series on the morphology of the best known meiolaniid, *Meiolania platyceps*. The skull morphology was described in Gaffney (1983), and the vertebral morphology in Gaffney (1985a). The present paper completes the morphologic series by describing the shell and limbs. A systematic review of all other known meiolaniids is presented here along with a review of the family. Lastly, there is a phylogenetic analysis of the relationships of the Meiolaniidae to other cryptodires.

This paper has been in preparation for over ten years and some of the taxonomic sections have already appeared in print (Gaffney, 1992; Gaffney et al., 1992). These sections are repeated here as updated and modified for this paper.

ACKNOWLEDGMENTS

My work on meiolaniids began in 1976 and since that time I have been dependent on the support and encouragement of many institutions and individuals. I am particularly grateful to the Australian Museum in Sydney, New South Wales, for their support of the project. In 1980 they awarded me a visiting curatorship which made it possible for me to study their meiolaniid collection, the world's largest, and to make new collections on Lord Howe Island.

Particular thanks and deep appreciation go to Dr. Alex Ritchie and Mr. Bob Jones of the Department of Palaeontology of the Australian Museum. In addition to collecting new specimens, they often went to heroic lengths to make their very large and sometimes unwieldy collection available to me.

Other institutions and individuals to whom I am grateful for access to specimens and information are: J. Pickett, Mining and Geological Museum, Sydney; A. Milner, C. Walker, S. Chapman, Natural History Museum, London; D. Megirian, Northern Territory Museum of Arts and Sciences, Darwin; N. Pledge, South Australian Museum, Adelaide; M. Archer, A. White, University of New South Wales, Sydney; G. McNamara, James Cook University, Townsville; R. Molnar, A. Bartholomai, Queensland Museum, Brisbane; T. Rich, National Museum of Victoria, Melbourne; P. Vickers-Rich, Monash University, Melbourne; I. Hutton, J. Dorman, Lord Howe Island.

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The figures are the work of Frank Ippolito and Ed Heck. Once again, their talent and skill will provide a permanent contribution in the form of high quality figures. Anna Schermerhorn improved the manuscript and devoted time to its preparation. Dr. Anne Burke and Ms. Amy Davidson prepared some of the specimens.

Dr. Richard Tedford, my colleague at the AMNH and the collector of central Australian meiolaniids, has often taken the time to help me in this project with his extensive knowledge of Australian paleontology. As in the past, I am very grateful to my colleagues Drs. Don Brinkman, Howard Hutchison, and Peter Meylan for making freely available to me information on specimens that they are currently working on. The cryptodire PAUP analysis had its origin in a 1992 meeting when Drs. Meylan, Hutchison, Brinkman, and I produced a data matrix and analysis to which all four of us contributed. I am again grateful to my three colleagues for allowing me to use the intellectual fruits of these efforts. Dr. Dirk Megirian has provided me with casts and information about *Meiolania brevicollis*.

This paper has been significantly improved by comments from Drs. Peter Meylan, Dirk Megirian, and Don Brinkman. I appreciate the time they took to read this.

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York
AM	Australian Museum, Sydney
BMNH	Natural History Museum, London
MM	Mining and Geological Museum, Sydney
NMV	National Museum of Victoria, Melbourne
NTM	Northern Territory Museum, Darwin
QM	Queensland Museum, Brisbane
SMNS	Staatliches Museum für Naturkunde, Stüttgart
TMP	Royal Tyrrell Museum of Palaeontology, Drumheller
UCMP	University of California Museum of Paleontology, Berkeley

SHELL MORPHOLOGY

CARAPACE (figs. 1–26)

The carapacial outline of *Meiolania platyceps* is ovoid, protuberant anteriorly, and lacking a cephalic notch of the sort seen in *Ordosemys* and *Macrobaena*. The sides are roughly parallel and the posterior margin is serrated. There is no caudal notch.

As restored, the carapace is moderately vaulted or arched (figs. 1, 2), more similar to those of testudinids like *Gopherus* rather than *Geochelone*. The degree of vaulting, however, is problematical. The only preserved carapace that is nearly complete, AM F:61110, is relatively flat but has been crushed to some extent. Photographs (fig. 3) of a complete shell, AM F:49141, before collection and consequent collapse, also show a flat carapace, but this specimen clearly collapsed along the costo-peripheral sutures. The preserved peripherals show that the carapace was vaulted. Smaller sections of carapace, particularly AM F:61402 (figs. 21, 22), that seem to retain the original shell curvature, also show a moderate degree of vaulting. The bridge peripherals (figs. 10, 31) are C-shaped in cross section rather than V-shaped, also consistent with a vaulted shell.

The surface of the carapace and plastron is coarsely textured with irregular grooves, pits, and foramina (figs. 3, 27, 83). Although there is no regular pattern to this texture, it is nonetheless distinctive enough to be distinguished from that of most other turtles in the Australasian fauna. The peripherals tend to be thick and the more medial parts of the carapace are much thinner.

Specimens with Large Portions of Carapace Preserved

AM F:57984 (figs. 12–15).—The restored skeleton, figures 1 and 2, (also Gaffney, 1983: fig. 1; Burke et al., 1983: figs. 1, 2, 4–8, 18) is based primarily on AM F:57984. The carapace consists of the anterior margin plus the central area of the carapace; bridge and posterior margins are missing. While the anterior margin appears to be undistorted, the central area is flattened—unusual for Lord Howe Island preservation. For the restoration, the central carapace area was cast in flexible rubber and fitted to a pre-determined shell curvature (based on a number of other specimens, but primarily on AM F:61402 and on extrapolations of the anterior margins in AM F:57984 and AM F:49141). The central area consists of two large pieces from the right and left series of costals, and these halves have a good series of contacts via posterior neurals. The anterior margin, however, does not have good contacts with the central section and it seems likely that the central section was placed too far forward in the restored cast. The position of the first thoracic rib is clear on both sides and the head of the first costal rib (left) is preserved in the central section. In the original restoration, the first costal rib head was placed slightly ahead of, rather than behind, the line of the first thoracic rib. It was thought at the time that these elements curved to produce this relationship, but this now seems unlikely. The distance between the two carapace sections is increased in the new restoration (figs. 5, 6) so that the first thoracic

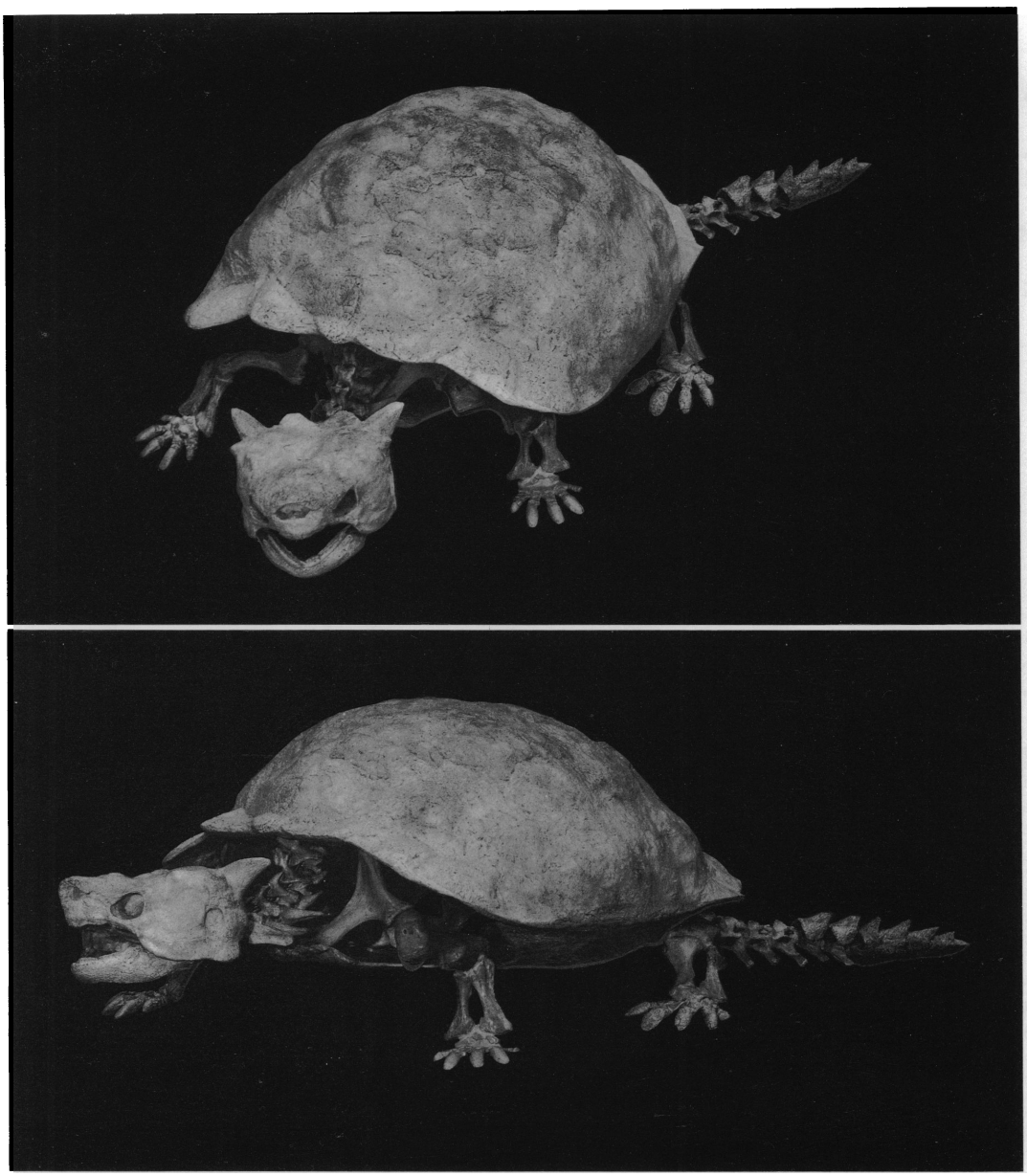


Fig. 1. Reconstructed skeleton of *Meiolania platyceps,* Pleistocene, Lord Howe Island, New South Wales. About 60% of the skeleton consists of AM F:57984. **Upper,** anterodorsal oblique view. **Lower,** anterolateral view.

and first costal ribs line up as they are in AM F:61110 and AM F:61402; that is, at right angles to the midline.

The restored cast probably also errs in having too much area between the last rib heads and the posterior margin of the carapace. Although this area is completely unknown in AM F:57984, based on the new restoration of AM F:61110, and some disarticulated elements, the posterior rib heads should be closer to the peripherals. The total length of the new restoration is only a few inches short-

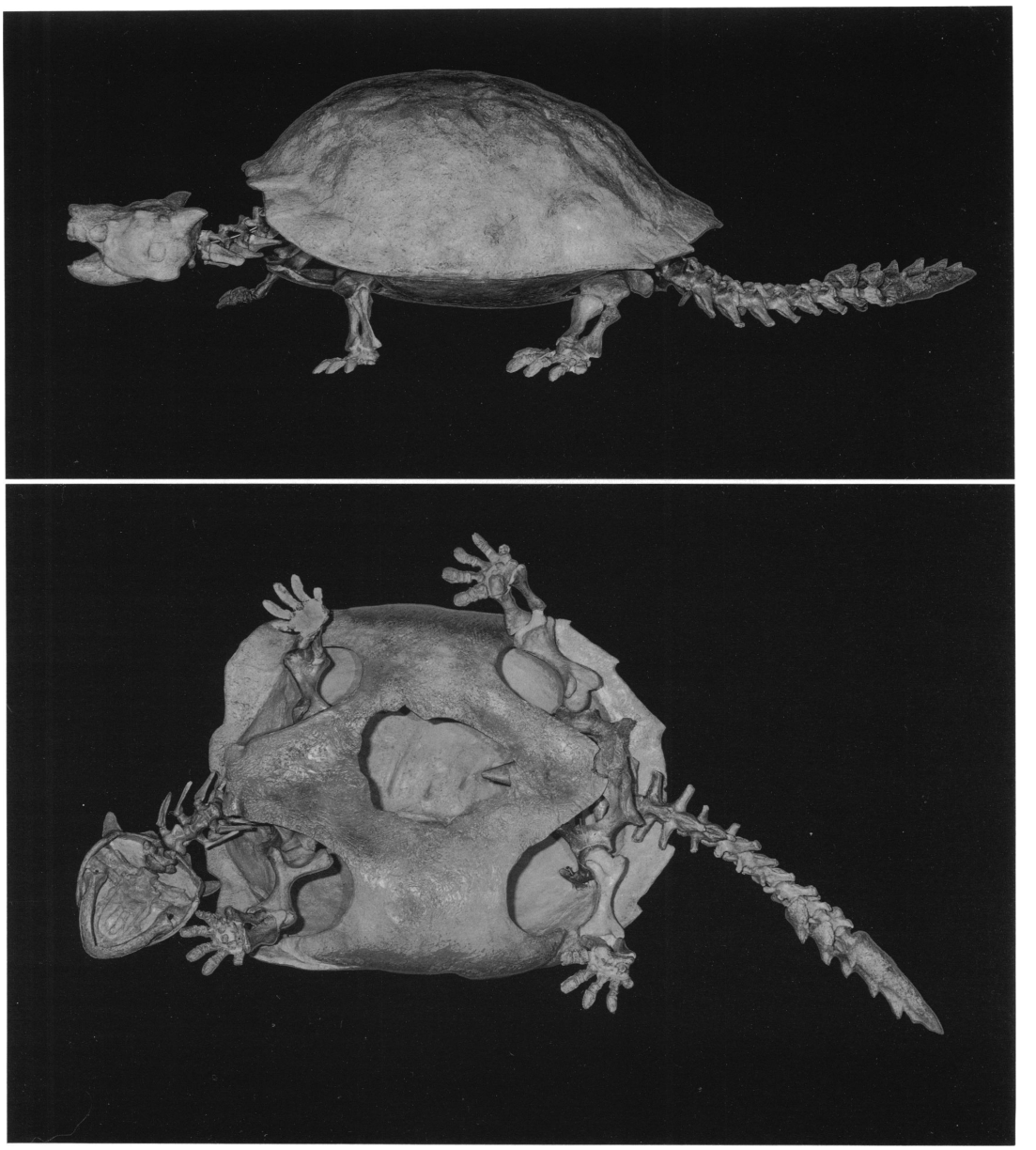


Fig. 2. Reconstructed skeleton of *Meiolania platyceps,* Pleistocene, Lord Howe Island, New South Wales. About 60% of the skeleton consists of AM F:57984. **Upper,** lateral view. **Lower,** ventral view, plastron is AM F:18775.

er than the old, but the position of the entire costal/rib head section is moved posteriorly.

AM F:61110 (figs. 17–20).—This specimen has the most complete carapace of any *Meiolania,* but some areas are broken and displaced so that a completely confident restoration is not possible. Only the internal surface is visible, the rest being encased in matrix. AM F:61110 is also difficult to restore because it is so different from the other specimens. AM F:61110 has a very narrow free edge on the peripherals and the body wall

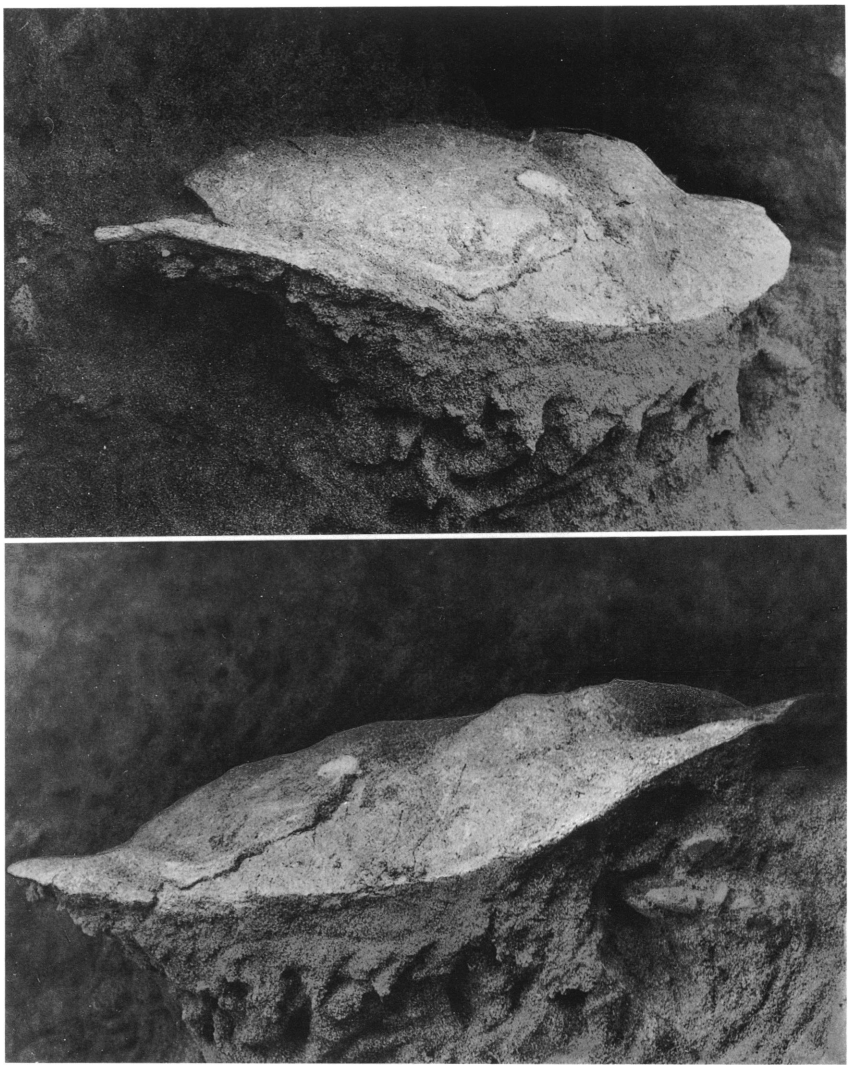


Fig. 3. *Meiolania platyceps,* AM F:49141, in situ in Ned's Beach Cliff, Lord Howe Island (locality 5 in Gaffney, 1983). Photo taken between July 20 and 22, 1959, probably by Elizabeth Pope, curator, Australian Museum. Along with the shell were articulated cervicals (described by Gaffney, 1985a) and limbs (figs. 41–44, 48). Most of the carapace and plastron were destroyed after these photographs were taken. The remaining articulated portions are shown in fig. 10. **Upper,** left side of shell in anterolateral view. **Lower,** posterolateral view of left side of shell.

margin is very close to the shell margin, in contrast to AM F:57984 and AM F:49141, both of which have a relatively large free edge, or overhang, on the peripherals.

The anterior margin on the left side is in good condition from the midline to the axillary buttress. There is a crack on the midline that slightly separates right and left halves of the anterior margin but this does not seem to have produced significant distortion. The right lateral margin of the carapace lacks natural edges but the left side has some of the bridge present and much of the remainder is a natural mold in the rock. The left posterior quadrant is broken free from the rest of the carapace and displaced anteromedially. Shifting this back and aligning it with the bridge and posterior margin produces a good

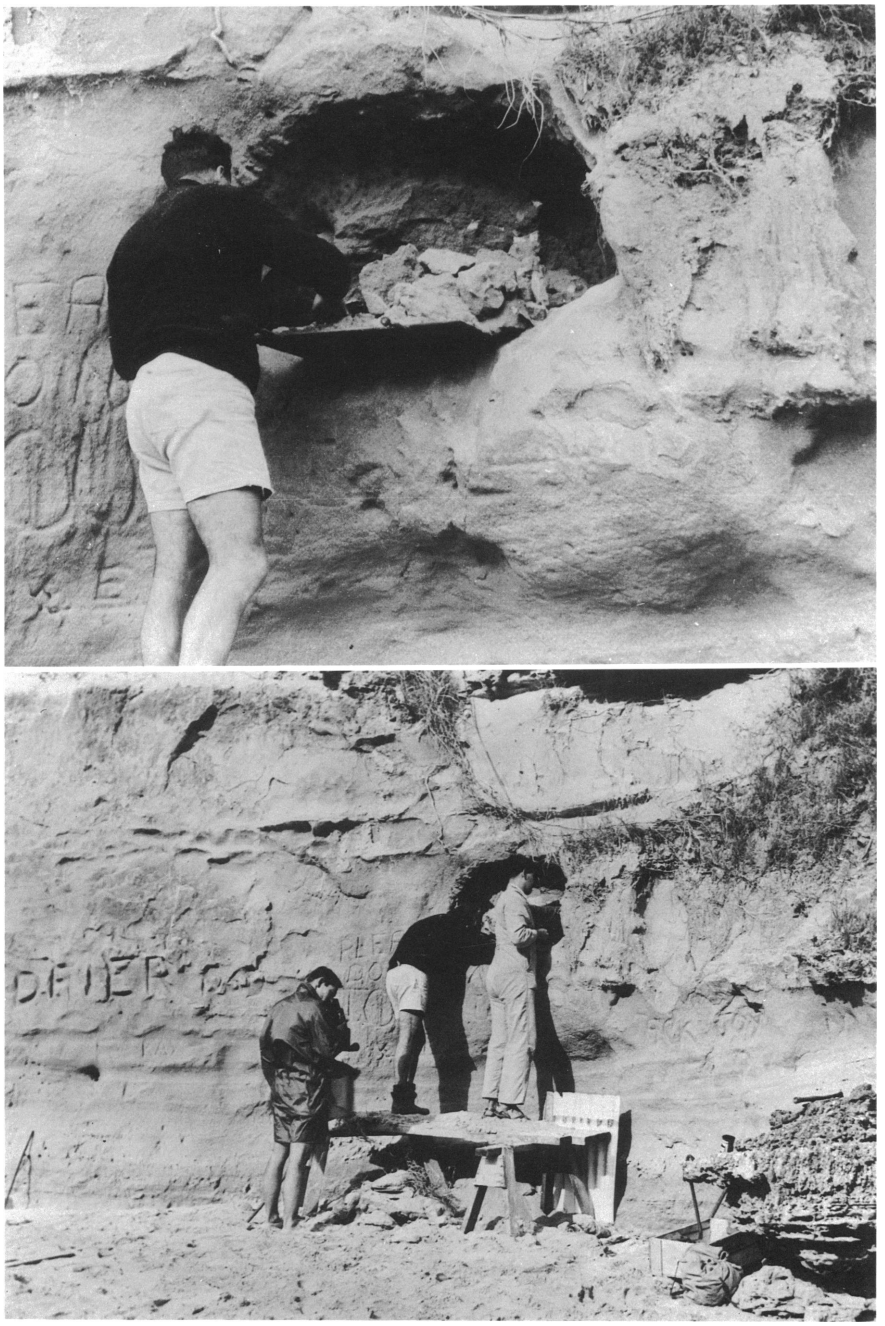


Fig. 4. Collecting *Meiolania platyceps,* AM F:49141, July 20–22, 1959, Lord Howe Island, New South Wales. Locality 5 of Gaffney (1983), Ned's Beach Cliff.

fit, and is the basis for the carapace outline (fig. 19).

The anterior thoracic vertebrae are articulated in their natural position, but beginning with the third thoracic, the more posterior centra are broken free and displaced to varying degrees and, as preserved, are unreliable indicators of the midline. Instead the posi-

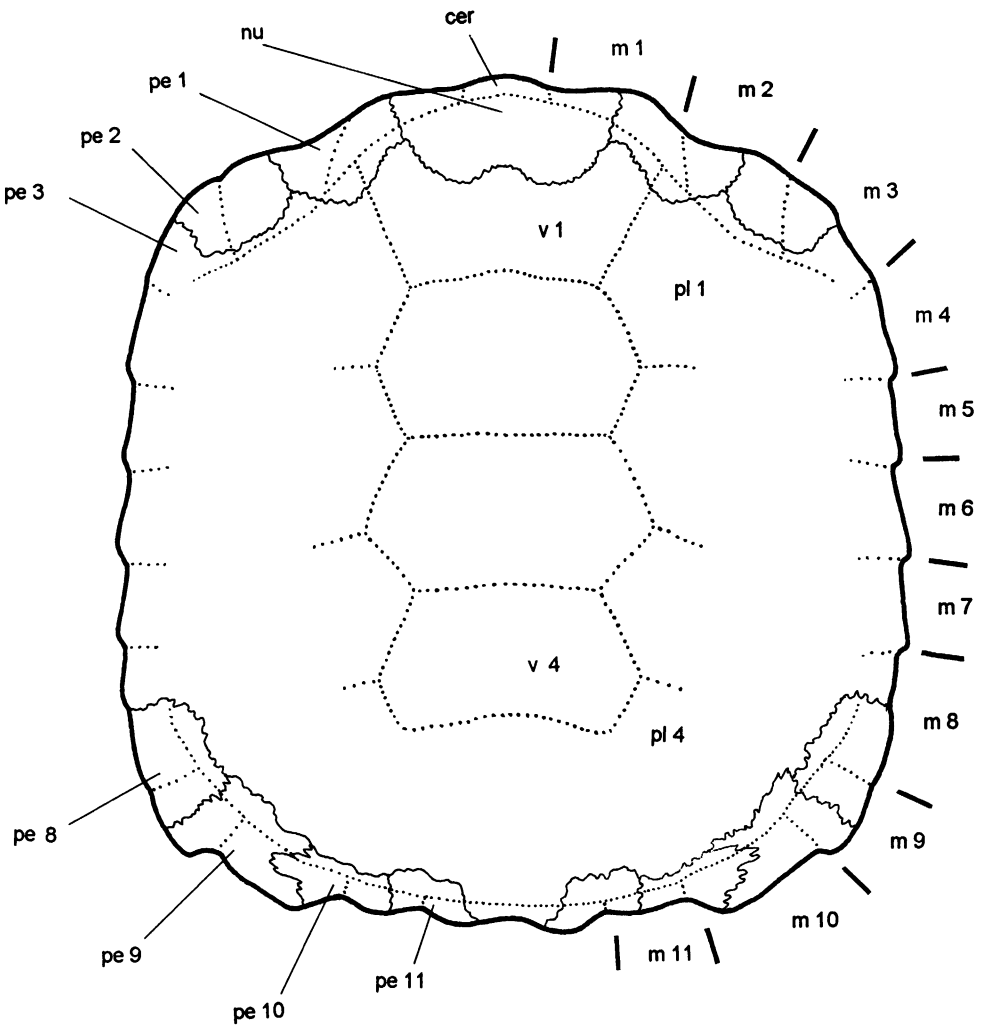


Fig. 5. Composite reconstruction of the carapace of *Meiolania platyceps* in dorsal view based on specimens as indicated in fig. 8. Sutures are solid, scales are dotted. Abbreviations: cer cervical scale, m marginal scale, nu nuchal bone, pe peripheral bone, pl pleural scale, v vertebral scale.

tions of the costal rib heads have been used to determine the midline. The principal source of error in this approach is the relatively poor preservation and ambiguity of the posterior rib heads and the possible displacement of carapace bones on the left side, beneath the overlying carapace fragment. The result could be wrong primarily in width of the posterior third of the carapace and in the positions of costal rib heads seven and eight. The maximum width of the carapace is different on both sides, but the left side has been interpreted as correct because it appears to be less distorted than the right.

AM F:49141 (figs. 3, 4, 10, 11).—This carapace was complete when discovered but was nearly destroyed during collecting (figs. 3, 4, also see Gaffney, 1983: 392). Although many pieces were collected, I have been able to piece-fit the carapace margin only back to marginal 10. Marginal edges and rib ends are preserved and by flipping from right to left a composite restoration (fig. 11) can be made, as with the other two shells. Unfortunately,

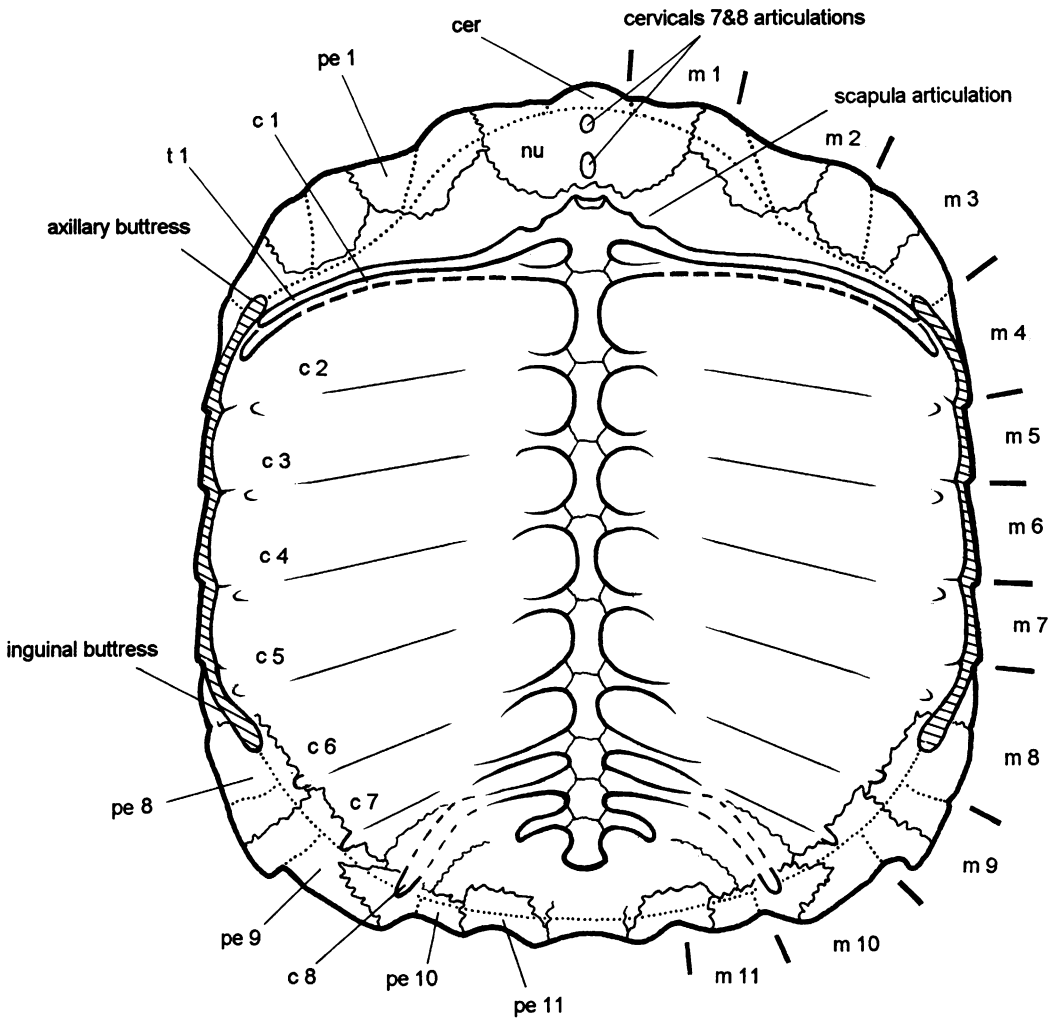


Fig. 6. Composite reconstruction of the carapace of *Meiolania platyceps* in ventral view based on all available specimens. Abbreviations: c costal rib or rib trace, cer cervical scale, m marginal scale, nu nuchal bone, pe peripheral bone, t thoracic rib.

the absence of any midline center posterior to the cervical scute makes the posterior width conjectural, but I have restored it with roughly parallel sides, as appears to be the case in AM F:61110.

NUCHAL (figs. 5, 6, 14, 21)

The nuchal region is preserved in AM F:57984, AM F:61110, AM F:49141, AM F:61402, AM F:184, AM F:220, AM F:81925, and a disarticulated partial nuchal, AM F:18791. Only this last specimen shows sutures. The nuchal is broader anteriorly than posteriorly as in most turtles. The sides taper posteriorly so that the suture with the first peripheral trends posteriorly and slightly medially. In the anterior part of the nuchal/first peripheral suture, the first peripheral sends a process medially into a pocket in the nuchal. The contact with the first costal is not completely preserved in AM F:18791 but as preserved it trends irregularly posteromedially. There is a curved contact, convex anteriorly, for the first neural bone on the midline.

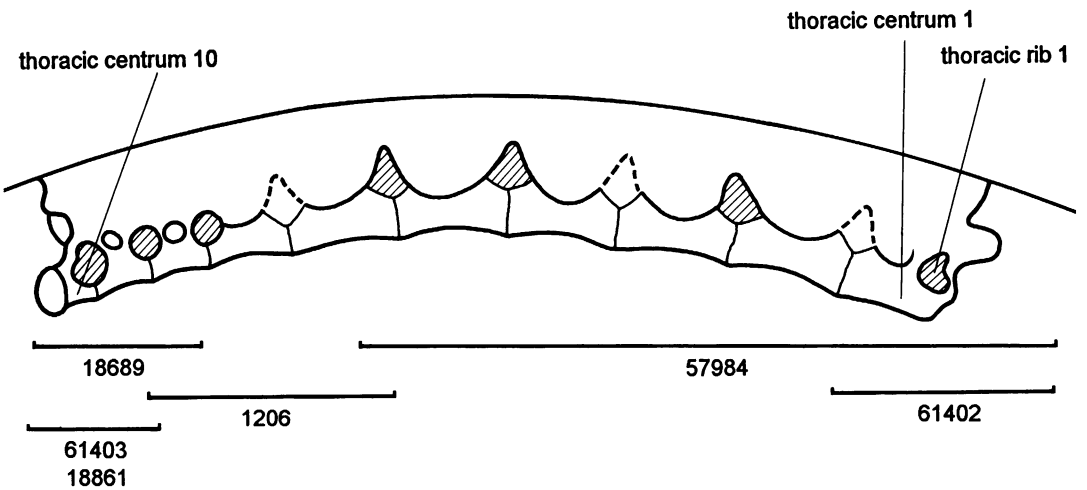


Fig. 7. *Meiolania platyceps.* Restored thoracic vertebrae in right lateral view. Numbers refer to AM F specimens that preserve portions of the thoracic vertebrae. Anterior to the right.

The dorsal surface of the nuchal (fig. 12) has shallow troughs for the sulci, except in AM F:61402 (fig. 21) where they are the more normal grooves, which delimit a small, rectangular cervical scute, the first marginal scale, and first vertebral scale. The cervical scale area is a raised convexity, thickest in AM F:184 and thinner in AM F:61402 and the other specimens. The anterior part of the scale area protrudes anteriorly in AM F:57984 and AM F:49141 but to a lesser extent in the other specimens. Although not entirely clear, the cervical scale seems to be particularly shallow in AM F:61110.

The ventral surface of the nuchal (figs. 6, 21, 22) shows two midline rugosities for the articulations of the neural spines of the last two cervical vertebrae. The anterior one for the seventh cervical is smaller and nearly circular, while the posterior articulation for the eighth cervical is larger, and more elongate anteroposteriorly. These facets and the corresponding articular surfaces on cervicals seven and eight (Gaffney, 1985a) indicate a movable contact rather than a tightly sutured one, as in *Proganochelys* (Gaffney, 1990), which has a sutured articulation between the nuchal and the neural spine of the eighth cervical but no articulation with the seventh cervical. *Ordosemys* (Brinkman and Peng, 1993a) has a loose articulation between the nuchal and the eighth cervical. Chelonioids also have an articulation between the nuchal and the eighth cervical (Gaffney and Meylan, 1988).

There is no indication of costiform processes of the nuchal bone.

First Peripheral (figs. 5, 6, 10, 12)

The region of the first peripheral is preserved in AM F:57984, AM F:49141, AM F:61402, AM F:81923, and AM F:61110, and two disarticulated partial first peripherals, AM F:18854 and AM F:18799, preserve sutural edges.

AM F:18854 is a nearly complete first right peripheral lacking only an area along the posterolateral margin. The bone forms the posterior half of the first marginal scale and the anterior half of the second marginal, which has only a shallow convexity anteriorly. There is a shallow, broad and poorly defined groove on the dorsal surface marking the first/second marginal sulcus. The contact with the nuchal is distinctive in that the first peripheral has medially directed interdigitations that fit into an embayment on the nuchal.

AM F:18799 is the lateral half of a first left peripheral showing the entire contact with the second peripheral and the large pocket on the ventral surface for the reception of a pro-

cess from the second peripheral. AM F:81923 is also a first left peripheral/first marginal area but no sutures are present.

In *Xinjiangchelys, Ordosemys,* and most turtles the first vertebral scale contacts the second marginal scale, but in *Meiolania,* as in many testudinids, a first marginal/first pleural contact prevents this.

Second Peripheral (figs. 5, 6, 10, 12)

The region of the second peripheral is preserved in AM F:49141, AM F:57984, AM F:6110, and AM F:61402. There are also some disarticulated second peripherals: AM F:184 (right), AM F:220 (left), and AM F:18858 (left). AM F:18798 may be a second (probably left) peripheral but it may also be a posterior peripheral.

Some of the second peripherals, as exemplified by AM F:18858, have a protrusion along the anterior margin covered by the second marginal scale. This protrusion ends at the sulcus with marginal three forming a step along the edge of the shell. This step can be seen in AM F:184 and AM F:220 as well as AM F:18858. AM F:61402, AM F:49141, and AM F:61110 lack this step; it is indeterminable in AM F:57984.

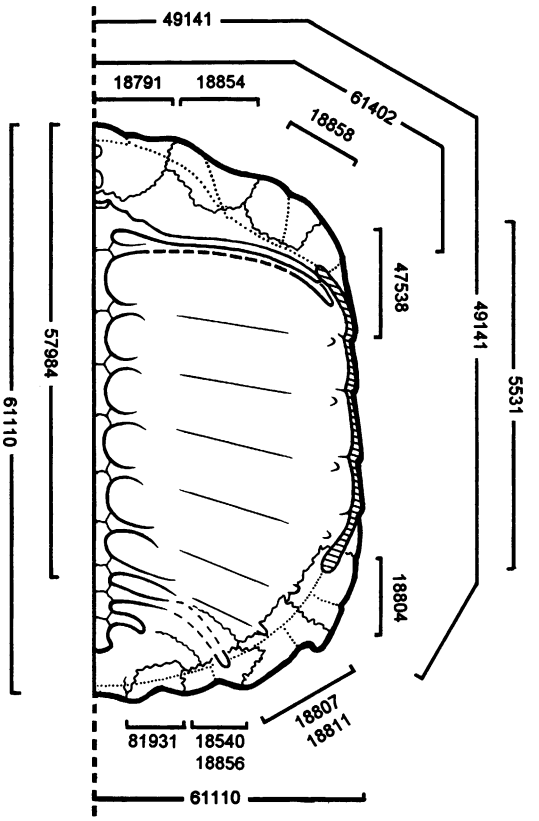


Fig. 8. Specimens used in the composite reconstruction of the carapace of *Meiolania platyceps.* All are Australian Museum (AM F) catalog numbers. For thoracic centra specimens see fig. 7.

Third Peripheral (figs. 5, 6, 14, 15, 21, 22)

There are no disarticulated third peripherals with clear sutures, but AM F:47538 appears to be a third peripheral with damaged margins, and I am using the limits of this specimen as the margins of the third peripheral in the reconstruction (figs. 5, 6). The area is also preserved in AM F:57984, AM F:61110, AM F:81927, AM F:49141, and AM F:61402. The third peripheral is a complex bone, the components of which are best seen in AM F:57984 (fig. 15) and AM F:61402 (figs. 21, 22). It is a flat but thickened bone that bears the attachment of the axillary buttress of the plastron. It also receives the distal end of the first thoracic rib, and, at least to some extent, the distal end of the first costal (= second thoracic) rib. In AM F:57984 the swollen distal end of the plastral buttress fits into a pocket on the third peripheral, and the attachment is open. In AM F:49141 (visible only in part), AM F:61402 (fig. 21), AM F:47583, and AM F:81927 the plastral contact is fused with no suture but the fusion area is recognizable. Just posterior (internal) to the buttress is the distal end of the first thoracic rib, completely free in AM F:57984 but variably fused in the other specimens. The rib shaft and rib end are only fused in part in AM F:49141. They are more completely fused in AM F:61402 and entirely fused in AM F:47538. All specimens, however, retain a pit or pocket on the inside of the buttress marking the very end of the first thoracic rib.

The shaft and distal end of the first costal

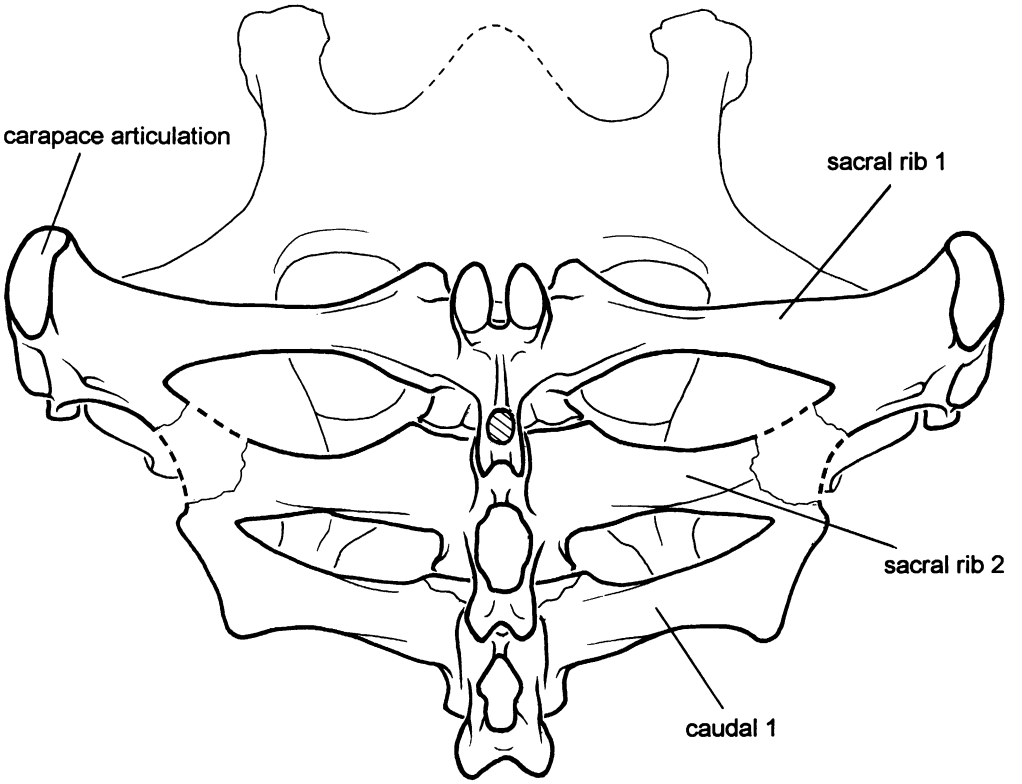


Fig. 9. *Meiolania platyceps,* reconstructed sacral vertebrae in dorsal view, based on AM F:49141.

rib (the second thoracic) are best seen in AM F:49141 (fig. 11) and AM F:61402 (fig. 21). Although the shaft of the first costal rib is completely integrated into the costal, the rib end fits into a pocket where it articulates with the peripheral. The first costal rib end is posterolateral to the end of the first thoracic rib and within and posterior to the plastral bridge attachment. The axillary buttress, then, extends well onto peripheral three but does not reach peripheral two, nor does it extend onto the costal.

The lateral extension of the first thoracic rib meets the axillary buttress in sinemydids, such as *Sinemys* (Brinkman and Peng, 1993b)

←

Fig. 10. *Meiolania platyceps,* AM F:49141, dorsal view of carapace consisting of articulated peripheral bones. See also fig. 3 for this specimen when discovered.

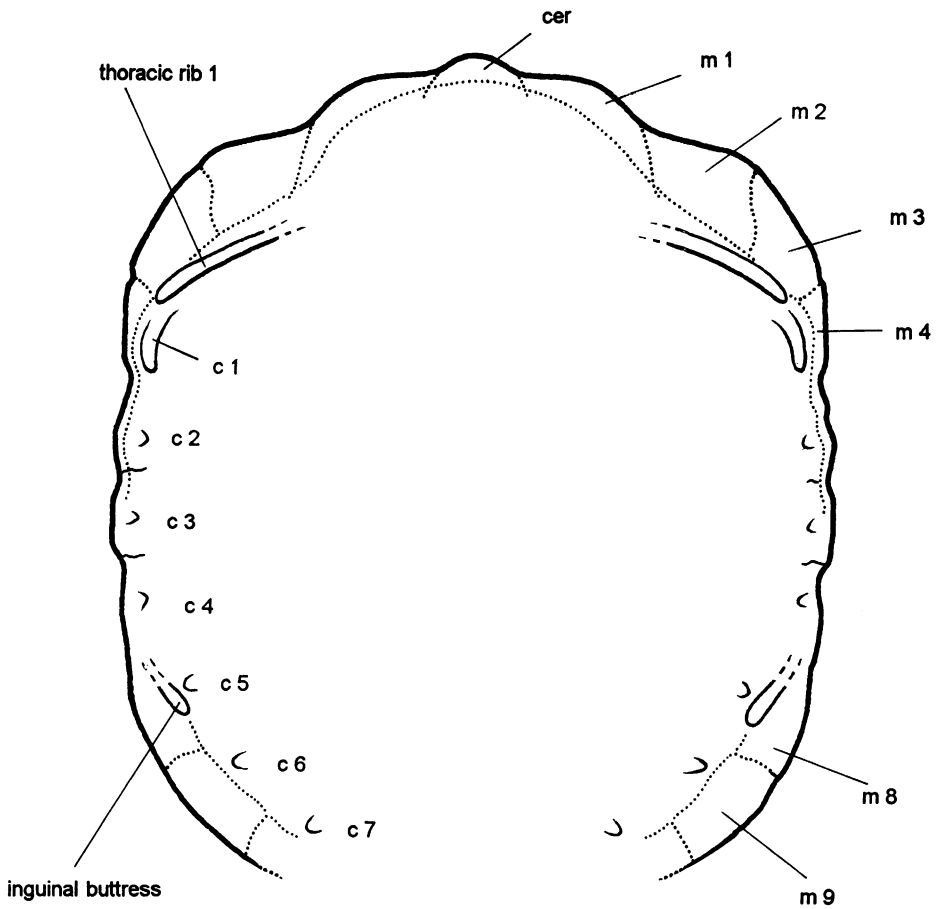


Fig. 11. *Meiolania platyceps,* AM F:49141, reconstructed dorsal view of carapace. Abbreviations: c costal rib end (showing position on ventral surface), cer cervical scale, m marginal scale.

and *Ordosemys* (Brinkman and Peng, 1993a), and is interpreted here as the primitive condition for eucryptodires. In *Ordosemys* the axillary buttress extends farther anteriorly onto the second peripheral, in contrast to *Meiolania* in which the buttress only reaches the third peripheral. The first thoracic rib is also slightly shorter in *Ordosemys* than in *Meiolania.*

Bridge Peripherals (peripherals 4–7, figs. 5, 6, 10, 11, 31)

The bridge peripherals are not well preserved on any of the *Meiolania* specimens and this description relies on fragmentary material. The best bridge series is AM F:49141, with AM F:5531 (AM F:5533, AM F:18326, AM F:5532 all being the same individual as AM F:5531), and AM F:1208 (fig. 31; Anderson, 1925, plate 30) preserving significant sections. AM F:61110 has a small area of bridge preserved on the left side, and AM F:17733 and AM F:241 are fragments of bridge peripherals. None of the specimens with bridge areas show sutures. The sulci on them are shallow, broad, and indistinct but roughly discernible, the principal landmarks being the distal ends of costal ribs.

Despite the wide variations between individuals seen in the free edges of the anterior and posterior peripherals of *Meiolania* specimens, the bridge peripherals are relatively

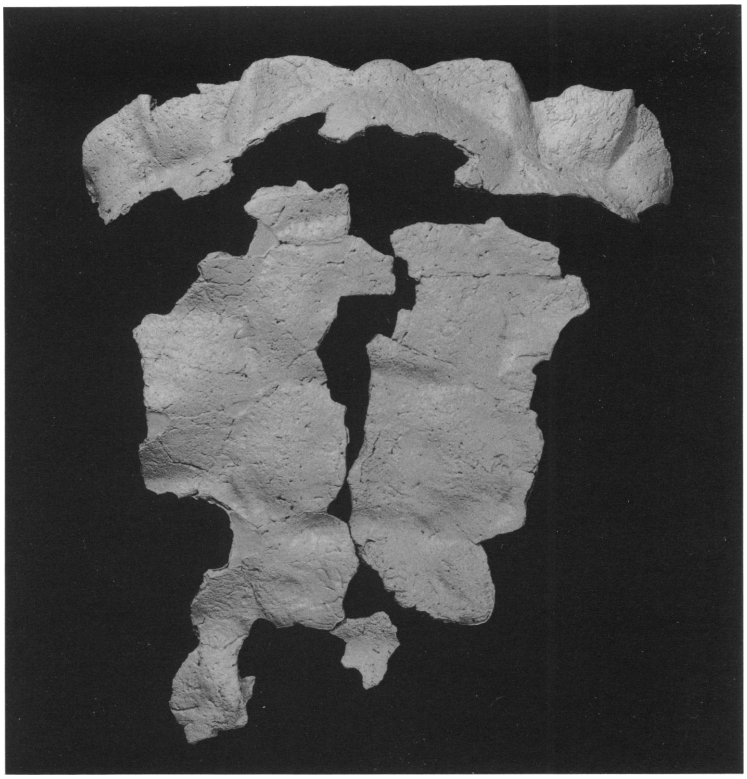


Fig. 12. *Meiolania platyceps,* AM F:57984. Dorsal view of cast of carapace.

uniform. All are C-shaped in cross section and show very obtuse angles between the broadly curved dorsal and ventral plates with a low, rugose carina running horizontally along the outside of the bridge. The carina in AM F:241 is somewhat smoother than the carinae in AM F:49141 and AM F:5531. The carina is a continuation of the free edge of the more anterior and posterior peripherals.

AM F:49141 (fig. 11) preserves the costal rib endings continuously from costal rib 1 to costal rib 5 on both sides. These rib ends presumably mark the positions of peripherals 3 through 7. There are indistinct depressions that can be interpreted as sulci in most specimens, and these are best seen on the left side of AM F:49141 and the right side of AM F:5531. The rib ends terminate in a pocket that has a foramen penetrating through to the outside surface in the right costal four rib of AM F:49141 and the right costal four rib of AM F:5531. On the left side of AM F:49141 there are cracks where the sutures should lie and they may represent these sutures. Near the left costal 3 rib of AM F:49141 there is what appears to be a costoperipheral suture but it is only visible on the internal surface. As in most other cryptodires, the bridge of *Meiolania* is made up of peripherals 4 to 7.

Seventh Peripheral (figs. 5, 6, 10, 11)

The area of peripheral 7 is preserved in AM F:61110, AM F:49141, and AM F:5531, but the only suture available is the anterior edge of AM F:18804 (fig. 23), which is a disarticulated eighth peripheral. AM F:18804 has both the sixth costal rib and the inguinal buttress of the plastron. Peripheral 7 forms the posterior part of the bridge and bears the distal end of costal rib 5. It is also the area bearing portions of marginals 7 and 8. The peripheral 7 region in AM F:61110 (figs. 17–19) is damaged and poorly preserved, AM

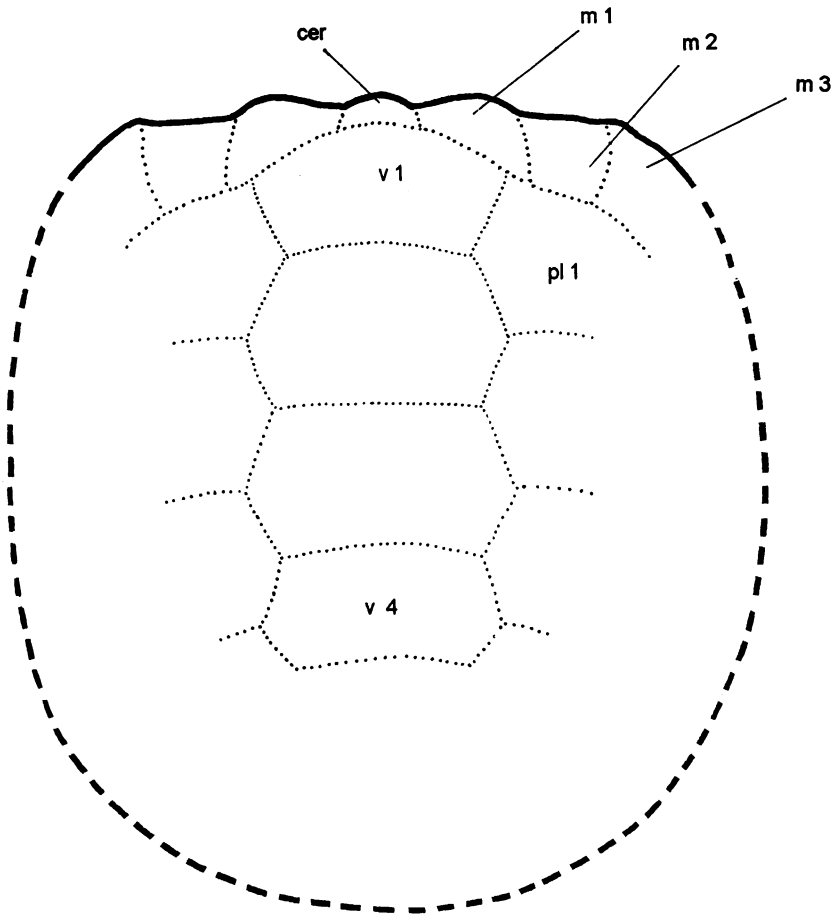


Fig. 13. *Meiolania platyceps,* AM F:57984. Reconstruction of dorsal surface of carapace. Abbreviations: cer cervical scale, m marginal scale, pl pleural scale, v vertebral scale.

F:49141 and AM F:5531 (including AM F:5533, AM F:5532, AM F:18326 which are all one individual) have no sutures but the left side of each has a series of peripherals from costal rib 1 to costal rib 6. The inguinal buttress of the plastron in AM F:5531 (fig. 6) lies roughly between costal rib ends 5 and 6 but in AM F:49141 (fig. 11) the buttress is more anteriorly placed and is nearly in contact with costal rib end 5.

On the dorsal surface, the sulcus dividing marginal scales 7 and 8 is just anterior to the position of costal rib end 5 in AM F:49141 and AM F:5531. In AM F:49141 the peripheral overhang is better developed than in AM F:5531. In AM F:61110 the peripheral overhang, the free edge outside the visceral margin, is barely developed in comparison to that of the other specimens, but a distinct ridge is clearly present at the position of the inguinal buttress. Posteriorly, around the carapace margin, a ridge (figs. 17, 18, 19) marks the visceral margin.

Eighth Peripheral (figs. 5, 6, 23)

AM F:18804 (fig. 23) is a disarticulated eighth peripheral with well-preserved anterior and posterior sutures, and attachment pits for the inguinal buttress and costal rib 6. Other specimens with this area preserved are AM F:61110 (fig. 19), AM F:49141 (fig. 11),

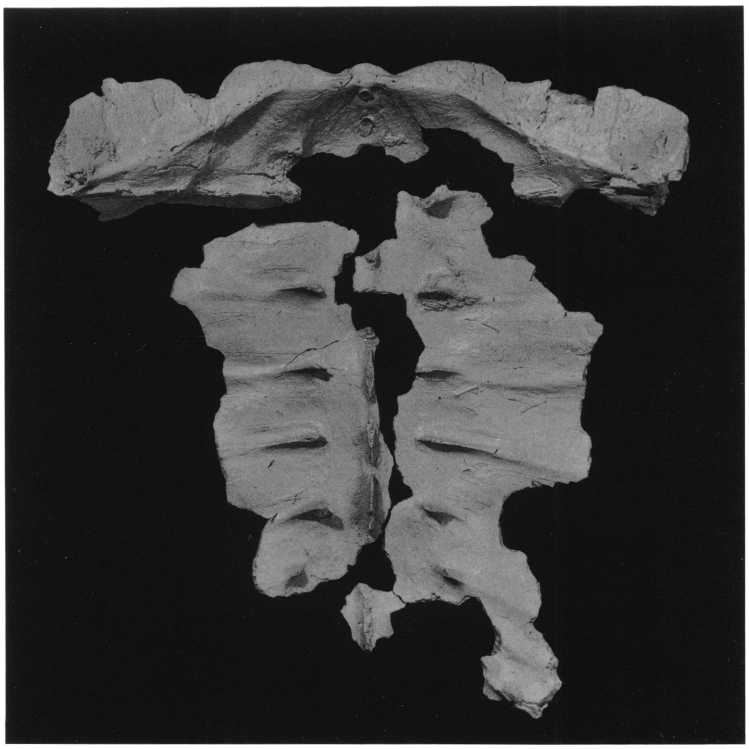


Fig. 14. *Meiolania platyceps,* AM F:57984. Ventral view of cast of carapace.

AM F:5531, AM F:18320 (same individual as AM F:18324), and AM F:81922. The ventral surface of AM F:18804 (fig. 23) shows the inguinal buttress extending from the anterior margin of the peripheral almost halfway along the length of the peripheral. There is some variation in the distance between the inguinal buttress and the end of costal rib 6. In AM F:18804, costal rib end 6 is an excavation on the posterior half of the eighth peripheral and is separated from the buttress scar by a relatively narrow area of bone. Compared with AM F:18804, in AM F:5531 the distal end of costal 6 is farther from the buttress, and in AM F:49141, costal 6 is even farther from the buttress. It is difficult to be precise in these comparisons because the actual size of the shells being compared is unknown, but I would hypothesize that AM F:49141 is a distinctly larger individual than AM F:5531 and that AM F:18804 is a slightly smaller individual than AM F:49141 but larger than AM F:5531. The variation in the relative position of costal rib end 6 to the buttress is probably due to the different sizes of individuals involved. However, the relative positions of buttress, costal rib end, and the sulci of marginals 7/8 and 8/9, are the same in all specimens, showing that the inguinal buttress ends on peripheral eight.

Ninth Peripheral
(figs. 5, 6, 11, 19, 24, 25)

Two well-preserved ninth peripherals, AM F:18807 (fig. 24) and AM F:18811 (fig. 25), are right and left mirror images of each other and possibly from the same individual. These show rib ends, sutures, and have the anterior parts of the tenth peripherals attached. Other specimens with this area preserved are AM F:61110 (fig. 19) and AM F:49141 (fig. 11), but no sutures are visible in these shells.

Peripheral 9 in *Meiolania* specimens, AM F:18807 and AM F:18811, is very distinctive, having a marked serration at the sulcus

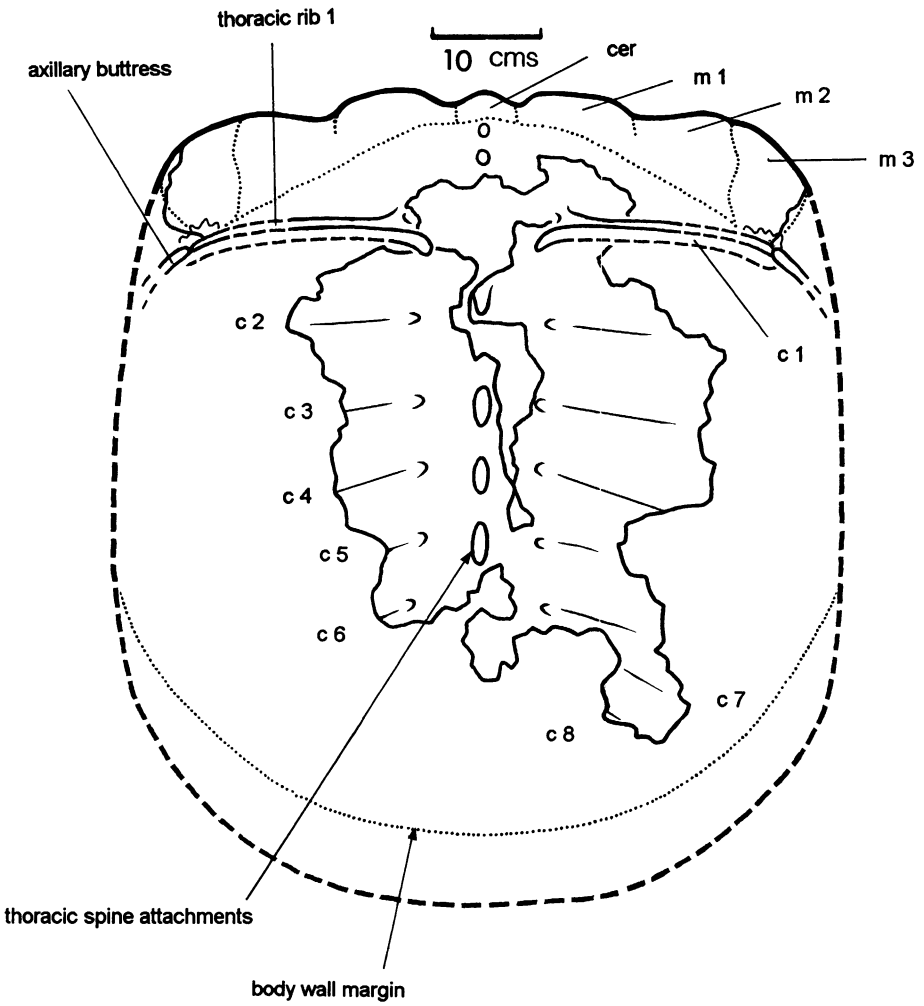


Fig. 15. *Meiolania platyceps,* AM F:57984, key to fig. 14, ventral view of carapace. Abbreviations: c costal rib trace, cer cervical scale, m marginal scale.

between marginals 9 and 10. The serration begins on peripheral 8 which flares strongly along its length. The posterior margin of disarticulated peripheral 8, AM F:18804 agrees in general size and shape with the anterior edge of AM F:18807 but AM F:18804 is thinner in cross section and the sutures do not agree, demonstrating that two individuals are represented.

The serration formed by the marginal 9/10 sulcus is nearly absent in AM F:49141. Although the edge is worn and the most lateral portion of the sulcus is broken off, the "tooth" or flare just anterior to the sulcus (i.e., the posterior part of marginal 9) in AM F:18807 and AM F:18811 is mostly absent, with only a rounded convexity present. AM F:61110 has only a shallow concavity along the peripheral edge to mark the marginal 9/10 sulcus, there is no flaring, and no "tooth" or serration, although the position of the sulcus is apparent.

The pit for the distal end of costal rib 7 is a particularly well developed tunnel in AM

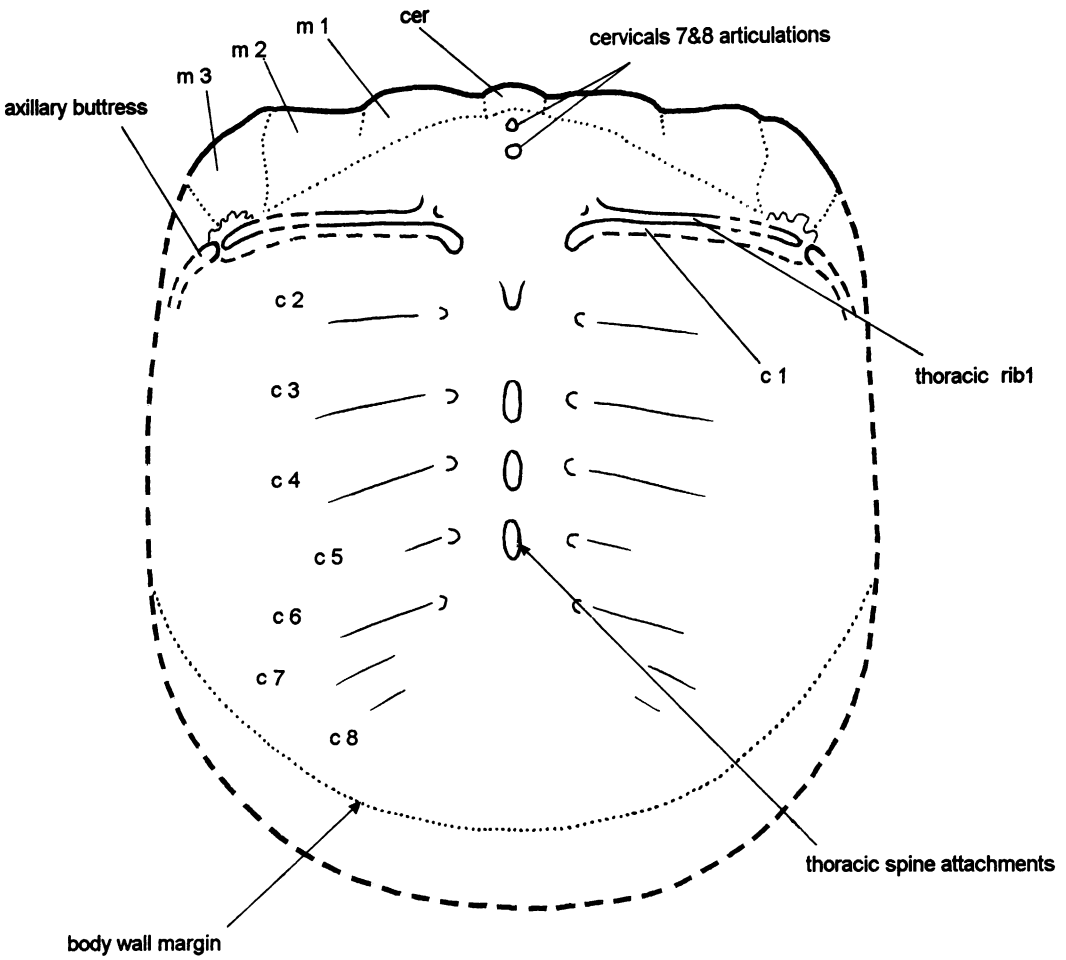


Fig. 16. *Meiolania platyceps,* AM F:57984. Reconstruction of ventral surface. Abbreviations: c costal rib trace, cer cervical scale, m marginal scale.

F:18807 and AM F:18811. Only the anterior half of this pit is preserved in AM F:49141 and it is not a tunnel, only an indentation, open ventrally.

The contact between peripherals 9 and 10, seen in AM F:18807, AM F:18811, and AM F:18540 (a disarticulated peripheral ten) is V-shaped. Proximally, it trends anterolaterally then turns sharply posteromedially to bisect the large serration cusp formed by marginal 10.

Tenth Peripheral (figs. 5, 6, 19, 24, 26)

The anterior part of peripheral 10 is preserved in AM F:18807 (fig. 24) and AM F:18811 (fig. 25), two nearly complete right tenth peripherals are AM F:18856 (fig. 26) and AM F:18540, and the region is preserved, without sutures, on both sides of AM F:61110 (fig. 19). Other probable tenth peripherals, are: AM F:81921 (right), AM F:220 (left), AM F:9056 (right), and AM F:18390 (right). The tenth peripheral has a flared edge anteriorly where it forms the posterior part of the marginal 10 serration cusp, and it narrows posteriorly where the edge is close to the body wall margin. In AM F:18807, the serration flare of marginal 9 is well defined and reversed at its cusp. The marginal 10 serration flare on this specimen, however, is rounded, not reversed, and the degree of flar-

ing is much less. While the degree of flare of the ninth marginal varies considerably among the specimens (compare AM F:61110 [fig. 19] and AM F:18807 [fig. 24], for example), the degree of flaring in the area of the tenth marginal shows much less variation. In AM F:61110 (fig. 19) the flare is present but less extensive than in any of the other specimens. Nonetheless, this relatively low "serration" is more clearly defined than any other marginal scale sulcus in AM F:61110 and allows identification of the marginal 10/marginal 11 sulcus.

Costal rib 8 is preserved for most of its length in AM F:18856 (fig. 26) and AM F:61110, but the rib head and connection to its thoracic centrum is missing in all specimens. In AM F:61110 the rib trace is recognizable only by being raised slightly, but there are no sutures. AM F:18856, however, shows sutures and preserves most of the eighth costal as well as the tenth peripheral. The costal rib in this specimen is straight and exposed ventrally where it enters the rib pit in peripheral 10. In the other peripherals the rib pit and distal rib end is covered ventrally. In AM F:18807 and AM F:18811 there is a ledge ventral to the rib pits extending along the medial edge of the body wall margin from just anterior to costal rib pit 7 to just posterior to costal rib pit 8. The peripheral 9/peripheral 10 suture lies between the rib pits. Medially, about two-thirds of the distance along the shaft of costal rib 8 is an articulation facet, small in AM F:18856 and large in AM F:81921, for the articulation of the ilium. It is not apparent in AM F:61110 but it may have been lost in preparation.

The posterior part of peripheral 10 has a straight margin and is relatively narrow. In AM F:18856 and AM F:18540 the free edge turns upwards posteriorly. In both of these specimens, as well as AM F:61110, the body wall margin is very close to the posterior outer edge of the peripheral. The region is not preserved in any other specimen.

Eleventh Peripheral (figs. 5, 6, 17–19)

The only specimen definitely preserving the posterior margin of the carapace between peripheral 10 and the midline is AM F:61110 (fig. 19), but no sutures, sulci, or other landmarks are visible. AM F:81931 possibly represents a disarticulated peripheral 11. However, the primary basis for this identification is that it doesn't look like any of the other peripherals. There is no sign of a rib pit and it differs strongly in shape from the anterior peripherals. Given the high degree of variability in *Meiolania platyceps,* anything is possible, but this specimen is quite distinct from any other *Meiolania* peripheral, and all the others that are complete enough, can be identified.

If AM F:81931 is an eleventh peripheral, then it is probably a right because there is a ridge (the body wall margin) on one side separating a visceral surface from a free edge allowing identification of the ventral surface. The body wall ridge, however, lies close to the anterior margin of the bone and does not intersect with what is preserved of the ridge on peripheral 10 in other specimens. AM F:18540, a disarticulated peripheral 10, has the body wall ridge very close to the free edge, inconsistent with the position of the body wall ridge in AM F:81931. The complimenting sutures of each bone, however, agree convincingly when aligned with the free margins. The difference in relative position of body wall ridges could be due to individual variation of the same sort seen in the posterior peripherals of AM F:61110 versus AM F:49141. The free margin of AM F:81931 has a large indentation separating two projections, the anterolateral one supporting the marginal 11 serration and the posteromedial one supporting marginal 12. There is no indication of these projections on AM F:61110, the only other specimen preserving this region.

There is no information in any specimen of *Meiolania* about pygal or suprapygal bones. The only thing that can be gleaned from AM F:61110 (figs. 17–19) is that the midline seems to have an indention, consistent with a midline sulcus separating the right and left twelfth marginals. If there is a pygal bone it would appear to have a roughly parasagittal contact with the eleventh peripheral, AM F:81931. However, AM F:81931 also has another sutural surface facing anterodorsomedially, one which is continuous with the presumed parasagittal pygal contact. This roughly triangular sutural area may be for an overlapping contact with a suprapygal, the usual anteromedial contact in the eleventh peripheral of

Fig. 17. *Meiolania platyceps,* AM F:61110, ventral view of carapace with associated postcranial elements in situ.

eucryptodires. This seems the most likely arrangement for *Meiolania* but medially meeting eleventh peripherals, or even a divided pygal, cannot at present be ruled out.

Costals (figs. 5, 6, 12–22, 26)

The costals are best seen in AM F:57984 (figs. 12–16), in which both dorsal and ventral surfaces are prepared, and in AM F:61110 (figs. 17–19), in which only the ventral surface is visible. In both specimens the sutures are fused. The costals in *Meiolania platyceps* are thin. Large pieces of costals as well as costal fragments are rare in the Lord Howe Island outcrops and also in museum collections.

There are some individual specimens of costals and parts of costals that are informative. AM F:1207 (a group number) includes a fragment with combined seventh and eighth right costal rib heads and an apparently unassociated larger area of carapace consisting of the plate portion of two costals. AM F:18773 is the proximal portion of what is probably a fifth right costal showing sutures; AM F:18800 is a posterior costal, probably the left seventh; AM F:18799 (including

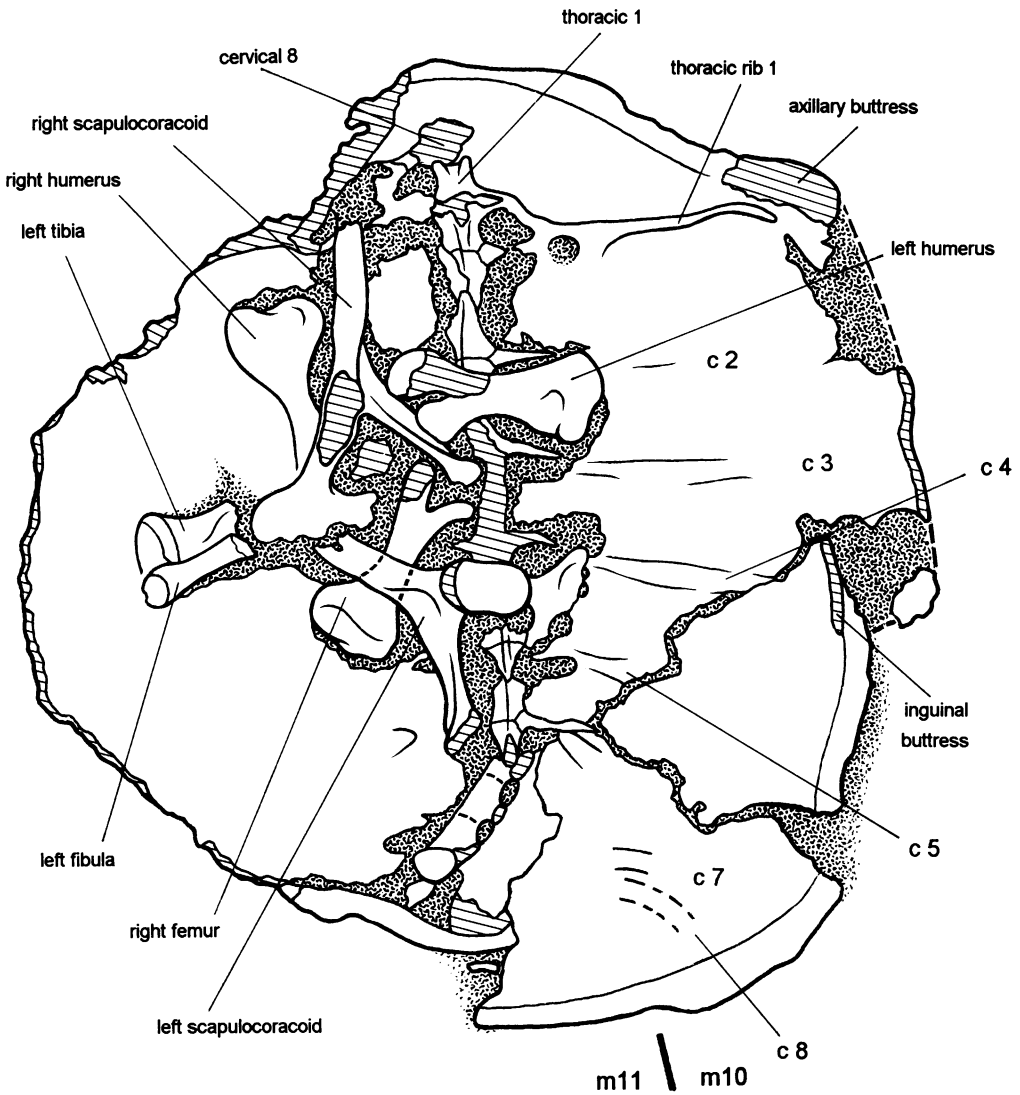


Fig. 18. *Meiolania platyceps,* AM F:61110, ventral view of carapace, key to fig. 17. Abbreviations: c costal rib trace, m marginal scale.

part of AM F:18856 which articulates with AM F:18799) consists of the plate portion of two costals; and AM F:81930 is the proximal part of costal 2, 4, or 6, with sutures.

The first thoracic rib in *Meiolania* (figs. 6, 16, 21) is very long and extends distally to lie on or close to the third peripheral, just behind the axillary buttress attachment. In *Plesiochelys* (Solothurn Museum 101) the first thoracic rib also reaches the axillary buttress, as in *Proganochelys* (Gaffney, 1990), the presumed primitive chelonian condition. In *Meiolania* the first thoracic rib may articulate with the first costal bone by a suture (AM F:57984, figs. 14, 15, 16) or by fusion (AM F:61402, AM F:61110, fig. 19), or it may be fused proximally and sutured laterally (AM F:49141, figs. 10, 11). The first costal rib trace and distal rib end are discernible in all the specimens in which this area is preserved.

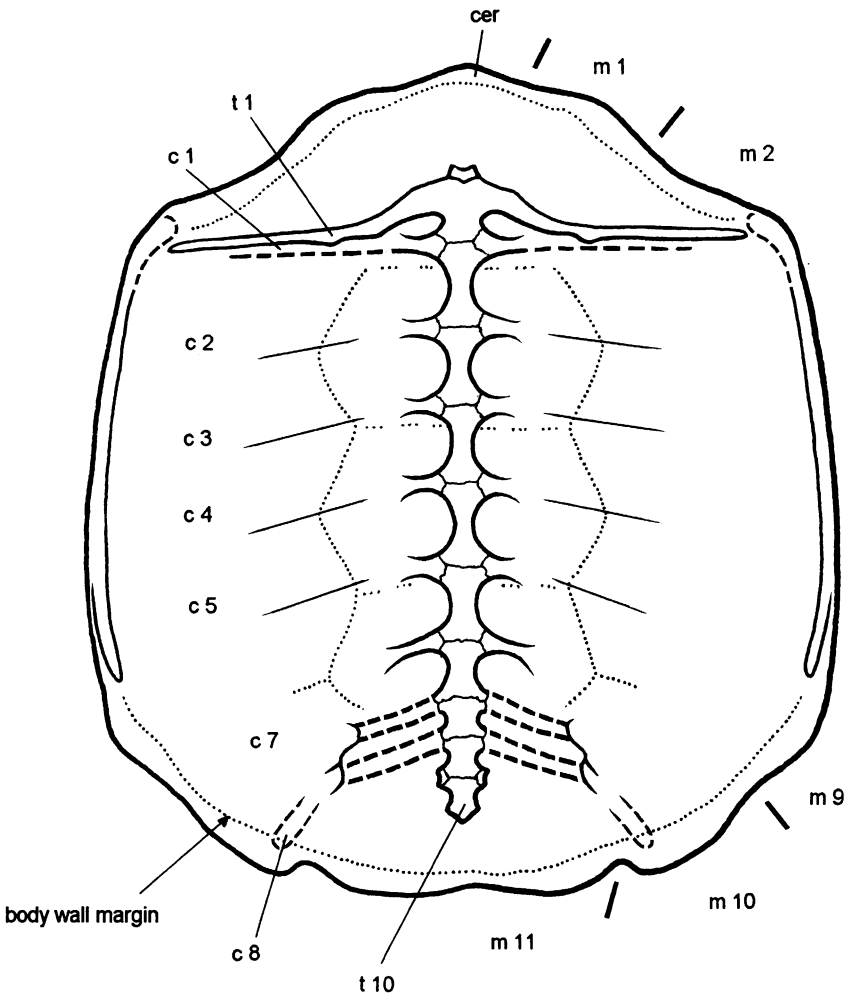


Fig. 19. *Meiolania platyceps,* AM F:61110, reconstruction of carapace in ventral view. Abbreviations: c costal rib trace, cer cervical scale, m marginal scale, t thoracic rib or centrum.

Although there are no intercostal sutures in any of the partial carapaces, there are presumably eight costals because there are eight costal rib heads, rib traces, and rib terminal ends. The rib traces of the anterior costals are nearly perpendicular to the midline, but posteriorly the rib traces trend more posterolaterally from the midline. Intercostal sutures are present on some of the disarticulated elements but due to the great range of individual variation and poor definition of scale sulci, I have been unsuccessful in identifying any of these with a particular costal in one of the more complete shells. AM F:18773, which may be a fifth right costal, and AM F:18799, which consists of two costals somewhere between the second and sixth, show intercostal sutures that are roughly parallel but seem to diverge distally, as in many turtles. The vertebral/pleural sulci are very broad and difficult to recognize on most single fragments of costals but AM F:81930 seems to bear the junction of a vertebral and two pleurals, making it a second, fourth, or sixth costal. Only the proximal part of the costal is preserved but this is one of the few elements showing a neural contact. The medial margin of this bone is a straight sutural

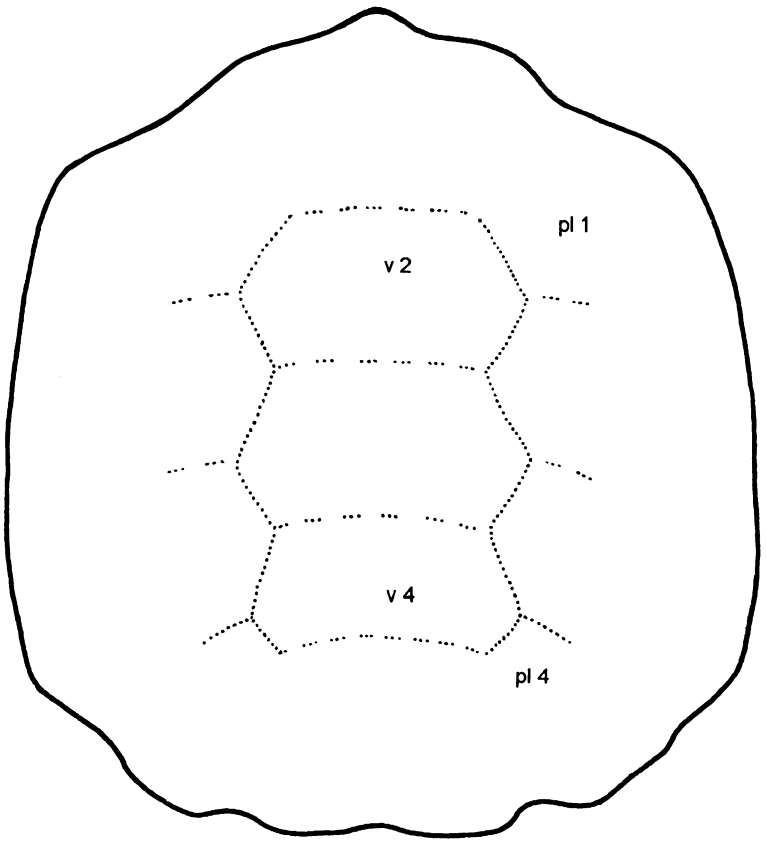


Fig. 20. *Meiolania platyceps,* AM F:61110, reconstructed dorsal view. Abbreviations: pl pleural scale, v vertebral scale.

edge that suggests that the adjacent neural is four sided rather than six sided.

The rib heads and/or rib traces of costals 7 and 8 can be seen in AM F:1207, AM F:57984 (figs. 15, 16), and AM F:61110 (fig. 19). Costal 8 itself is preserved in AM F:18800 and AM F:18856 (fig. 26). These show that the rib/costal plate attachments of costals 7 and 8 are farther from the midline than in the other costals; that is, the costo-vertebral tunnel is larger posteriorly. The costal 8 rib attachment is farther from the midline than the costal 7 rib attachment. This condition is similar to that described in *Proganochelys* (Gaffney, 1990) and also occurs in *Kayentachelys* and baenids but not in plesiochelyids, or chelydrids.

In most Polycryptodira except *Chelydra* and trionychoids (Meylan and Gaffney, 1989), the tenth thoracic rib contacts the eighth costal, often at a swollen area bearing the iliac articulation (Bojanus, 1819). This does not seem to be the case in *Meiolania.* Although it cannot be definitely determined, it is very likely that the tenth thoracic rib does not reach the eighth costal. There is no *Meiolania* carapace with all costal and thoracic ribs preserved without damage, but AM F:61110 has all eight costals and costal ribs on one side or the other, and the thoracic centra from 1 to 10 are present. Unfortunately, the tenth thoracic rib is broken off close to its centrum and the visceral surface of the eighth costal was somewhat damaged during preparation so the condition of the tenth thoracic rib is not determinable from this specimen alone.

Fig. 21. *Meiolania platyceps,* AM F:61402, left anterolateral portion of carapace. **Upper,** dorsal view; **middle,** ventral view; **lower,** anterior view.

However, AM F:18856 (fig. 26) is a well-preserved eighth costal plus tenth peripheral, and it shows the eighth costal rib head and trace with no articulation for a tenth thoracic rib. In both this specimen and AM F:61110 the rib shaft of the eighth costal has portions of a suture between it and the costal plate, initially suggesting that this was the tenth thoracic rib. AM F:18856 has intercostal sutures and it is clear that there is no other rib head or trace (i.e., an eighth costal rib) on this bone.

AM F:18800 is another eighth costal that has sutures. It agrees with AM F:18856 in the anterior intercostal suture, which in *Meiolania* differs from the usual cryptodiran condition. These two specimens show that the ventral expression of the intercostal suture between costals 7 and 8 is straight but the dorsal suture is S-shaped because the eighth costal overlaps the seventh costal medially and the seventh costal overlaps the eighth costal laterally.

The tenth thoracic vertebra (figs. 6, 7) is preserved in AM F:61110, AM F:18689, AM F:61403, AM F:18861, and AM F:372. Of these, only AM F:372 has the rib preserved, which is broken laterally. However, the most complete rib, the left, tapers strongly, and if it were extrapolated laterally, it would terminate before reaching the costal. All of the tenth thoracics show a fused or ankylosed anterior central articulation with the eighth costal centrum (= ninth thoracic) and a strongly convex, hemispherical posterior central articulation with the first sacral.

AM F:1207 (a group number) includes a proximal fragment of costals 7 and 8, bearing the rib head bases. These show in cross section that there is a thickened area of bone centered approximately on the costal 6/costal 7 suture. AM F:57984 also shows this feature which is expressed as a low convexity on the dorsal surface in the anteromedial region of the fourth pleural scale (figs. 12, 13).

Neurals

Unfortunately no neural bones with sutures are preserved. Neurals are presumably present in AM F:57984 (figs. 12–16) and AM F:61110 (figs. 17–20). A costal bone, AM F:81930, shows a medial suture with a neural. This is the only evidence that neurals were present in *Meiolania.*

Carapace Scales (figs. 5, 10–13, 19–25)

The scale areas of *Meiolania* vary a great deal in degree of expression among the preserved shells. In AM F:61402 (figs. 21, 22) the sulci are neatly incised and discrete as in

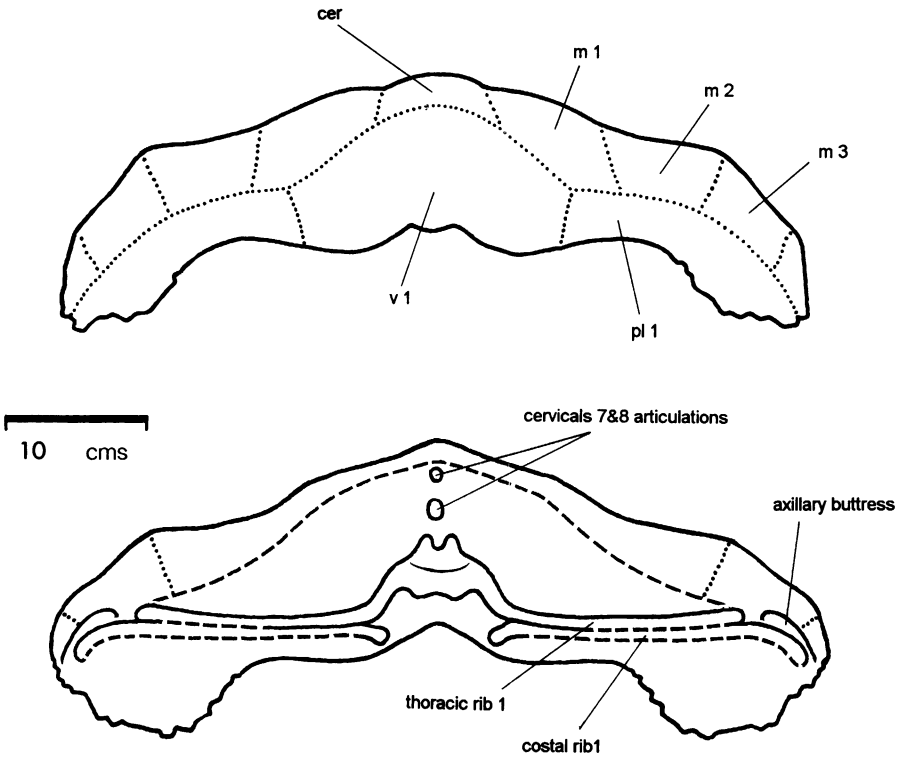


Fig. 22. *Meiolania platyceps,* AM F:61402, reconstructed anterior portion of carapace in dorsal view (upper) and ventral view (lower). Abbreviations: cer cervical scale, m marginal scale, pl pleural scale, v vertebral scale.

most other turtles, but in the other *Meiolania* shells, such as AM F:49141 (fig. 10) and AM F:57984 (fig. 12), the sulci are shallow grooves, often not clearly incised. The cervical scale and the anterior marginals, however, are clear in all specimens with this area preserved.

The cervical scale of *Meiolania* is four-sided, particularly as seen in AM F:18791 and AM F:61402 (figs. 21, 22). The anterior or free margin is curved, convex anteriorly, best developed in AM F:57984 (figs. 12, 14). The lateral sulci converge anteriorly. The cervical scale area is protuberant and raised in AM F:57984, AM F:18791, and AM F:49141 (figs. 10, 11), but it is flat in AM F:61402 (figs. 21, 22).

The posterior sulcus of the first marginal continues posterolaterally from the posterior margin of the cervical scale to reach the sulcus separating the first vertebral from the first pleural. The first marginal is five sided, contacting both first pleural and first vertebral. AM F:61402 (figs. 21, 22) shows this arrangement particularly well. In AM F:57984 (fig. 12) the sulcus expression is less pronounced and the scale appears to be more triangular. The area of the first marginal is upturned along the anterior margin in AM F:61402 (fig. 21). But in AM F:57984 and AM F:49141 the edge extends anteriorly as a flat plate. AM F:57984 and AM F:49141 also differ from AM F:61402 in having a very thick, raised lateral margin to the scale area, completely absent in AM F:61402. The separation between the first marginal and the second marginal in AM F:57984 and AM F:49141 is a rounded step from the higher plane of the first marginal to the lower plane of the second. In AM F:61402 both marginals are on the same level.

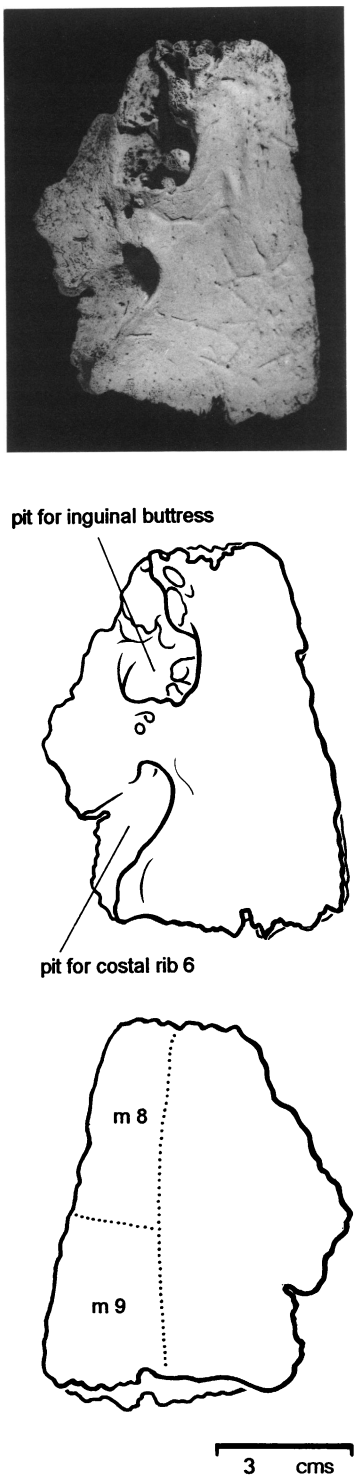


Fig. 23. *Meiolania platyceps,* AM F:18804, left peripheral 8. **Top and middle,** ventral view; **bottom,** dorsal view. Abbreviation: m marginal scale.

In AM F:57984 (fig. 12) and AM F:49141 (fig. 10), the area of marginals 2 and 3 form a single, large extension anterior to the body wall margin that is thick but flat in cross section. This extension, the free edge of the shell, is developed to a lesser extent in AM F:61402 (fig. 21) and it is absent in AM F:61110 (fig. 19). This degree of variation is very unusual within a species. The sulcus between marginals 2 and 3 is broad and low, except in AM F:61110 where it is better defined. AM F:18858, AM F:184, and AM F:220 show a step or protrusion where this sulcus meets the margin, but this is not seen in AM F:49141 (fig. 10) and AM F:61402 (fig. 21); it is not determinable in AM F:57984. Marginal 4 is the transition from a relatively flat peripheral to the obtuse angle of the bridge peripherals.

The more posterior marginals are described in the section on peripherals.

The vertebral and pleural scales in *Meiolania* (fig. 5) are best seen in AM F:57984 (figs. 12, 13), AM F:61110 (figs. 19, 20), and AM F:61402 (figs. 21, 22). In AM F:61110 only the visceral surface is visible, the dorsal surface is still encased in matrix, but the sulci outlining vertebrals 2, 3, and 4, are visible as ridges on the visceral surface (fig. 19). This is also the condition in AM F:57984 which has both surfaces visible showing that the carapacial bone is relatively thin, the sulci are broad, although ill defined, and relatively deep, producing the ridges on the visceral side. This results in the central part of the carapace consisting of broadly undulating bone (fig. 12). Possibly, the shell of *Meiolania* had thick scales, as in some Recent testudinids, which also have thin, undulating costal bones.

Only the first four vertebrals of *Meiolania* are known (fig. 5). They are wider than long, wider than in most Polycryptodira (*sensu* Gaffney and Meylan, 1988) but not as wide as in *Kayentachelys* or *Proganochelys.* The first four vertebrals are about equal in width, the first three are equal in length with the fourth vertebral slightly shorter than the others. The first vertebral differs from the others in its anterior margin which is convex anteriorly rather than straight.

Only the first four vertebral/pleural sulci are preserved. Small sections of the medial parts of the interpleural sulci for pleurals 1 to 4 are visible in AM F:57984 (figs. 12, 13).

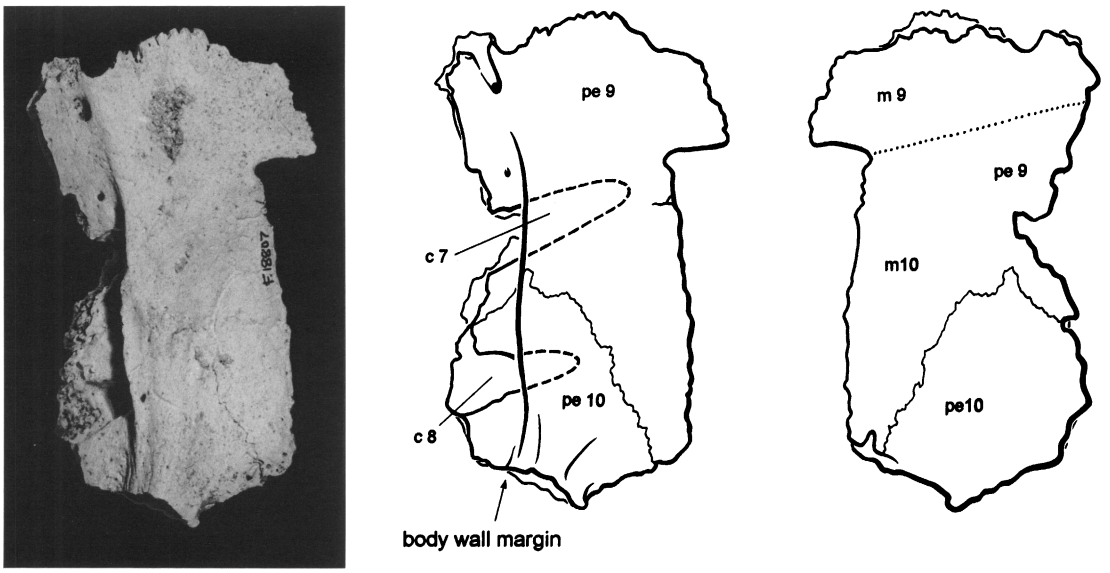


Fig. 24. *Meiolania platyceps,* AM F:18807, left peripherals 9 and 10. **Left and center,** ventral view; **right,** dorsal view. Abbreviations: c costal rib termination pits, m marginal scale, pe peripheral bone.

On the anterior peripherals preserved, the marginal/pleural sulci seem to lie close to or on the peripheral/costal sutures, or slightly more on the peripherals. There are no pleural sulci identifiable on the bridge areas preserved but the posterior peripherals show the marginal/pleural sulci lying well onto the peripherals.

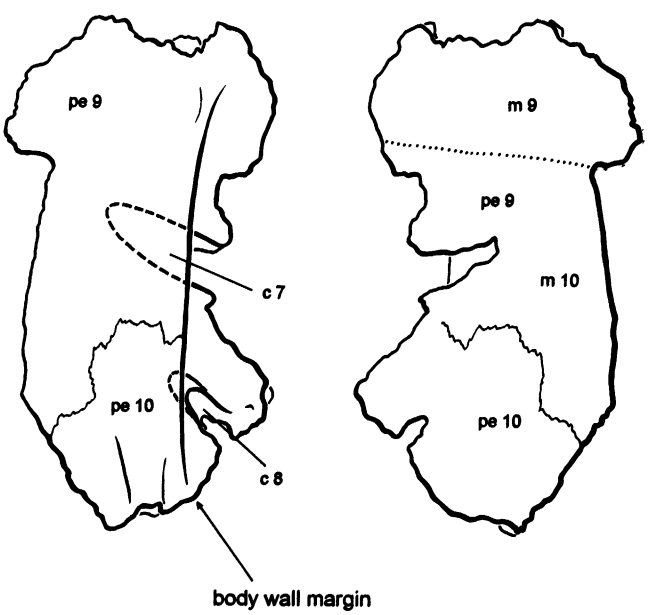
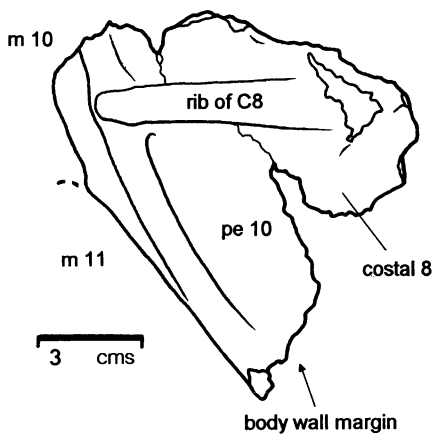


Fig. 25. *Meiolania platyceps,* AM F:18811, right peripherals 9 and 10. **Left,** ventral view; **right,** dorsal view. Abbreviations: c costal rib termination pit, m marginal scale, pe peripheral bone.



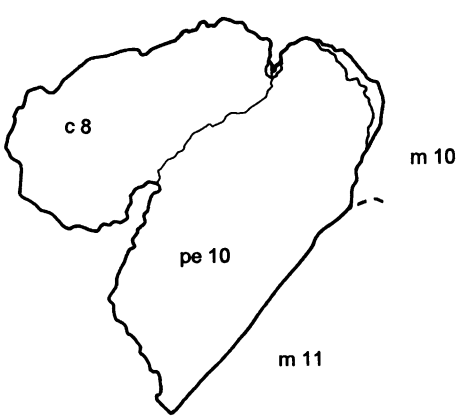


Fig. 26. *Meiolania platyceps,* AM F:18856, right costal 8 and peripheral 10. **Upper and middle,** ventral view; **lower,** dorsal view. Abbreviations: c costal bone, m marginal scale, pe peripheral bone.

Thoracic Vertebrae
(figs. 6, 7, 17–19, 21, 22)

The first thoracic vertebra (figs. 6, 7) is present in AM F:57984, AM F:61402 (figs. 21, 22), AM F:61110, AM F:49141, AM F:213 (two first thoracics from two individuals), and AM F:1200.

The first thoracic vertebra has a concave central articulation anteriorly, wider than high, and a platycoelous articulation posteriorly. The first thoracic vertebral rib is solidly fused to the centrum. The rib is very long, extending to the axillary buttress of the plastron (fig. 6). The free part of the rib from centrum to costal is stout and heavier than the other thoracic ribs and has an anteriorly directed spur, near the costal attachment, for the articulation of the dorsal process of the scapula. The appearance of the bone surface on the spur, carapace, and scapula, suggests that a synovial joint type of articulation was present.

The prezygapophyses of the first thoracic are very close together and are fused ventrally, allowing very little movement of the eighth cervical. The prezygapophyses are virtually an anterodorsally opening pocket on the neural arch of the first thoracic. The neural spine is a flat blade fused to the carapace as in the other thoracic vertebrae.

The centrum of the first thoracic is roughly V-shaped in cross section, the midline keel is more rounded than in the immediately posterior thoracics but not flattened as in the most posterior thoracics. In ventral view the centrum is constricted in the middle and expanded at either end for the rib articulations and the neural canal is open for the vertebral nerves. The neural canal is nearly circular in cross section. The rib of the second thoracic vertebra has a synarthrosis with the posterior part of the first thoracic vertebra, as in all turtles. The articulation with the second thoracic centrum is also a typical vertical synarthrosis.

AM F:61402 (figs. 21, 22) is the best preserved first thoracic vertebra with its associated rib and carapace attachment. The vertebra is slightly crushed and displaced but comparisons with AM F:61110, the only other specimen preserving this region intact, sug-

gest that there has been very little displacement. The rib of the first thoracic curves posterodorsolaterally to contact the costal wall posterior to the front of the centrum. The rib of the first thoracic is either fused or suturally attached to the overlying costal depending on the specimen, but the rib remains as a bladelike ridge, distinct from the costal. The first costal rib (the second thoracic rib) is attached to the costal just posterior to the first thoracic rib attachment, both being on the same thickened region of costal one.

The thoracic centra for the vertebrae from the first costal (second thoracic) to the last thoracic (thoracic 10), are present in their entirety only in AM F:61110 (figs. 17–19) and they are not well preserved. AM F:57984 has at least portions of six thoracic centra (fig. 7) and AM F:1206 has a series of three. AM F:1206 probably consists of costal ribs 5 through 7, that is, thoracic vertebrae 6 through 8. From AM F:61110 and some of the disarticulated specimens, it can be seen that costal rib 7 attaches to the costal plate more laterally than in the anterior costals and that the costovertebral tunnel of costals 7 and 8 is relatively large (as in other relatively primitive cryptodires). This is the case in AM F:1206. In this specimen, costal rib 5 is very deep and flat, with only a small slit for the costovertebral tunnel, costal 6 has a larger opening with the rib less bladelike, and costal 7 has a nearly circular free rib and a large costovertebral tunnel.

The second thoracic is known from AM F:61110 and a small section in AM F:57984. AM F:61110 and AM F:57984 also contain thoracics 3 through 5, although 5 in AM F:61110 is mostly covered. AM F:1206 overlaps slightly with AM F:57984 on the fifth thoracic and continues posteriorly with the sixth and seventh thoracics. AM F:61110 also has thoracic 6 and part of 7. The eighth thoracic is present in AM F:232 (part), AM F:18689 (part), and AM F:61110 but thoracics 9 and 10 are in AM F:61110, AM F:18689, AM F:232, AM F:18861, and AM F:61403. AM F:372 is a thoracic 10.

Thoracic centra 2 through 7 are similar to each other in shape and are about the same in length. They are roughly U-shaped in cross section, although the thoracics of AM F:61110 have a more acute ventral keel than the others. The centra are all constricted to some extent and are expanded at the rib attachments. The neural canal in cross section is an elongate oval, higher than wide, with the roof flattened by the neural spine except in the most anterior and most posterior vertebrae. The vertebral nerve exits have curved ventral edges formed by the centra and, for thoracics 5 through 7 (and probably 2 through 4) straight dorsal edges formed by the ventral edges of the neural spines. Thoracics 6 and 7 have smaller openings and are similarly shaped to the more anterior thoracics, but thoracics 8 and 9 (as seen in AM F:61110) and AM F:18861) differ markedly from all the other thoracics by having circular foramina for the nerve exits (fig. 7).

The thoracic centra all articulate with each other by vertical ankyloses or complete fusion. Where sutures are visible, the thoracic rib heads articulate by means of roughly triangular ankyloses with three facets (one for the neural arch and one for each vertebra). Although there is a tendency for the posterior rib articulation area on each centrum to be slightly smaller than the anterior rib articulation, all the rib heads from thoracics 1 through 7 have well-developed articulations on two centra.

The keel along the ventral edge of the thoracics is lost posteriorly and thoracic 10 is nearly flat on its ventral surface. Thoracic 10 has a free rib, unattached to a costal, and this can be seen in AM F:372. This rib tapers strongly as it extends from the centrum, to a small, flat blade. The end is broken in AM F:372 so its extent is not known, but its small size suggests that it was not very much longer. The last thoracic, the tenth, has a nearly hemispherical, convex posterior central articulation surface. It is wider than high and fits into the deep concavity of the first sacral. The neural spine of the tenth thoracic has nearly vertical postzygapophyses formed on a swelling of the neural spine.

Sacral Vertebrae (fig. 9)

Meiolania has two sacral vertebrae and in some specimens a first caudal that is fused to them. There is a great deal of variation in the

pattern of the central articulations. The available material is: AM F:49141 (sacrals 1, 2, and first caudal, all fused together, most ribs preserved, the best specimen and figured in fig. 9), AM F:18687 + 18703 (sacrals 1 and 2 from same individual, used in 1982 AMNH cast), AM F:9067 (sacrals 1 and 2 fused), AM F:18691 (sacral 2), AM F:18695 (probably a first caudal but fused anteriorly to the sacrum), AM F:1201 (sacral 1), AM F:367 (probably sacral 2), AM F:206 (probably a first caudal), and AM F:10780 (probably sacral 1).

The sacral centra are distinctly wider than high, with a flat ventral surface and no hemal spine swellings. The rib bases are very large (AM F:1217) and occupy most of the lateral part of the centrum. The rib of the first sacral lies entirely on the centrum but the rib of the second sacral extends onto the first sacral to a small extent. The anterior central articulation of the first sacral is a deep, hemispherical concavity for the articulation of the tenth thoracic central articulation. The depth and extent of this articulation is not duplicated by any of the other *Meiolania* vertebrae. The central articulation between sacrals 1 and 2 is a vertical synarthrosis in AM F:49141, AM F:18687 + 18703, AM F:9067, and AM F:208, but in AM F:1217, a second sacral, the articulation is somewhat concave and may not be a synarthrosis. AM F:10780 has a deep anterior concavity, as in all other first sacrals, but it has a formed, convex posterior central articulation. The convexity is irregular but it still differs markedly from the other specimens. AM F:10780 is best interpreted as a first sacral, with an anomalous posterior articulation, but it could also be interpreted as a second sacral with an anomalous anterior articulation. In any case, of the seven preserved first/second sacral articulations, two are anomalous in being partially or fully formed rather than synarthritic. I interpret this as individual variation.

The prezygapophyses of the first sacral are close together but do not meet and are nearly vertical. The postzygapophyses of the first sacral are small and placed at the base of the neural spine and are only slightly separated from the neural spine. The matching prezygapophyses of the second sacral are small, close together, but are not joined. The articulation between zygapophyses, visible in AM F:459141, AM F:9067, and AM F:18687 + 18703, is not synarthritic.

The neural arches of the sacrals enclose a circular neural canal and a pair of round, lateral foramina between the arches for the spinal nerves. The neural spine of the first sacral is broken off in all specimens. The neural spine of the second sacral, present in AM F:49141 and AM F:9067, is a stout blade that rises above the level of the zygapophyses and has a posteriorly inclined, flat articulation surface on the top where it contacts the carapace.

The sacral ribs can be seen in part in AM F:9067, AM F:18687 + 18703, and are most complete in AM F:49141. Distal ends of the ribs are preserved in AM F:81949 (a right pelvis). As in all turtles, the first sacral rib is the strongest, being particularly larger in AM F:18687 + 18703 and AM F:9067, but in AM F:49141 the second rib joins it as a small projection posteromedially. In AM F:49141 (fig. 9), however, the second rib is large distally where it is broken off, and the nature of the contact, although not preserved, would appear to be much larger.

The posterior central articulation of the second sacral shows a lot of variation. In AM F:18703 + 18687, AM F:208, AM F:1217, and AM F:18691, the centrum is a shallow concavity, wider than high. But in AM F:9067 the articulation is a rounded convexity and in AM F:49141 (fig. 9) the first caudal and the second sacral are fused in a vertical ankylosis. The shallow convexity of the anterior central articulation of the first caudal AM F:61409 (Gaffney, 1985a) suggests that individual was also concave in the second sacral, but AM F:18695 is another first caudal (based on haemal spine swellings) like AM F:49141, that has an ankylosis as its anterior central articulation. In AM F:49141 (fig. 9) the rib of the fused first caudal is thinner but otherwise about the same size as the second sacral rib. The first caudal rib expands distally and is fused anterolaterally to the second sacral rib. The first caudal rib has a short spur or projection posterolaterally. The only other first caudal with a rib is AM F:61409 (Gaffney, 1985a: fig. 14) and this rib, although

similar to AM F:49141 proximally, appears to taper off and end short of the rib in AM F:49141.

AM F:211 is an asymmetric vertebra that is probably a pathologic first caudal. The anterior central articulation is very similar to that in AM F:61409 and is the basis of the identification. But the posterior articulation is convex also and the left hemal swelling is enlarged into what looks like more of a hemal arch. The two anomalies together produce an unusual vertebra; but finding a biconvex first caudal emphasizes the variation in this series of vertebrae.

PLASTRON (figs. 27–31)

Material available: The anterior lobe of the plastron in *Meiolania platyceps* is complete only in AM F:18775, but useful portions are preserved in AM F:923, AM F:64434, AM F:1208, AM F:5522, AM F:49141, AM F:57984, AM F:18323, and AM F:18256. Some sutures are visible in AM F:18256, AM F:57984, AM F:923, and AM F:1208, but in most specimens the sutures are fused.

The epiplastron (fig. 27) is a paired, curved element, meeting on the midline at the front of the plastron and forming a dorsal process. None of the specimens show a midline suture, but in AM F:18256 there is a transverse entoplastron/epiplastron suture on the dorsal surface and a more jagged but also transverse suture on the ventral surface. These show that the entoplastron is not exposed at the front of the plastron. The epiplastra have only a narrow contact in ventral view and a broader contact dorsally. The sloping nature of the epiplastra/entoplastron contact is visible in AM F:18256. The epiplastron tapers posterolaterally and is actually separated along the suture from the hyoplastron distally in AM F:923 and AM F:1208. The suture is the same on the dorsal and ventral surfaces.

The epiplastra of *Meiolania* form a dorsal process on the midline (fig. 27) that extends posterodorsally over the entoplastron. This process is preserved in AM F:49141, AM F:57984, AM F:923, AM F:1208, AM F:18256, and is most complete in AM F:18775. The process is apparently a "stop" or base for the acromion process of the scapula, which articulates with the entoplastron. In contrast to the dorsal processes of the epiplastra in *Proganochelys* and *Kayentachelys,* which are paired processes not articulated to the scapula, this process in *Meiolania* is a single, unpaired, midline process. In AM F:18775 and AM F:57984, the dorsal part of the process bifurcates in the direction of the scapula, and it is quite possible that this bifurcation was present in the other plastra as well. The degree of development of the process in *Meiolania platyceps* varies from relatively narrow in AM F:49141 to relatively broad in AM F:18775 and AM F:18256.

The entoplastron of *Meiolania platyceps* (fig. 27) has distinct sutures only in AM F:18256, AM F:1208 (fig. 31), and AM F:57984. It is roughly oval with a long posterior median process. The entoplastron separates the hyoplastra anteriorly on both dorsal and ventral sides and the median process extends posteriorly over the medially meeting hyoplastra. The extent of the median process is not determinable but it is unlikely to be as long as in *Proganochelys.* The contacts of the entoplastron with epiplastra and hyoplastra, as seen in AM F:1208 (fig. 31) and AM F:18256 are strongly interdigitating.

The dorsal surface of the entoplastron (fig. 27) has paired, articular facets for the articulation of the scapulae. These facets are preserved in AM F:18775 (fig. 27), AM F:1208 (fig. 31), AM F:57984, AM F:49141, AM F:18256, AM F:923, and AM F:18323. The facets are raised tubercles covered by articular contact bone and are wider than long in dorsal view. A scapular fragment is preserved in articulation with these facets in AM F:923.

The anterior lobe of the plastron (fig. 27) in ventral view shows a distinctive, paired, gular projection in most specimens. The gular projection is best developed in AM F:18775 in which it is acuminate but not as extensive as in *Proganochelys.* The gular is more rounded in AM F:49141 and AM F:923, but in AM F:18323 the gular scute area does not project at all.

Meiolania lacks the more common, neatly incised scale margins seen in the plastron of most turtles. The gular scute (fig. 27) is bordered posteriorly by a broad, shallow trough, deepest laterally and merging medially with

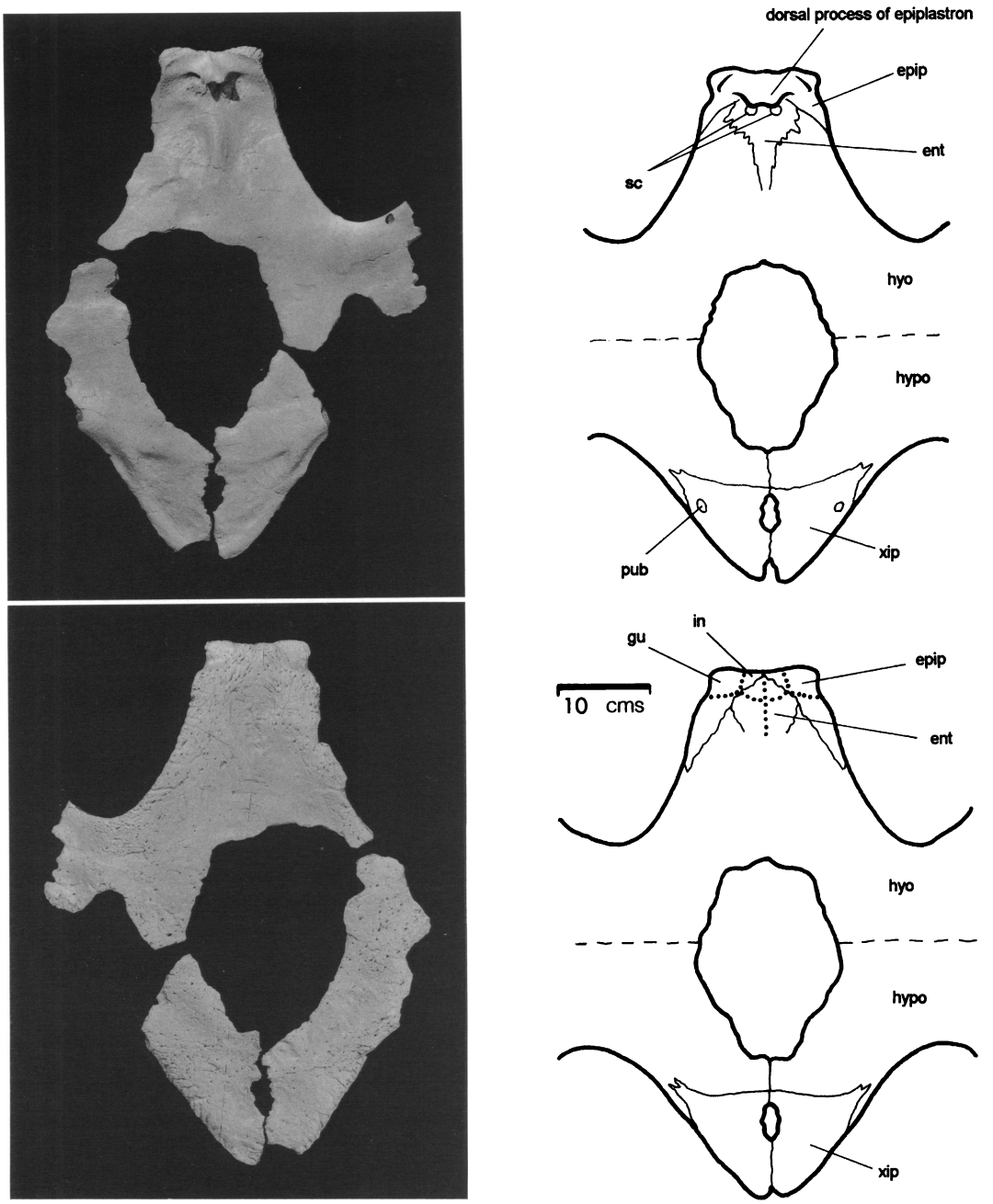


Fig. 27. *Meiolania platyceps,* AM F:18775, plastron in dorsal view (upper row) and ventral (lower row) view. Reconstructions on right side are composites that include sutures from other specimens. Abbreviations: ent entoplastron, epip epiplastron, gu gular scale, hyo hyoplastron, hypo hypoplastron, in intergular scale, pub articulation surface for pubis, sc articulation surface for scapula, xip xiphiplastron.

Fig. 28. *Meiolania platyceps,* AM F:18775, as restored for articulation with carapace of AM F:57984 in reconstructed skeleton. Bridge areas restored from AM F:49141, AM F:1208, and AM F:5522-5523.

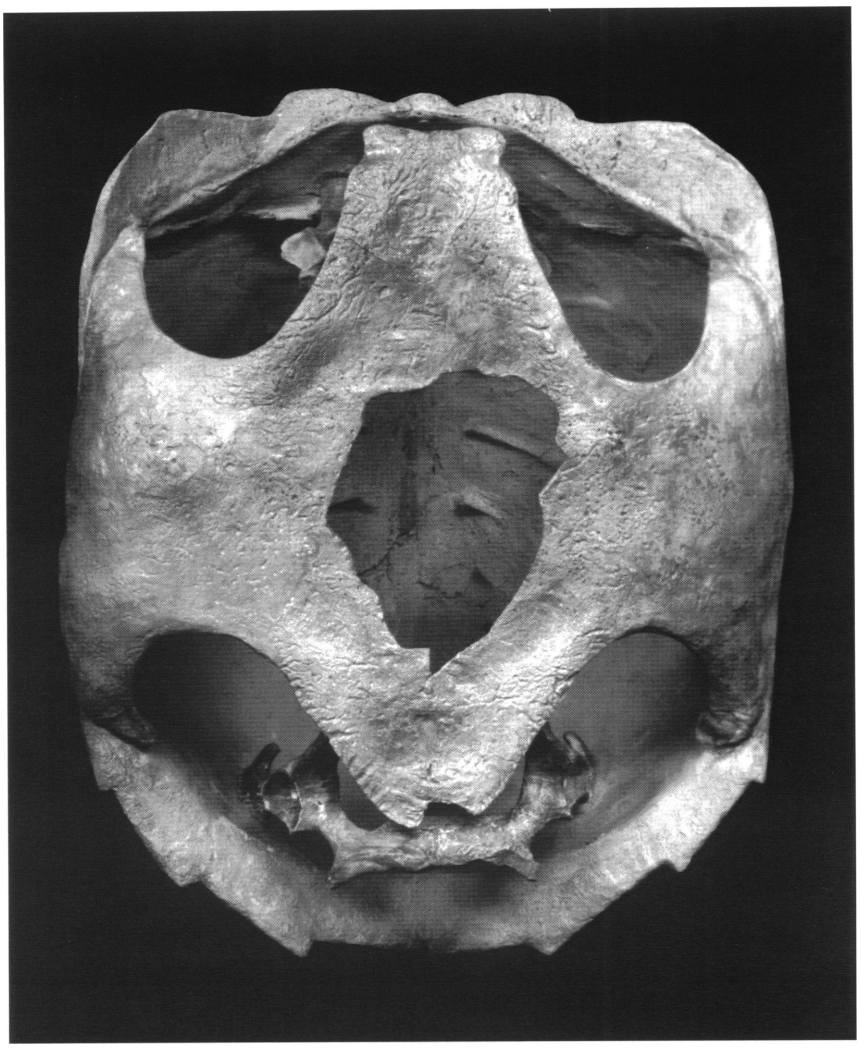


Fig. 29. *Meiolania platyceps,* reconstructed shell with limb girdles in ventral view. Carapace is primarily AM F:57984, plastron is AM F:18775.

the intergular. In AM F:18775 and AM F:923 the gular trough is best developed, while in AM F:49141 the distinctions among the gulars and intergulars are barely visible. The intergular scute in *Meiolania* (fig. 27) is a ventral boss or convexity separated from the gular by a difference in level rather than a sulcus. In AM F:57984 there is a midline trough with paired lateral ridges and this is interpreted as a midline separation of two intergular scales. The posterior margin of the intergular is only a very shallow trough seen best in AM F:18775 and AM F:923. The lateral margin of the anterior lobe tends to have thickened edges, the more medial areas being thin except in the midline where the entoplastral process lies.

The hyoplastron is preserved in AM F:18775 (fig. 27), AM F:1208 (fig. 3), AM F:57984, AM F:49141, AM F:923, AM F:5522 and AM F:64434 (fig. 30). The hyoplastron forms the anterior bridge region

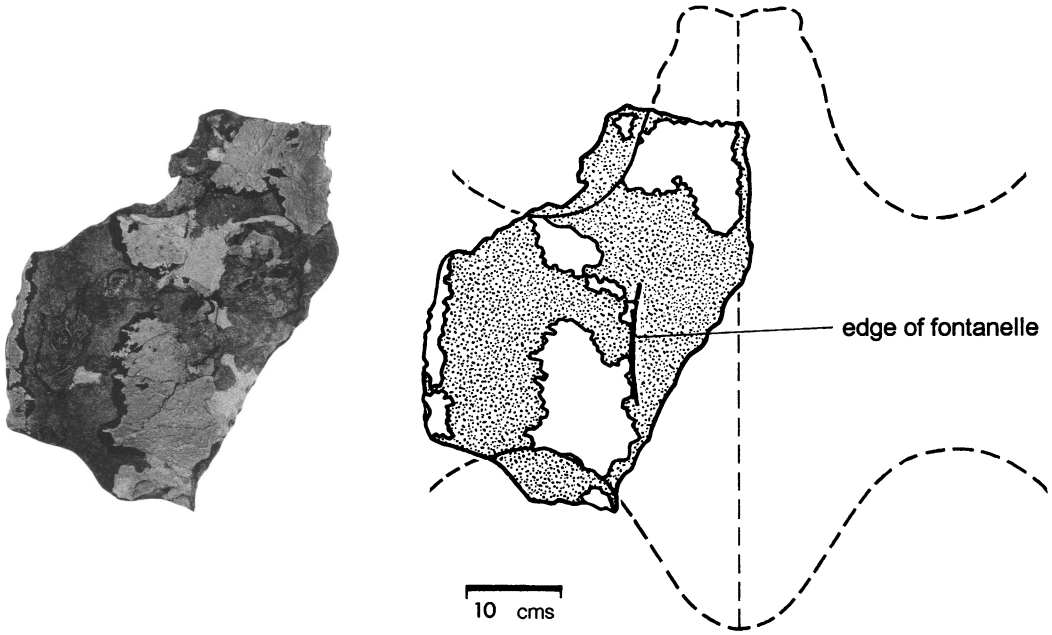


Fig. 30. *Meiolania platyceps,* AM F:64434, ventral view of incomplete plastron.

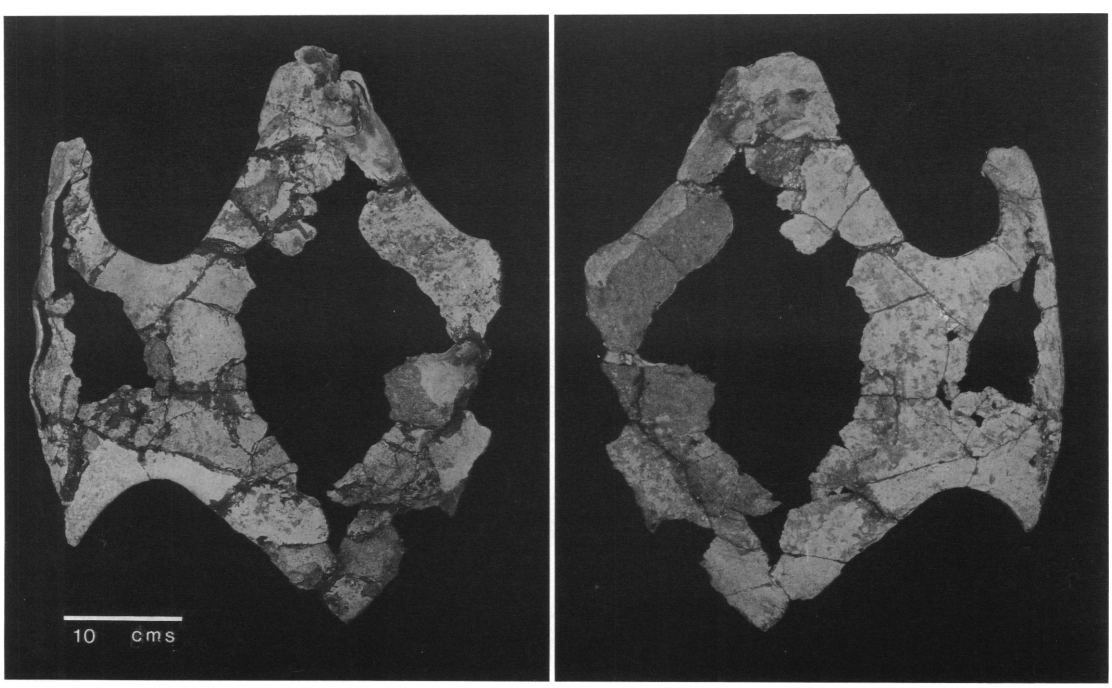


Fig. 31. *Meiolania platyceps,* AM F:1208, plastron and bridge area in dorsal (left) and ventral (right) views. Also figured in Anderson (1925: pl. 30) prior to further preparation.

and the axillary buttress. The axillary buttress is a sheet of bone curving medially around the forelimb opening then curving anterodorsolaterally to reach peripheral three but not the costals. Although both the axillary and inguinal buttresses reach the peripherals and are sutured to them, the bone between the buttresses is thin and only contacts the peripherals by a series of digitate processes. This condition is best seen in AM F:1208 (fig. 31) and AM F:5522. The peripherals themselves have very thin ventral edges and are not thick enough to have the pits to receive the plastral processes seen in other taxa with ligamentous bridge attachments. The plastral bridge area in AM F:1208 is figured by Anderson (1925, pl. 30, fig. 1) before extensive preparation took place and while the peripherals and plastron were held together in situ by matrix. In this figure, the digitate processes can be seen particularly well. In this specimen the digitate processes barely reach the peripherals but in some other specimens, like AM F:49141, the processes may have reached the peripherals and fused with them producing a series of small fontanelles.

The plastral area between inguinal and axillary openings is preserved in AM F:49141, AM F:1208, AM F:64434, and to some extent in AM F:5522. This area is thickened at the anterior and posterior edges and thin in the middle. No definite sutures are present but in AM F:49141, AM F:1208, and AM F:5522 there are growth lines and centers of ossification that suggest the absence of mesoplastra and a transverse contact between hyoplastron and hypoplastron. The absence of a mesoplastron in *Meiolania platyceps* is consistent with a specimen of *Meiolania brevicollis* (Megirian, 1992).

The plastron of *Meiolania platyceps* has a large, irregularly shaped, midline fontanelle, margins of which are preserved in AM F:49141, AM F:64434 (fig. 30), AM F:1208 (fig. 31), AM F:18775 (fig. 27), and AM F:5522. The fontanelle is particularly susceptible to variation and few of the preserved margins that are comparable are the same in any two specimens. The fontanelle is formed by hypoplastra and hyoplastra and occupies the area between the anterior and posterior lobes with more of the fontanelle in the posterior region of the plastron than in the anterior region.

The posterior plastral lobe of *Meiolania* (fig. 27) is slightly shorter and more acuminate than the anterior lobe, ending in a gentle taper. In AM F:5522 the posterior lobe is slightly more blunt than in AM F:18775. The very acuminate anterior and posterior lobes of AM F:1208 (fig. 31) are somewhat exaggerated by breakage but this specimen does differ from the other plastra in this feature.

The area of the hypoplastron is preserved in AM F:33741, AM F:18775 (fig. 27), AM F:57984, AM F:49141, AM F:1208 (fig. 31), and AM F:64434 (fig. 30). The hypoplastron forms the inguinal buttress, which curves posteriorly contacting the bridge peripherals and ending on peripheral eight. The buttress does not extend onto the costals. Hypoplastron/xiphiplastron sutures are visible in AM F:57984 and the disarticulated xiphiplastron AM F:18853. This suture is similar to other turtles, with a notch or process near the lateral edge. In AM F:18775, the posterior lobe has a midline suture that is open and has a small fontanelle. It is possible that the thin, relatively open plastron of *Meiolania* had some degree of kinesis as well as flexion.

On the external surface of some specimens, the lateral edge of the posterior lobe has a series of short grooves, as in AM F:18775 (fig. 27), trending anteromedially but more regularly than the other grooves and foramina covering the surface. The internal surface of the posterior lobe in AM F:49141 and AM F:5522, has a raised tubercle on the xiphiplastron, anterolaterally, for the articulation of the pubis. AM F:18775 and AM F:18853 lack the tubercle but have a rugosity.

AM F:18853 is a disarticulated xiphiplastron of a presumed juvenile. It is much smaller than the other plastra and has an open anterior suture, and median fontanelles alternating with median interdigitations as in most juvenile turtles. AM F:18781 may also be a xiphiplastron from a juvenile.

Only the gular and intergular scales are determinable on the plastron on *Meiolania platyceps*. Close examination of the external surfaces in all the plastral specimens has failed to reveal other scale sulci.

LIMB MORPHOLOGY

SHOULDER GIRDLE (figs. 17, 18, 32)

Material available: AM F:210, glenoid; AM F:369, glenoid; AM F:924, scapula with glenoid part of coracoid; AM F:5535, shoulder girdle fragments; AM F:9065, glenoid portion of scapula; AM F:10784, scapula; AM F:10785, scapula; AM F:10786, scapula; AM F:18253, scapula and glenoid part of coracoid; AM F:18369, scapula fragment; AM F:18376, glenoid; AM F:18377, glenoid; AM F:18378, coracoid fragment; AM F:18496, coracoid and glenoid portion of scapula, figured in Anderson (1925: pl. 38, fig. 1), same individual as AM F:1208, plastron; AM F:18546, scapula fragment; AM F:18726, scapula; AM F:18727, scapula; AM F:18728, scapula fragment; AM F:18729, scapula fragment; AM F:18730, glenoid fragment; AM F:18731, coracoid and glenoid; AM F:18732, scapula; AM F:18733, right coracoid; AM F:18734, glenoid; AM F:18735 (fig. 32), coracoid; AM F:18736, scapula; AM F:18737, coracoid; AM F:18849, coracoid; AM F:18850, scapula fragment; AM F:19360, right scapula; AM F:19775, shoulder girdle; AM F:20508, glenoid; AM F:49141, AM F:57984 (fig. 32), right and left shoulder girdles, part of associated skeleton; AM F:61110 (figs. 17, 18), right and left shoulder girdles, part of associated skeleton; BMNH R681, coracoid; BMNH R686, scapula fragment; BMNH R693b, glenoid; BMNH R693d, scapula fragment; BMNH R9639, scapula fragment; BMNH R9654, scapula fragment.

There are over 40 elements that are identifiable as belonging to the shoulder girdle of *Meiolania platyceps.* Of these, only AM F:18496, a left coracoid and scapula, has been figured (Anderson, 1925: pls. 30, 38, fig. 1). Other important specimens include a right and left scapula and partial coracoid, AM F:57984 (fig. 32); a complete right scapula, AM F:18733; a nearly complete right coracoid, AM F:19360; right and left shoulder girdles, AM F:61110 (figs. 17, 18); partial right and left shoulder girdles, AM F:49141.

The shoulder girdle elements in *Meiolania platyceps,* the scapula and coracoid, are usually fused at the glenoid, but the contact suture can be determined by articulating a scapula, AM F:19360, and a coracoid, AM F:18733, both of which preserve the sutural surface. The shoulder girdle of *Meiolania* has the typical chelonian triradiate shape. It is more massive than in most casichelydians, but similar to testudinoids.

The dorsal process of the scapula in *Meiolania* is relatively thick when compared with *Glyptops,* baenids, chelydrids, and emydids, but similar to some testudinids. The process is essentially a straight cylinder with a rounded dorsal end bearing an articular surface. The articular surface, as in all turtles, articulates with the carapace, and the articulating surface of the carapace is still attached to the scapula in AM F:57984 and AM F:19360.

The more ventral or acromial process joins the dorsal process at about 120°. Most turtles join at about 90°, but testudinids and chelonioids have greater angles apparently due to their relatively deep shells (Walker, 1973). This is consistent with the relatively deep shell of *Meiolania.* The two processes of the scapula form a bony web, well developed in *Meiolania* as it is in some testudinids. The glenoid is not supported by a neck. The acromial process is a stout, straight cylinder, similar to the dorsal scapular process but shorter. It articulates with the anterior part of the plastron, where a distinctive forked process forms a medial stop for the acromion.

A complete coracoid is not known for *Meiolania platyceps* but AM F:18735 is nearly complete and is the basis for figure 32. The coracoid of *Meiolania* is fan shaped and short as in testudinids. *Glyptops* also has a short, fan-shaped coracoid, more fan shaped and extensive than in *Meiolania.* Baenids, chelydrids, and emydids generally have a long coracoid, one that matches or exceeds the length of the acromion. A long coracoid is generally found in swimming turtles (Walker, 1973), and the short one is presumably related to a more terrestrial habitus.

PELVIS (figs. 9, 33)

Material available: AM F:189, right pelvis; AM F:190, acetabulum; AM F:219, acetab-

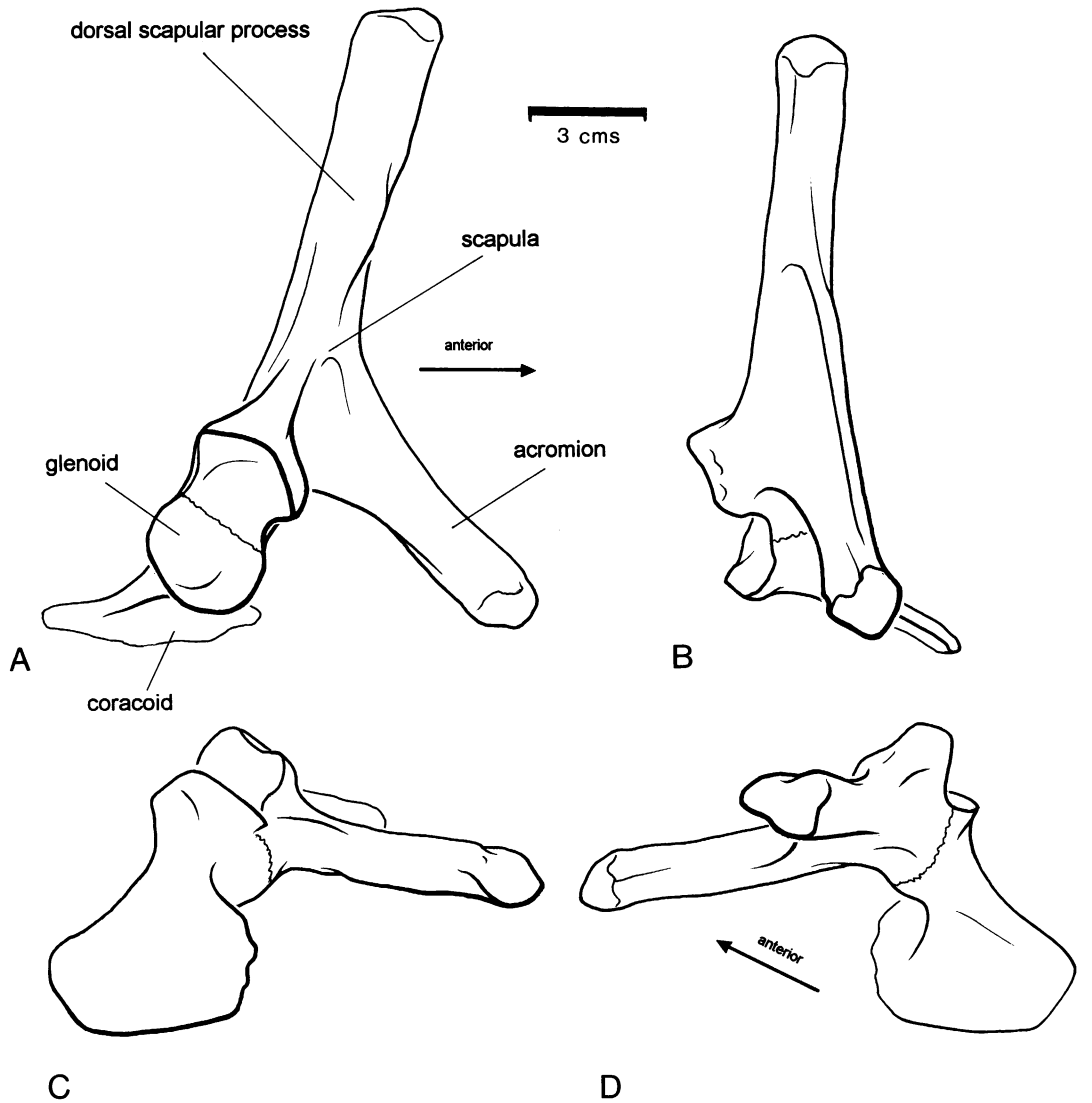


Fig. 32. *Meiolania platyceps,* right shoulder girdle, based primarily on AM F:57984 with coracoid from AM F:18735. **A,** Lateral; **B,** anterior; **C,** ventral; **D,** dorsal.

ulum; AM F:1205, both acetabula plus ischium; AM F:1214, left ilium; AM F:1219, right pubis and (?) ischium; AM F:3296, left pelvis; AM F:5476, acetabulum; AM F:5529, both pubes; AM F:5756, right acetabulum and part of ilium; AM F:9057, right ilium plus acetabulum; AM F:17735, acetabulum; AM F:18251, left acetabulum and ilium; AM F:18258, left acetabulum and ilium; AM F:18497, pelvis, figured in Anderson (1925, pls. 30, 39), same individual as AM F:1208; AM F:18823, left acetabulum and ilium; AM F:18824, acetabulum; AM F:18825, right pelvis; AM F:18826, acetabulum; AM F:18848, left pubis; AM F:20509, right pubis; AM F:49141, both ilia, fragments of acetabulum; AM F:57984, fragments of right and left acetabula; AM F:81949, right pelvis;

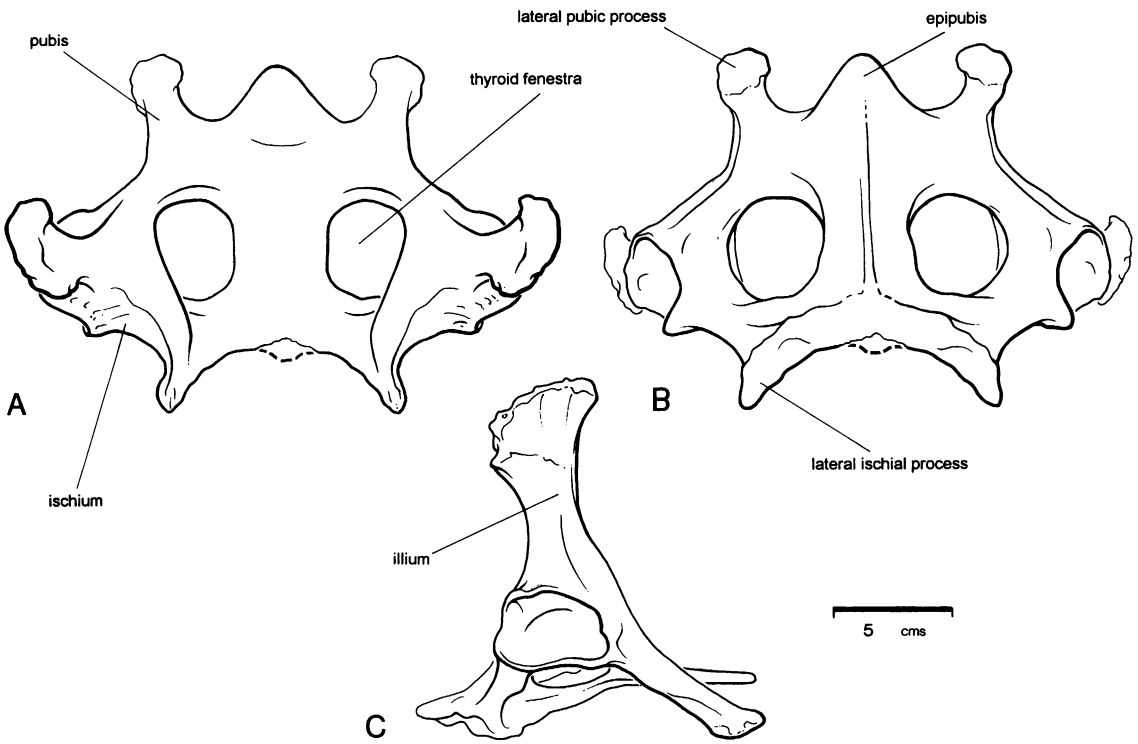


Fig. 33. *Meiolania platyceps,* composite reconstruction of pelvis based on all available specimens, primarily AM F:18825, AM F:18497, and AM F:97549. **A,** Dorsal; **B,** ventral; **C,** right lateral.

BMNH R687, ilium; BMNH R693e, ilium; BMNH R9641, ischium fragment.

Although there are over 25 specimens identifiable as parts of the pelvis, none is complete. A partial pelvis of a small individual, associated with a plastron was figured by Anderson (1925, pls. 30, 39; AM F:18497, same individual as AM F:1208). This remains one of the most complete pelves available. The figures are accurate but it should be noted that plate 39, figs. 2 and 3, are in a different orientation than the figures presented here. Another *Meiolania* partial pelvis, a left ilium and acetabulum, was figured by Owen (1886b: pl. 32). I have been unable to identify the specimen in the collections of the Mining Museum, Sydney, the Natural History Museum, London, or the Australian Museum. The figure nonetheless is accurate compared with other specimens.

Other important specimens are: a right ilium and acetabulum, AM F:18825, a left ilium and acetabulum, AM F:18823, right and left pubes, AM F:5529; a right pubis, AM F:1219; a right pelvis, AM F:189.

The pelvis (see Zug, 1971; Walker, 1973; Ruckes, 1929 for general discussions of chelonian pelves) of *Meiolania platyceps* is not known from complete specimens, and the illustrations (fig. 33) are restored from a series of specimens. The sutures in the pelvis are usually fused.

The ilium in *Meiolania platyceps* agrees with Zug's (1971: 38) "spool shaped" pattern seen in chelydrids and testudinids, relatively straight, extending dorsally from the acetabulum. In most cryptodires the ilium fans out at the top (i.e., baenids) or is directed posterodorsally (chelydrids, most testudinoids). In *Meiolania* the ilium becomes narrower

TABLE 1
Humerus Measurements (mm)

	Maximum length	Maximum proximal width	Maximum distal width
Meiolania platyceps			
AM F:16850 + 16848	205	–	110
AM F:18750	174	110	90
AM F:925	–	145[1]	–
AM F:20505	153	90	73
AM F:405	–	–	95
AM F:20506	161	90	75
AM F:18677	151	83	69
AM F:57984	–	101	–
Meiolania brevicollis			
NTM P923-3	160	94	73
NTM P895-55	168	115	94

[1] Broken.

dorsally (AM F:18825, AM F:18823). The dorsal third of the ilium has a tubercle posteriorly and an indentation anteriorly, producing a jog in the shaft. This closely fits the shape of the sacral ribs that articulate on the medial surface of the jog. The ilium in *Meiolania* is also directed dorsally rather than posterodorsally as in most cryptodires. Testudinids, however, also have a dorsally directed ilium, and perhaps this is related to a common habitus rather than phylogeny. The dorsal end of the ilium has an articular surface for the carapace.

The ischium of *Meiolania* is similar to chelydrids (for example) in having well developed lateral ischial processes and a plastral contact surface including the processes and extending to the midline. In *Meiolania* the ischium is somewhat more massive and has an extensive pubis/ischium contact on the midline, widely separating the thyroid fenestrae. Wide separation of the thyroid fenestrae also occurs in *Glyptops* and baenids, as well as testudinoids (Walker, 1973). Widely separated thyroid fenestrae seem to be primitive for turtles even though the condition does occur, possibly as a reversal, in many living turtles.

The pubis in *Meiolania* has a lateral pubic process or pectineal process that extends anteriorly and slightly laterally to articulate with the plastron. The process is similar in size to that in chelydrids and apparently slightly larger than in baenids. There is an epipubis that curves anteriorly on the midline about as far anteriorly as the lateral pubic processes. The epipubis is ossified, as in baenids, not calcified cartilage as in some recent cryptodires. The epipubis of baenids is much larger than that of *Meiolania.*

HUMERUS (figs. 17, 18, 34)

Material available: AM F:405, distal end of right, figured in Anderson (1925, pl. 38, figs. 4, 5); AM F:925, proximal end of left; AM F:1048, proximal end of left; AM F:1204 (part), two humeri- complete left humerus figured in Anderson (1925, pl. 38, figs. 2, 3), and damaged proximal end of humerus; AM F:5475, two left humeri, both proximal ends AM F:5755, right, lacking proximal end; AM F:9058, distal end of (?) left; AM F:16847, distal end of right; AM F:16849, proximal end of right; AM F:16850, right; AM F:16851, left lacking proximal end; AM F:17730, distal end of right; AM F:17732, left lacking proximal end; AM F:18738, left; AM F:18739, left; AM F:18741, right; AM F:18742, right; AM F:18744, left lacking proximal end; AM F:18748, right; AM F:18749, right lacking proximal end; AM F:18750, right, figured in Anderson (1930, pl. 48); AM F:18760, right lacking proximal end; AM F:19361, left; AM F:19362, right; AM F:20505, right; AM F:49141, both right and left, incomplete; AM F:57984, right and proximal end of left; AM F:81982, distal end of left; AM F:82002, distal end of right; AM F:82003, distal end of left; AM F:82005, proximal end of right; AMNH 20941, partial humerus; AMNH 20942, partial humerus; AMNH 20943, humeral shaft; AMNH 20944, distal end; AMNH 20945, distal humerus; AMNH 20946, proximal end; AMNH 20986, distal end; AMNH 20996, humeral shaft; BMNH R693c, distal end; BMNH R684, left distal end.

The humerus of *Meiolania platyceps* varies in size (table 1) from the smallest nearly complete specimen (AM F:18742) at approximately 125 mm, to the 205 mm long AM

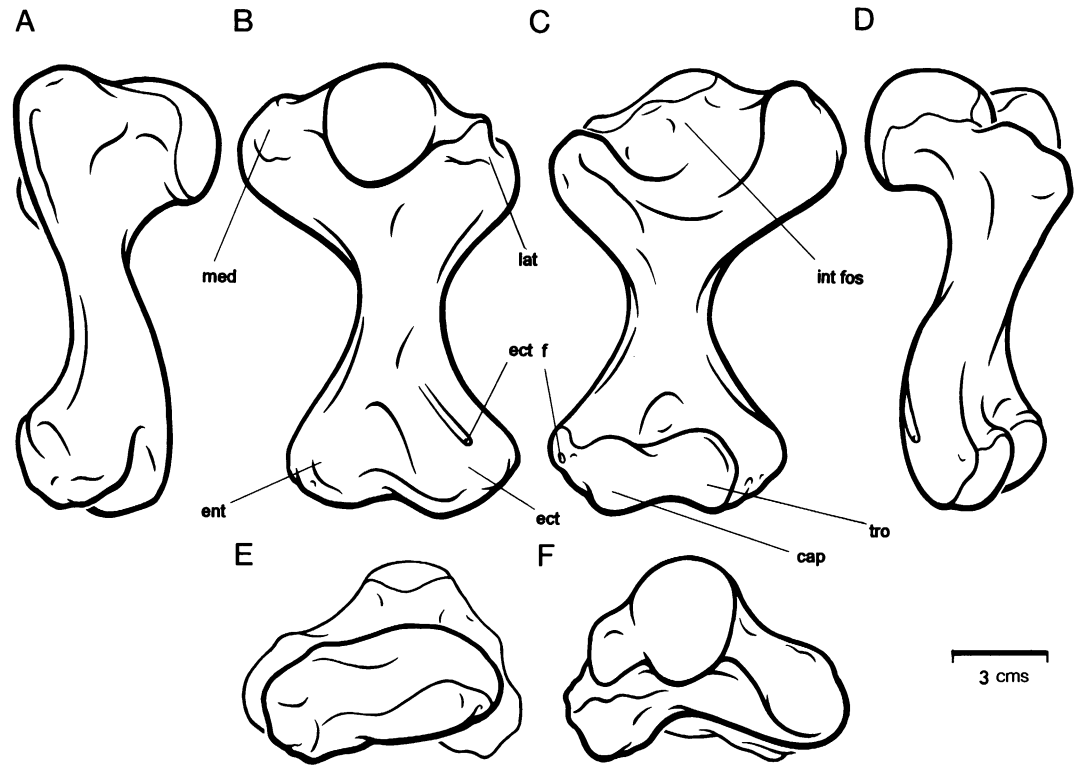


Fig. 34. *Meiolania platyceps.* Right humerus, composite based on AM F:57984, AM F:8677, and AM F:20506. **A,** Posterior; **B,** dorsal; **C,** ventral; **D,** anterior; **E,** distal; **F,** proximal. Abbreviations: cap capitellum, ect ectepicondyle, ect f ectepicondylar foramen, ent entepicondyle, int fos intertubercular fossa, lat lateral process, med medial process, tro trochlea.

F:16850 (including AM F:16848). The humeri also differ in the degree of expression of surface features and some, such as AM F:18677, are unusually rugose on the shaft. The general shape of the humerus in *Meiolania* is more like *Proganochelys* than other primitive cryptodires. Both ends are expanded and the proportions are stocky and massive. Primitive cryptodires, such as *Glyptops* and baenids, have narrower distal and proximal ends, and less massive proportions, but the more advanced eucryptodires have even narrower humeri.

The proximal articulation surface or head of the humerus in *Meiolania* is hemispherical as in *Proganochelys* but agrees with other casichelydians in being narrower anteroposteriorly. As in other casichelydians, the humeral head in *Meiolania* is separated off the main body of the humerus to a greater degree than in *Proganochelys.* The anterior (preaxial) margin of the humeral head has a distinct shelf or shoulder that is present in *Proganochelys* and most cryptodires. The shelf is well developed in *Meiolania* and slightly more separated from the head than in *Glyptops* and baenids.

The proximal expansions of the humerus in *Meiolania* are large and well developed, as in *Proganochelys.* Both agree in having the expansions roughly equal in size, but in *Proganochelys* the medial process is smaller than the lateral, while in *Meiolania* the medial process is larger. The condition in *Meiolania* is characteristic of cryptodires. The relative sizes of the medial and lateral processes in *Meiolania* agree with *Glyptops* and baenids. Most eucryptodires, such as chelydrids,

TABLE 2
Ulna Measurements (mm)

Meiolania platyceps	Maximum length	Maximum proximal width	Maximum distal width
AM F:18827	109	56	47
AM F:81951	105[1]	53	43
AM F:49141 (right)	—	—	—
AM F:49141 (left)	113	59	57
AM F:57984	98	48	42
AM F:18829	101	52[2]	48[2]

[1] Broken, probably 108.
[2] As restored.

trionychoids, and testudinoids, have the lateral process significantly smaller than the medial process. This may be a synapomorphy somewhere in the vicinity of Eucryptodira.

The distal end of the humerus in *Meiolania* has the typical chelonian double convexity, with the radial articulation, the capitellum, anteriorly, and the ulnar articulation, the trochlea, posteriorly. The articular surface in *Meiolania* is raised and distinct, as in *Glyptops,* but most living cryptodires have a poorly differentiated articular surface.

The ectepicondylar foramen is present in *Meiolania* as a distinct canal, extending from a long groove on the dorsal surface, through the ectepicondyle to open on the ventral surface. The foramen is very similar to that in *Glyptops* and baenids. Many living cryptodires have the canal open as a groove.

ULNA (figs. 35, 43, 44)

Material available: AM F:207 (part), right; AM F:223, proximal end of left; AM F:9061, proximal end of right; AM F:18827, right, associated with forefoot, figured in Anderson (1930: pl. 47, fig. 1; pl. 48); AM F:18829, left, used in cast; AM F:18830, right; AM F:18831, right; AM F:18839, left; AM F:18843, right; AM F:18847, left; AM F:49141 (figs. 43, 44), right with damaged proximal end, left with damaged proximal end; AM F:57984, right, used in cast, associated with most complete individual known to date; AM F:81951, right; AM F:82011, proximal end of right.

There are 15 specimens identifiable as ulnae of *Meiolania platyceps,* however, only four (AM F:57984, AM F:18829, AM F:18827, AM F:81951) are complete. The olecranon seems particularly susceptible to breakage, thus the relatively few ulnae measured (table 2). There is variation in degree of rugosity development, for example, in the tubercle for the attachment of the bicipital tendon. The tubercle is most developed in AM F:81951 and only slightly developed in AM F:57984. This does not seem to be correlated with size; AM F:81951 is 105 mm long while AM F:18827, a longer ulna at 109 mm, has less development of rugosity on the tubercle. There is little size variation among the complete ulnae but the largest ulna, AM F:18830, is roughly 15% larger than what seems to be the smallest, AM F:18843.

The ulna of *Meiolania* is generally similar to the ulna of *Proganochelys* and other cryptodires. It is stockier than in most turtles, however, and resembles testudinids in this feature. The ulna of *Meiolania* can be readily derived from that of *Proganochelys* by enlarging both ends and making the proportions more massive.

Proximally the ulna of *Meiolania* has a well developed olecranon on its proximodorsal margin. The triceps muscle/ligament system attaches on the olecranon, which tends to be well developed in more primitive turtles and lost in more modern turtles, i.e., the Polycryptodira. *Proganochelys* (Gaffney, 1990) and baenids have a relatively well-developed olecranon (Hay, 1908; Russell, 1934), larger than in *Meiolania,* as does *Glyptops.* Among eucryptodires, however, chelydrids (Gaffney, 1990) have a poorly developed olecranon, while TMP 87.2.1 and *Toxochelys* (Zangerl, 1953) have olecranons that can barely be recognized.

The sigmoid notch (Romer, 1956) is the proximal articular surface of the ulna, and usually has a compound curved surface in amniotes. This surface is simplified in *Proganochelys,* faces more proximally, and has a smaller arc of curvature than in generalized amniotes. Casichelydians extend this trend to a greater degree. *Meiolania* has a well defined sigmoid notch that is more similar to *Proganochelys* than to chelydrids. The entire

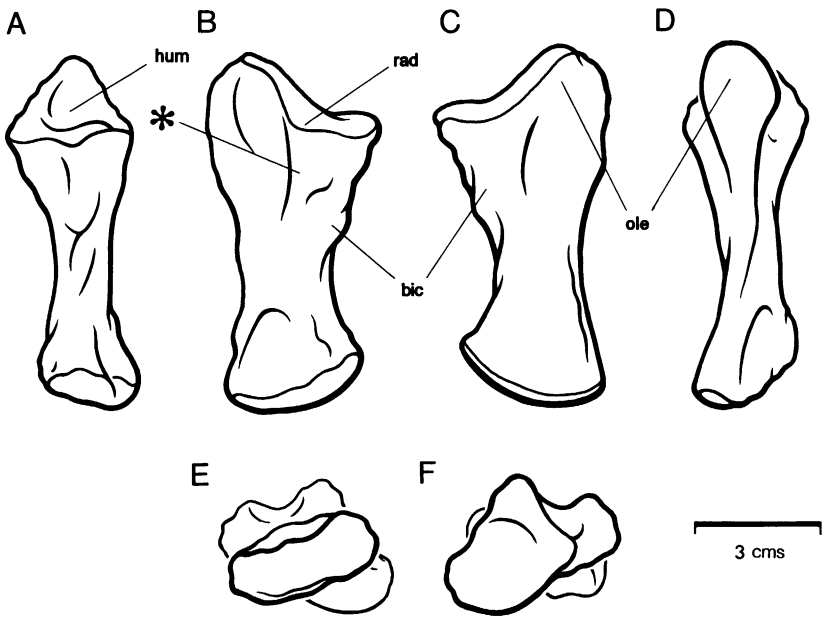


Fig. 35. *Meiolania platyceps.* Right ulna, AM F:57984 with restoration from AM F:18829 and AM F:18827. **A,** Medial; **B,** dorsal; **C,** ventral; **D,** lateral; **E,** distal; **F,** proximal. Abbreviations: bic bicipital tubercle, hum humeral articulation, ole olecranon, rad radial articulation, * see text for discussion of this feature.

articular surface is well defined in *Meiolania,* as in *Proganochelys* and in contrast to most eucryptodires. However, some testudinids (i.e., *Stylemys,* Hay, 1908, fig. 493) have an olecranon and sigmoid notch that is similar to that in *Meiolania.* This possibly relates to the presumed terrestrial life style of both.

The proximal end of the ulna has two articulation surfaces, the large proximally facing humeral surface and the small, dorsomedially facing radial surface. In most Polycryptodira these surfaces blend together and are not distinct. In *Meiolania,* however, they are unusually distinct, even more than in *Proganochelys.*

A sharp distinction of the *Meiolania* ulna from most, if not all other turtles, is the degree of development of a ridge on the dorsal surface of the ulnar shaft (described in *Proganochelys* by Gaffney, 1990: 217). This ridge (indicated by an asterisk in fig. 35) begins proximally just lateral to the radial articulation surface and extends distally forming a partial trough for the radius which lies between the ridge and the medial edge of the ulna. The ridge is highest proximally, becomes lower distally, and disappears midway along the shaft. A similar but smaller ridge is present in *Proganochelys. Glyptops,* baenids, and chelydrids have slender shafts and virtually lack the ridge. No turtle that I am aware of, including testudinids, has this ridge developed to the extent seen in *Meiolania* and it may be a synapomorphy for the family. Presumably, the radio/ulnar ligaments (Haines, 1946) attached along this ridge as well as the medial edge of the ulna, indicating a particularly strong relationship between the radius and ulna.

The bicipital tubercle is a small rugosity about halfway along the ulnar shaft. It is the attachment point of the biceps profundus. The tubercle is about the same size in *Meiolania* and *Chelydra.* The shaft of the ulna is twisted in this region so that the long axis of the distal end is at an angle to the long axis of the proximal end. This twist is present in most turtles but is more obvious in *Meiolania* because of its more robust proportions.

The carpal articulation surface in *Meiolan-*

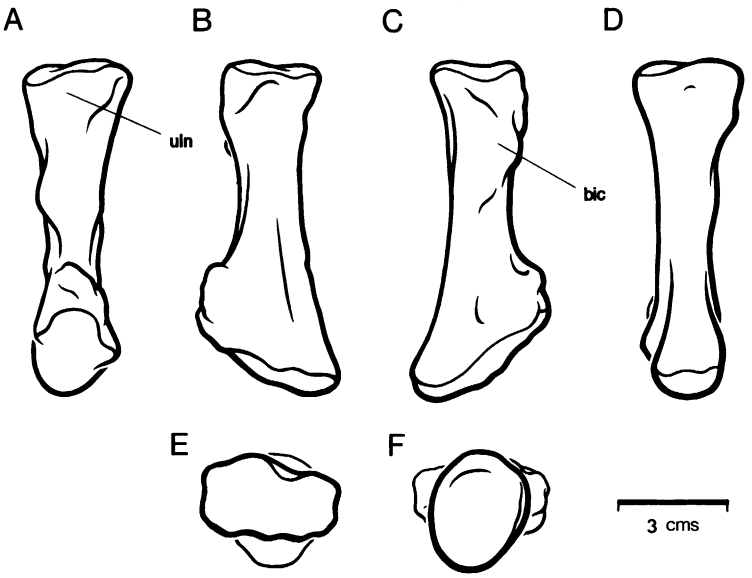


Fig. 36. *Meiolania platyceps.* Right radius, AM F:57984 with additions from AM F:5527. **A,** Lateral; **B,** dorsal; **C,** ventral; **D,** medial; **E,** distal; **F,** proximal. Abbreviations: bic biceps superficialis, uln ulnar contact area.

ia is strap shaped and differs from other turtles only in being relatively larger.

RADIUS (figs. 36, 43, 44)

Material available: AM F:207, two radii, a right complete, and a proximal end of a right; AM F:406, left; AM F:5527, left, used in cast; AM F:5528, right; AM F:18827, right, figured in Anderson (1930: pl. 48), part of associated forelimb; AM F:18828, right; AM F:20510, right; AM F:20511, right; AM F:49141 (figs. 43, 44), right radius lacking distal end, left radius damaged proximally, associated with articulated forefeet and partial skeleton; AM F:57984, right (fig. 36), used in cast, associated with most complete single individual known to date; AM F:61412, left, probably associated with carapace and partial skeleton AM F:61110; MM F:13845, right, figured in Owen (1888: pl. 36, figs. 5, 6).

The 16 preserved radii of *Meiolania platyceps* include three individuals, AM F:57984, AM F:49141, AM F:18827, with associated forefeet. The last two specimens have articulated forefeet. In all of these, however, the original position of the radius in the forefoot has been disturbed by postmortem agents of one sort or another. The specimen that retains positions closest to the life articulations is AM F:49141 (figs. 43, 44), in which the forelimbs seem to have been disturbed by the shrinking of soft tissues pulling the bony elements of the zeugopodium closer together, so that radius and ulna slightly overlap, overflexing the phalanges.

In addition to the associated specimens, the collection includes a number of complete radii, i.e., AM F:5527 (left), AM F:5528 (right, possibly these two were associated at one time), AM F:406, AM F:20510, AM F:207, and AM F:61412 (which is probably associated with AM F:61110, a skull, carapace and partial skeleton). Size variation among the complete *Meiolania* radii (table 3) ranges from the largest at 101 mm to the smallest at 76 mm. Some radii i.e., AM F:18827, have the rugosity on the lateral edge of the distal end, large and very rugose, while others, i.e., AM F:20510, nearly lack a rugosity here. This seems to be roughly correlated with size. The surface texture of the shaft also varies from smooth to moderately rugose, and this does not seem to be size related (i.e., AM F:57984 is relatively smooth and the same-sized AM F:5527 is rugose). The edge of the proximal

articulation surface is acute (AM F:61412) in some and rounded (AM F:406) in others.

The radius of *Meiolania* is very similar to the radius in *Proganochelys,* differing only in being more robust and stockier. The radius in turtles is relatively conservative morphologically, only in the swimming forms and in some testudinids does it depart very much from the norm.

The proximal end of the radius in *Meiolania,* as in other turtles, is oval in cross section, and slightly larger than the sections in the middle of the shaft. The distal end is expanded in the mediolateral plane. The proximal articulation articulates with the humerus and has a slightly concave surface. The lateral edge of the articulation and the rugose area just distal to the articular surface contacts the ulna. The distinct rugosity midway along the ventral surface of the shaft bears the attachment of the biceps superficialis (Walker, 1973). This rugosity is in a more distal position in *Macroclemys* than in *Meiolania*; in most turtles, however, it is poorly developed or absent. Distally, on the lateral edge of the ulna is a well developed rugosity for the more distal attachment of the radio/ulnar ligament. Based on Haines (1946) analysis, the unusually well-developed attachments of this ligament distally and proximally on opposing edges of the radius and ulna suggest that *Meiolania* had relatively restricted movement between radius and ulna.

The distal articulation of the ulna with the carpus is an elongate, expanded surface that has a distinct lateroproximal slope. It does not differ from other turtles except in being relatively more robust.

TABLE 3
Radius Measurements (mm)

	Max. length	Maximum proximal width	Maximum distal width
Meiolania platyceps			
AM F:18827	97	37	52
AM F:20510	82	25	40
AM F:61412	76	28	34
AM F:406	101	38	53
AM F:49141 (right)	—	41	—
AM F:49141 (left)	100	—	43
AM F:17661	77[1]	23	—
AM F:57984	88	30	39
AM F:5527	90	32	41
Meiolania brevicollis	88	27	20

[1] Broken, probably 81.

CARPUS AND MANUS
(figs. 37–44, 81, 82)

Material available (See table 4): The carpus of *Meiolania* is known from a number of specimens, none being perfectly preserved, however. AM F:49141 (figs. 41–44) is the best with both right and left carpi preserved in articulation. AM F:57984 (figs. 37, 38) has what appears to be a complete right carpus originally found in articulation but subsequently disarticulated. AM F:5542 and AM F:18835 have disarticulated carpal elements identified by comparison with the other specimens, and AM F:923 has a fragment of the medial centrale preserved in articulation with a partial manus.

The three best specimens, AM F:49141 (right and left) and AM F:57984, all agree in having seven carpal bones: four distal carpals and three proximal carpals. The three proximal carpals seem best identified as the ulnare, intermedium, and medial centrale. The ulnare is a block-shaped element with a flat surface for the ulna articulation proximally. A facet is also present for the intermedium, but the rest of the surfaces are broadly convex and protuberant with no distinct facets. The ulnare is the smallest of the proximal carpals.

The intermedium is a rectangular element differing from the ulnare and medial centrale in having flat facets on all four articular surfaces. It fits between ulna and radius proximally and ulnare and medial centrale distally with flat facets for each articulation.

The proximal carpus of *Meiolania* apparently has three elements rather than the four seen in *Proganochelys* and many other turtles (Gaffney, 1990). However, in many turtles the two centralia are fused (or the lateral centrale is absent) resulting in three proximal carpals. For example, in *Macroclemys* and *Chelydra* the two centralia usually form one elongate element with or without a suture or

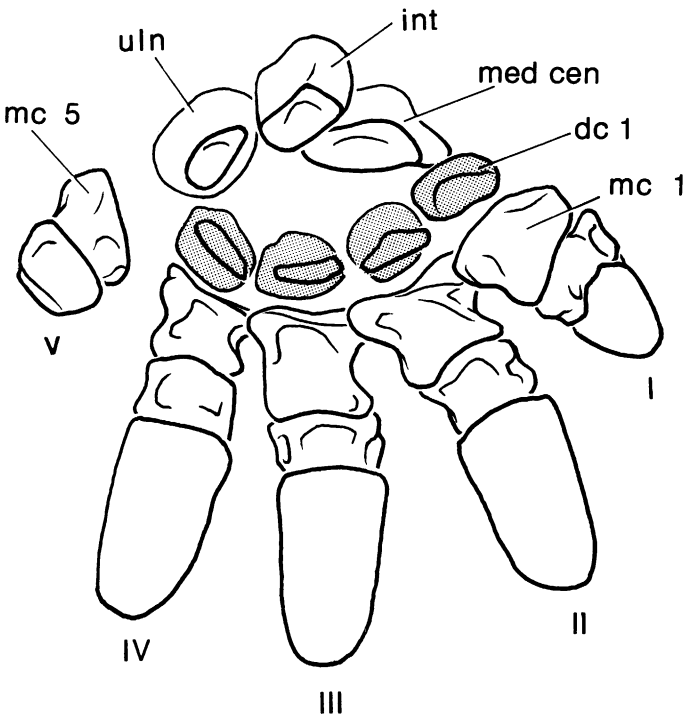


Fig. 37. *Meiolania platyceps,* AM F:57984, right manus in dorsal view. Terminal phalanx missing in digit V. Abbreviations: dc distal carpal (in stipple), int intermedium, mc metacarpal, med cen medial centrale, uln ulnare.

fusion zone apparent. In *Meiolania* the third element is large but not elongate and none of the specimens show any indication that it is two centralia fused. It seems best to identify it as the medial centrale and conclude that the lateral centrale is missing or unossified. It is unlikely that a separate lateral centrale is absent due to postmortem loss because both right and left carpi of AM F:49141 have this area preserved in articulation and there is no indication of it.

The medial centrale of *Meiolania* is the largest of the carpal elements and is irregular in shape. The distal surface is flat and may have a partial articulation with the first distal carpal at its medial edge. The proximal surface is a protuberant convexity contacting the intermedium proximolaterally and the radius proximomedially. The ventral exposed end is a rugosity and the dorsal exposed end is an irregular concavity ending in a hook-shaped spur laterally.

There is no evidence of a pisiform in *Meiolania* although this negative evidence is not definitive. If present, it would be expected in the left carpus of AM F:49141 because the fifth digit and associated osteoderms are intact and articulated in this specimen.

Meiolania has four distal carpals articulating with metacarpals I–IV. The fifth distal carpal, usually seen in other turtles is apparently absent in *Meiolania.* This condition does not appear to be the result of postmortem loss because the area is preserved in AM F:57984 and in the left foot of AM F:49141. The four distal carpals are similar in morphology. They are roughly tubular and somewhat wedge shaped with the narrow edge exposed on the dorsal surface. The ventral end has a rugosity on its exposed surface. Distal carpals three and four tend to be larger than distal carpals one and two. None of the distal carpals has well-formed articular facets, all the surfaces are convex. Each distal carpal is

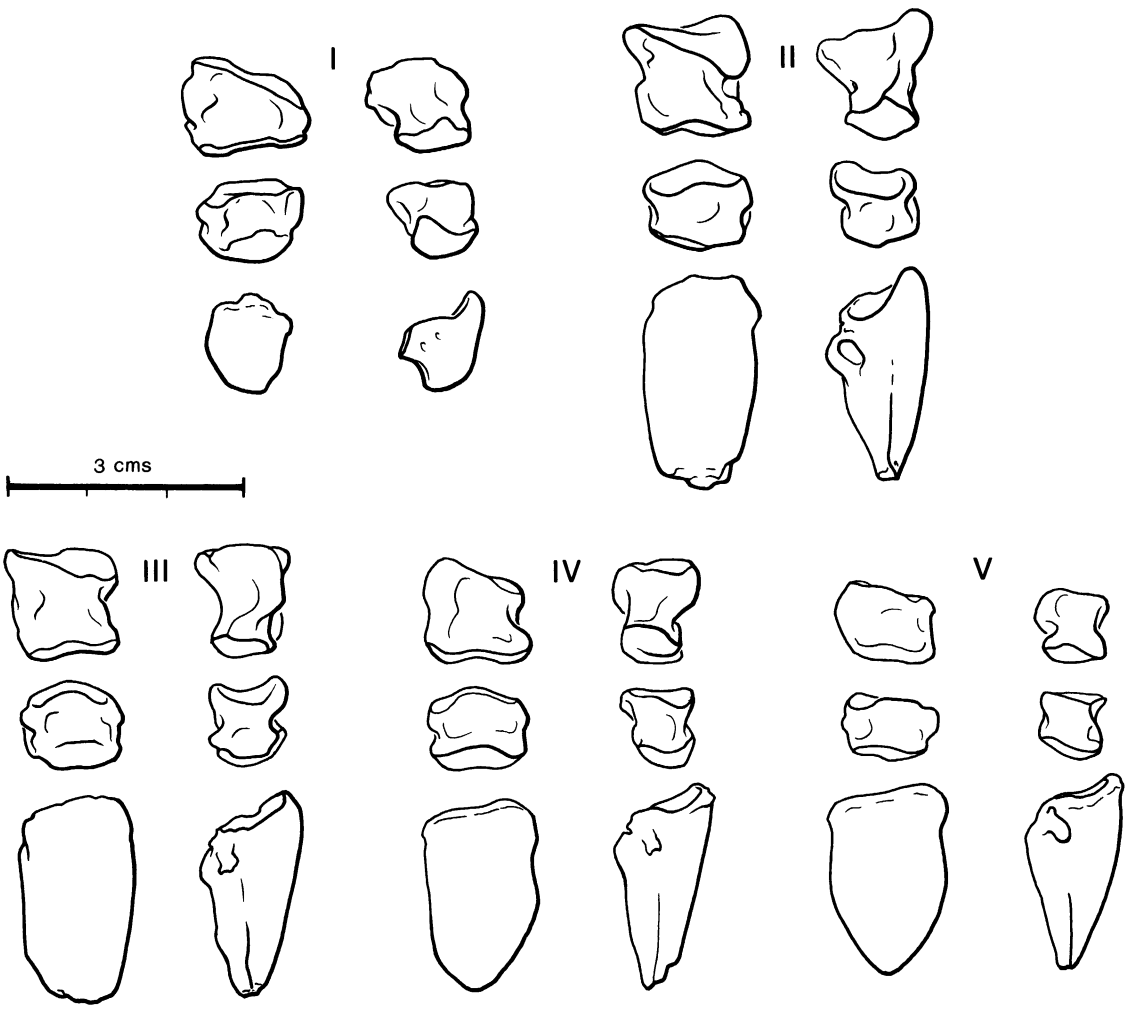


Fig. 38. *Meiolania platyceps,* AM F:57984, digits of right manus. Each digit is figured disarticulated in dorsal (left) and lateral (right) views. Proximal toward top of page. Ungual of fifth digit restored from AM F:49141.

most closely articulated with its associated metacarpal distally on a one to one basis, so that the first distal carpal articulates with the first metacarpal and so on. The fifth metacarpal does not articulate with any carpal.

The metacarpals of *Meiolania* are complete only in the right hand of AM F:57984 but good articulated series can also be seen in AM F:49141 (both hands) and disarticulated elements in AM F:5542 and AM F:18835. Metacarpals II–IV are similar in shape, with a broad proximal base, a constriction midway, and a distal expansion for the phalangeal articulation. Metacarpal I is wider than long, wedge shaped without a central constriction. Metacarpal V is also unlike the three central metacarpals in lacking the central constriction. It is block shaped and rectangular, similar to the phalanx articulating with it. Metacarpals I and II are subequal in size and larger than the others. Metacarpal size decreases from III to I. The bases of metacarpals I–IV have small articular facets for the overlapping articulation of the adjacent

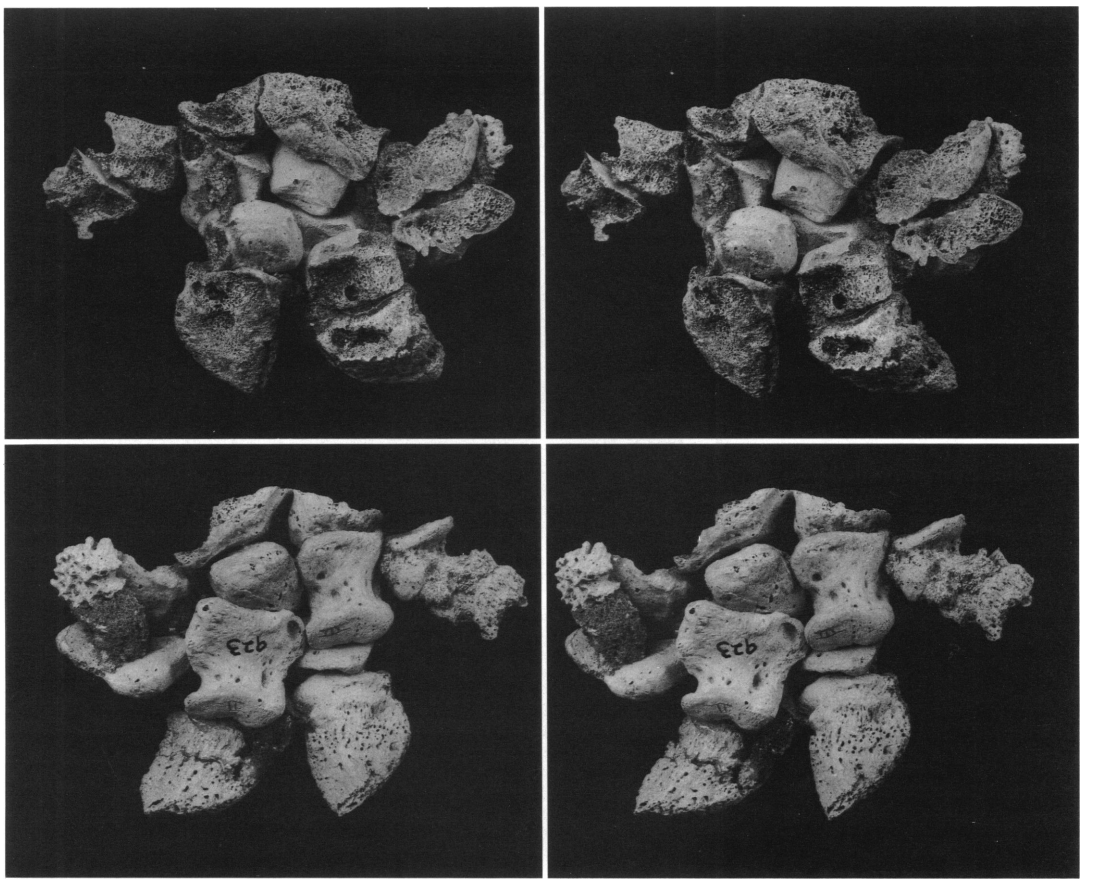


Fig. 39. *Meiolania platyceps,* AM F:923, stereophotographs of partial right manus in dorsal view (upper) and ventral view (lower).

metacarpal. Metacarpal V does not have an overlapping articulation with metacarpal IV.

The penultimate phalanx in all five digits of *Meiolania* is very similar in size and shape. They are all blocklike rectangular elements, wider than long, with only a slight indication of a midway constriction. The ventral proximal edge has a small rugosity for the flexor tendon attachment.

The ungual phalanges of *Meiolania* are broad, flat, and not recurved, similar to tortoises such as *Gopherus* (Auffenberg, 1966). In *Proganochelys* and most other turtles, such as chelydrids and emydids, the unguals are narrower, longer, more pointed, and recurved to some extent. In *Meiolania* the unguals II-V are very similar to each other but ungual I (preserved only in AMF:57984) is much smaller and is only a cap on the phalanx.

Meiolania has a manus digital formula of 2-2-2-2-2, as in *Proganochelys* (Gaffney, 1990) and some testudinids (Auffenberg, 1966). Baenids, pleurodires, and most cryptodires have a formula of 2-3-3-3-3, which Gaffney (1990) interpreted as primitive for turtles, with *Proganochelys* exhibiting an autapomorphy for this character. The same digital formula in *Meiolania* is also interpreted as an independent acquisition for that taxon as well as in those testudinids which have it.

Associated with both manus and pes of *Meiolania* are three types of dermal ossifications. One type is relatively dense bone with a smooth surface, which are sesamoids in flexor tendons. This type can be seen in the

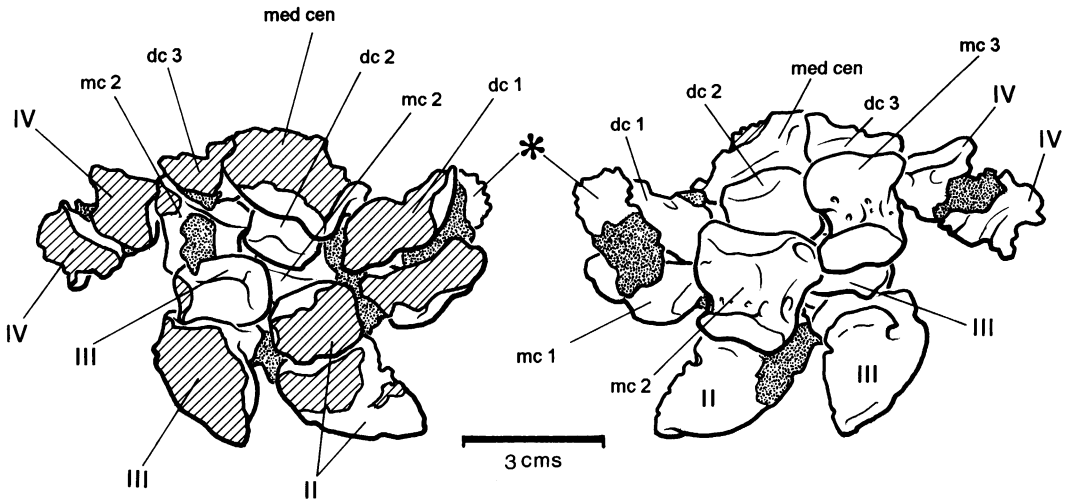


Fig. 40. *Meiolania platyceps,* AM F:923, partial right manus, key to fig. 39. Abbreviations: dc distal carpal, mc metacarpal, med cen medial centrale, * osteoderm. Roman numerals are phalanges and unguals.

right forefoot of AM F:49141, digit three, lying on the ventral surface of the penultimate phalanx (figs. 41, 42). This type of ossification also occurs in the extensor tendon of *Proganochelys* (Gaffney, 1990: 229) but not in the flexor tendon as in *Meiolania.* A second type of ossification seen in *Meiolania* feet are the disc- and cone-shaped bones very similar to the dermal armor ossicles seen in testudinids, usually covered with a scale, and partially exposed on the skin surface. These are common in some turtle groups. This ossification has a rough surface and is porous to some extent and can be seen in AM F:49141 right forefoot on the radius (figs. 41, 42). The third type of ossification has a very rough surface and is highly porous. Examples can be seen in AM F:923 right forefoot, near metacarpal I, (figs. 39, 40) and AM F:49141 left forefoot, near digit V (figs. 43, 44). These ossifications seem to be completely embedded in skin but their distribution and function is unclear.

FEMUR (fig. 45)

Material available: AM F:405, left; AM F:1203, right, figured in Anderson (1925: pl. 40, fig. 1, as apparent composite with AM F:16858); AM F:1552, left (cast); AM F:"1788," distal end of left; AM F:10773, left; AM F:16854, distal end of left; AM F:16855, distal end of right; AM F:16857, distal end of left; AM F:16858, right, figured in Anderson (1925: pl. 40, fig. 1, as apparent composite with AM F:1203); AM F:16870, distal end of right; AM F:18544, left; AM F:18751, right; AM F:18752, right; AM F:18755, right; AM F:18756, left, associated with hind foot (AM F:1833-4), figured in Anderson (1930: pl. 49, fig. 1); AM F:18759, left; AM F:18761, right; AM F:18762, right; AM F:18763, distal end of left; AM F:20507, right, probably associated with AM F:20505-6; AM F:49141, right; AM F:49141, left; AM F:61110 (figs. 17, 18), disarticulated right, associated with skull, carapace, postcrania; AM F:61110 (figs. 17, 18), left, attached to carapace; AM F:81955, right; AMNH 20950, proximal end; AMNH 20985, distal end; BMNH R684a, distal end of left; BMNH R846b, distal end; MM F:13824, femur; MM F:13825, left, figured in Anderson (1925: pl. 40, fig. 2).

Size variation in *Meiolania platyceps* femora is considerable (table 5). The longest fairly complete femur is AM F:1203 with a length of 213 mm. But AM F:1788 is a distal end

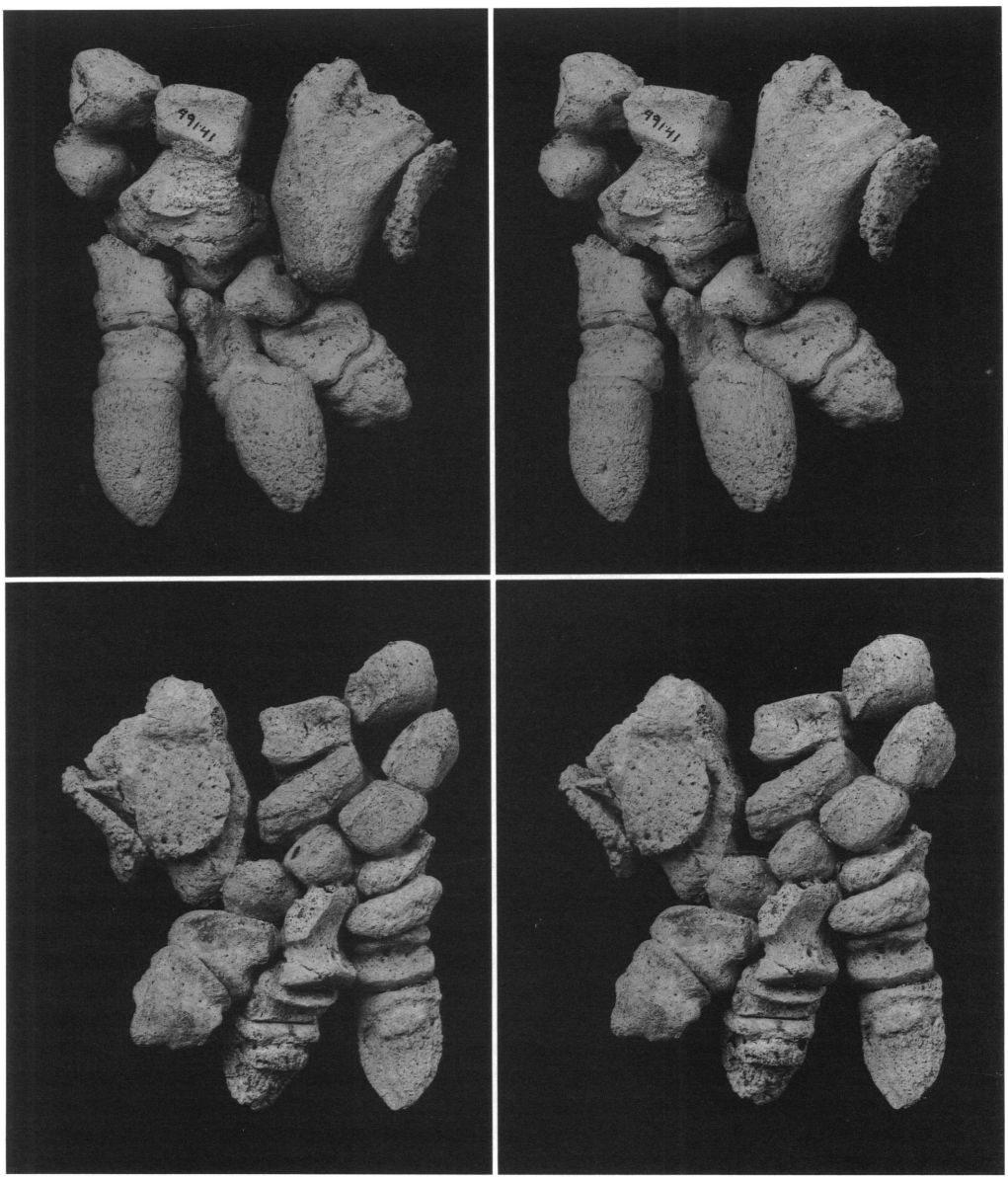


Fig. 41. *Meiolania platyceps,* AM F:49141, stereophotographs of partial right manus in dorsal view (upper) and ventral view (lower).

of a femur with a width that would indicate a length of 274 mm, if proportions are the same as in other femora. The smallest fairly complete femur is AM F:61110 at 134 mm. Besides variation in size, there is some variation in expression of surface rugosity and ossification of edges around articular surfaces. The intertrochanteric fossa in most *Meiolania* is a broad groove open ventrally. In a few *Meiolania* femora the fossae are partially closed off at the base of the trochanters. This is most developed in AM F:49141; it does not seem to be size related.

The femur of *Meiolania* is similar to the

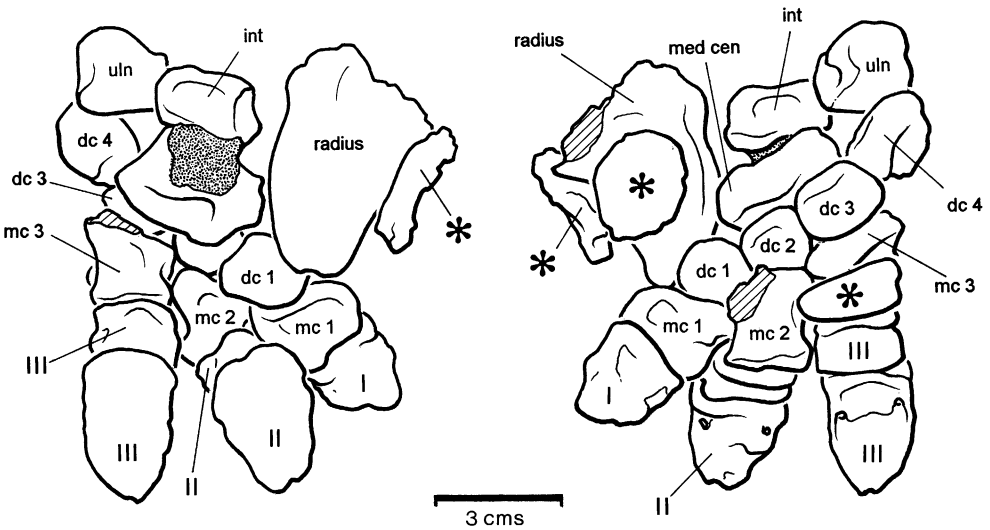


Fig. 42. *Meiolania platyceps,* AM F:49141, partial right manus, key to fig. 41. Abbreviations: dc distal carpal, int intermedium, mc metacarpal, med cen medial centrale, uln ulnare, * osteoderm. Roman numerals are phalanges and unguals.

femur of many other cryptodires, such as *Macroclemys.* As with the other limb bones, the femur of *Meiolania* is generally stockier and more robust, with wider ends, than in *Macroclemys.*

The proximal articulation of the femur with the acetabulum in *Meiolania* differs from *Proganochelys, Macroclemys* and most cryptodires in being rounder and more hemispherical, but it agrees in this feature with some testudinids. Zug (1971) concluded that a circular/spherical femoral head is associated with walking, terrestrial or bottom walking, as opposed to a more elongate head, which is associated with swimming. *Glyptops* and baenids have an elongate head, very similar to *Pseudemys,* while *Chelydra* and *Macroclemys* are more spherical, but not to the degree seen in *Meiolania.*

The trochanter minor is the more anterior of the two femoral trochanters. In *Meiolania* the trochanter minor does not extend proximally as much as the trochanter major but otherwise they are about the same size. Other than being slightly thicker, the trochanter minor of *Meiolania* agrees closely with that in *Macroclemys.*

The trochanter major in *Meiolania* is distinctly separated from the femoral head. In *Proganochelys, Glyptops,* baenids, *Macroclemys,* and many other cryptodires, the trochanter is connected to the head by a web of bone. A separate trochanter, however, is common in cryptodires, occurring in *Pleurosternon, Kallokibotion,* and emydids.

Between the two trochanters on the ventral surface is the intertrochanteric fossa. This curved surface does not vary much among the more primitive cryptodires, but in testudinids a web of bone extends between the trochanters to close the fossa ventrally. A few specimens (see above) of *Meiolania* have a partial development of a web but most do not.

The distal end of the femur in *Meiolania* consists of two poorly differentiated condyles, an anterior one bearing the anterior part of the tibial articulation, and a posterior one bearing the rest of the tibial articulation and the fibular articulation on its posterior margin. In *Meiolania* the ridge separating the tibial and fibular articulations is particularly well developed, more so than in *Proganochelys, Glyptops,* baenids, and *Macroclemys. Meiolania* has a large and well-developed fibular articulation extending posteri-

Fig. 43. *Meiolania platyceps,* AM F:49141, left forelimb in distal view (upper), ventral view (lower left) and dorsal view (lower right).

orly from the base of the fibular condyle. A well-developed fibular epicondyle is rare in cryptodires, although one very similar to *Meiolania* occurs in *Proganochelys. Glyptops,* baenids, and *Macroclemys* lack an expanded fibular epicondyle.

TIBIA (fig. 46)

Material available: AM F:209a, right; AM F:209b, right; AM F:209c, left; AM F:209d, left; AM F:213 (part), left; AM F:1202, left; AM F:5477, right; AM F:5526, left; AM

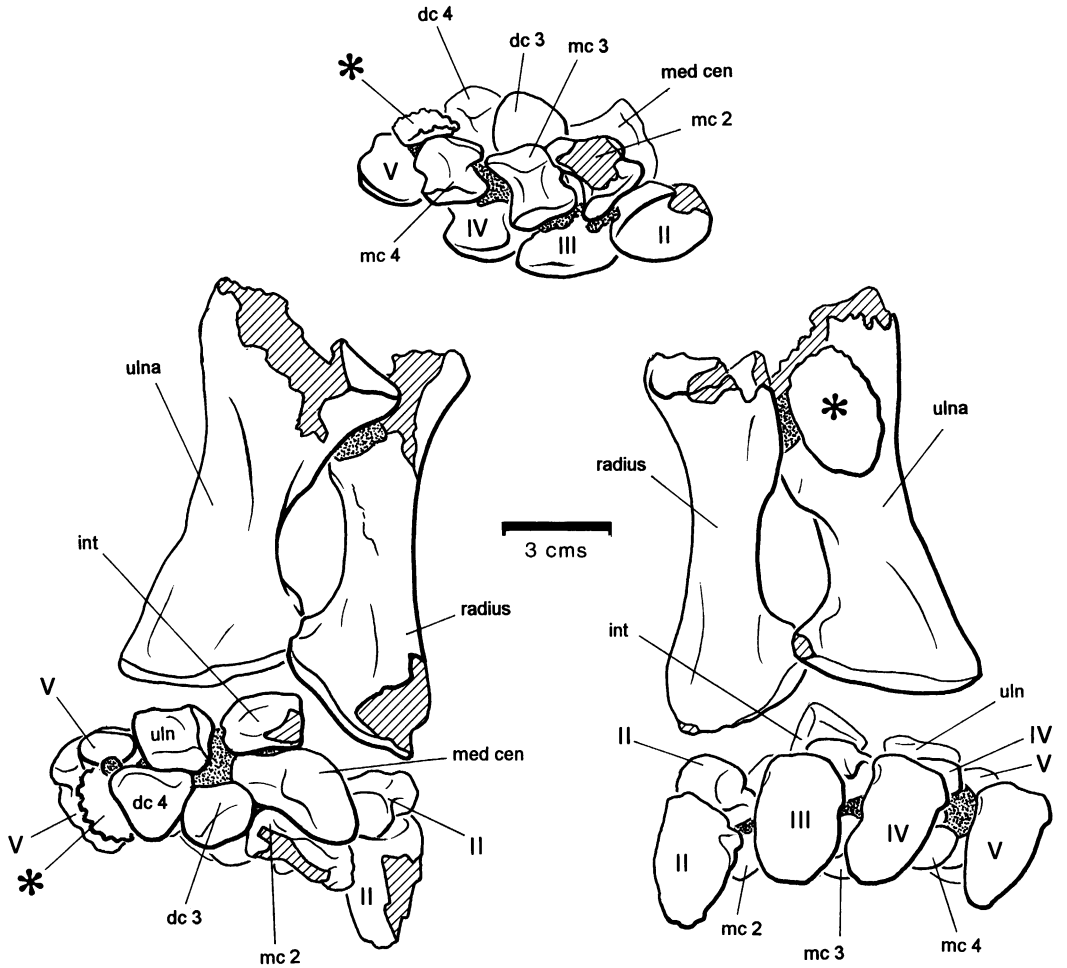


Fig. 44. *Meiolania platyceps,* AM F:49141, left forelimb, key to fig. 43. Abbreviations: dc distal carpal, int intermedium, mc metacarpal, med cen medial centrale, uln ulnare, * osteoderm. Roman numerals are phalanges and unguals.

F:18318, right; AM F:18319, left; AM F:18375, left; AM F:18547, left; AM F:18832, right; AM F:18833, left, used in cast; AM F:18833, left, figured in Anderson (1930: pl. 49); AM F:18836, left; AM F:18841, right; AM F:18842, right; AM F:18844, right; AM F:49141, left; AM F:49141, right; AM F:57984, right, used in cast; AM F:82008, left; AM F:82012, proximal end of right; AM F:82014, distal end of right; MM F:13844, left, figured in Owen (1888: pl. 36, figs. 1–4).

The tibia in *Meiolania platyceps* varies primarily in size (table 6), 70 mm the smallest and 110 mm the largest complete tibia, but tibial fragments AM F:82014 and AM F:82008 are larger.

Compared with other turtles, the tibia of *Meiolania* is stout and massive, more so than in *Proganochelys* and testudinids, which have the most robust of turtle tibias. Proximally the tibia is expanded to bear the articulation with the femur. There is a shallow, medial concavity for the medial condyle of the femur and a convex, lateral area for the trough between the condyles. *Meiolania* has a large rugose area on the dorsal side just distal to

TABLE 4
Preserved Material of Carpus and Manus

Meiolania platyceps	49141	57984	923	5542*	18835*
ulnare	L,R	-,R	-,-	L,-	-,-
intermedium	L,R	-,R	-,-	L,R	-,R
medial centrale	L,R	-,R	-,R	L,R	-,-
distal carpal 1	-,R	-,R	-,R	-,-	-,-
distal carpal 2	-,R	-,R	-,R	-,-	-,-
distal carpal 3	L,R	-,R	-,R	L,R	-,-
distal carpal 4	L,R	-,R	-,-	L,-	-,-
distal carpal 5	-,-	-,-	-,-	-,-	-,-
metacarpal I	-,R	-,R	-,R	L,R	-,-
metacarpal II	L,R	-,R	-,R	L,R	-,R
metacarpal III	L,R	-,R	-,R	-,R	-,-
metacarpal IV	L,-	-,R	-,R	L,R	-,-
metacarpal V	-,-	-,R	-,-	?L,-	-,-
phalanx I	-,R	-,R	-,R	-,-	-,-
phalanx II	L,R	-,R	-,R	L,R	-,R
phalanx III	L,R	-,R	-,R	-,R	-,-
phalanx IV	L,-	-,R	-,-	-,-	-,-
phalanx V	L,-	-,R	-,-	?,?	-,-
ungual I	-,-	-,R	-,-	-,-	-,-
ungual II	L,R	-,R	-,R	-,-	-,-
ungual III	L,R	-,R	-,R	-,-	-,-
ungual IV	L,-	-,R	-,-	-,-	-,-
ungual V	L,-	-,-	-,-	?,?	-,-

* Not articulated—identifications based on morphology only.

the femoral articulation, and this area bears the attachment of the patellar tendon. The attachment area is unusually broad and extensive, particularly when compared with *Glyptops,* baenids, and *Macroclemys.*

The proportions of the shaft of the tibia in *Meiolania* are as massive as in testudinids and appear to exceed them. Toward the distal portion of the shaft along its ventral edge, is an elongate rugosity, similar to one described in *Proganochelys,* (Gaffney, 1990: 239), but more rugose and larger. This ridge apparently bears the attachment of the popliteus (Walker, 1973), a muscle with fibers that pass ". . . diagonally from their origin on the tibial side of the fibula to their insertion on the fibular side of the tibia" (Walker, 1973: 89). The popliteus is described by Walker (ibid.) as a pronator of the foot, producing rotation of the tarsus by moving the fibula with respect to the tibia. The popliteal attachment area on the fibula in *Meiolania* is similarly enlarged and rugose. In *Meiolania* the massive proportions of tibia and fibula and the close proximity to each other of the tibial and fibular popliteus sites, suggests a relatively strong and perhaps less flexible relationship between tibia and fibula compared with other turtles.

The distal articulation surface on the tibia of *Meiolania* has the distinctive medial dome and lateral shallow concavity seen in most turtles. As in *Proganochelys,* the tibial/astragalocalcaneum contact is relatively tight.

FIBULA (fig. 47)

Material available: AM F:209 (part), right proximal end; AM F:5534, right; AM F:18832, right; AM F:18833, left, figured in Anderson (1930: pls. 47, 49, figs. 4–6;) used in cast; AM F:18837, right distal end; AM F:20512, right distal end; AM F:20513, left; AM F:49141, left distal end; AM F:50638, left.

The fibula of *Meiolania* (table 7) is only slightly thicker than the fibula of *Proganochelys* and is similar to the fibula in some testudinids. It is significantly more massive than the fibula in *Glyptops,* baenids, and *Macroclemys.* The remaining features of the *Meiolania* fibula are quite similar to the fibula in other cryptodires.

The proximal articulation surface is angled ventroproximally to articulate on the lateral condyle of the femur. This surface is similar in shape to *Proganochelys* and *Macroclemys* but it is relatively much larger. The shaft of the fibula in *Meiolania* is also relatively thicker than in other turtles. The distal articulation surface of the fibula is expanded mediolaterally as in other turtles but to a greater degree. The thickened ridge on the ventral side of the articulation surface provides a relatively wide contact surface with the astragalocalcaneum in *Meiolania,* it is usually smaller in other turtles.

TARSUS AND PES (figs. 48–52)

Material available (see table 8): The hind foot of *Meiolania* is known from an articu-

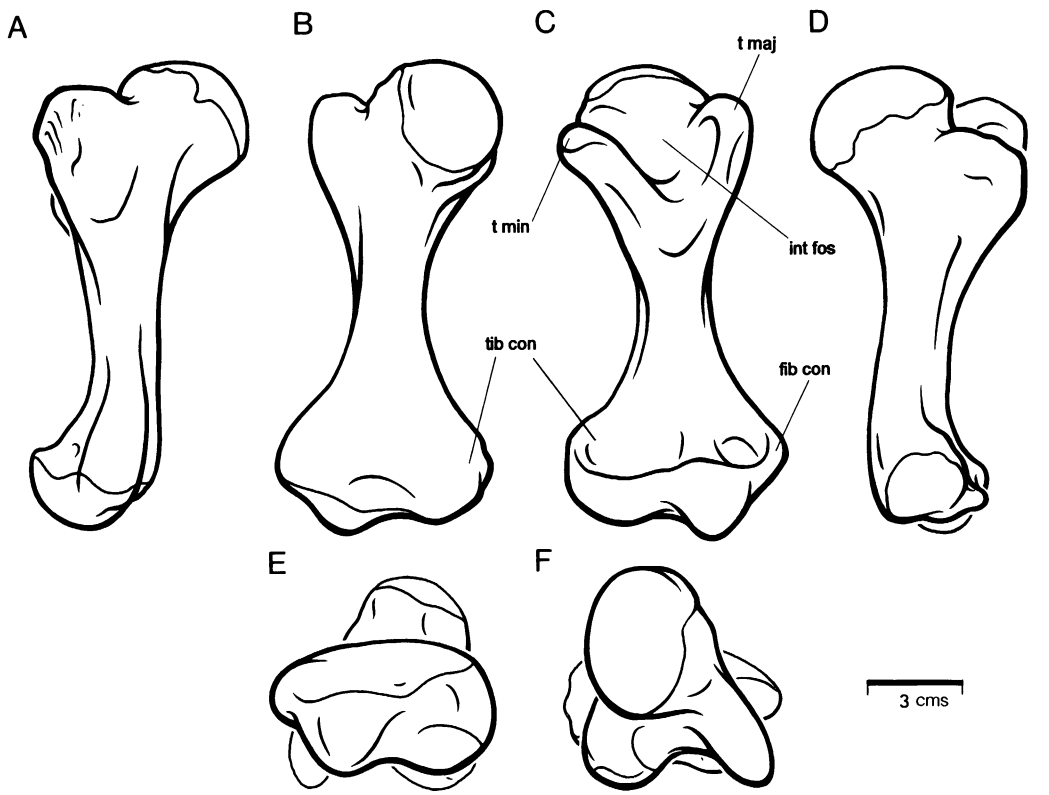


Fig. 45. *Meiolania platyceps.* Right femur, AM F:57984 with additions from AM F:18756. **A,** Posterior; **B,** dorsal; **C,** ventral; **D,** anterior; **E,** distal; **F,** proximal. Abbreviations: fib con fibular condyle, int fos intertrochanteric fossa, t maj trochanter major, t min trochanter minor, tib con tibial condyle.

lated right foot of AM F:57984 (figs. 51, 52), a partially articulated left foot of AM F:49141 (fig. 48), a partially articulated left foot of AM F:18833, and disarticulated elements in AM F:5542 and 5543 (see also Appendix 2 in Gaffney, 1983).

The astragalus and calcaneum of *Meiolania* (figs. 48–50) are completely fused with no indication of a suture in any of the three available specimens. *Proganochelys* and many casichelydians have a suture zone between these elements (Gaffney, 1990). There is also no indication of a centrale, either as a separate ossification or as an area set off by a suture. The shape of the astragalocalcaneum does not vary a great deal in turtles (Rabl, 1910; Zug, 1971), and that bone in *Meiolania* compares closely with the condition seen in *Proganochelys,* baenids, and chelydrids. It is an irregular, blocklike element tapering laterally. Proximally there is a concave articulation surface for the tibia medially and the fibula laterally. The tibial surface has a low ridge that fits a trough on the distal end of the tibia. In *Meiolania* the tibia and fibula meet distally and the two astragalar articulation surfaces meet to form a ridge (fig. 49), in contrast to the trough seen in *Proganochelys* and some other turtles (Gaffney, 1990). Distally the astragalocalcaneum of *Meiolania* has a convex swelling forming part of the plantar surface of the foot, somewhat larger and better developed than in *Proganochelys.*

The distal tarsals of *Meiolania* are poorly preserved and only two are known from an articulated specimen (AM F:49141 left hindfoot, fig. 48). A number of disarticulated dis-

TABLE 5
Femur Measurements (mm)

Meiolania platyceps	Max. length	Max. proximal width	Max. distal width
AM F:18756	171	69	77[1]
AM F:61110	134	47	58[1]
AM F:57984 (right)	162	65	—
AM F:57984 (left)	165	—	67[1]
AM F:49141 (right)	194	—	—
AM F:49141 (left)	189	—	—
AM F:18759	138	48[1]	60
AM F:18755	175	71	80
AM F:1552 (cast)	196	80	96
AM F:"1788"	—	—	112
AM F:81955	—	79	—
AM F:10773	135	44	55
AM F:18752	130	42	55
AM F:20507	154	60	68
AM F:16858	194	70+?[1]	94
AM F:1203	213	80	89[1]
AM F:17665 (*mackayi*)	—	38[2]	—

[1] Broken.
[2] Estimated.

TABLE 6
Tibia Measurements (mm)

Meiolania platyceps	Maximum length	Maximum proximal width	Maximum distal width
AM F:49141 (right)	110	55	42
AM F:49141 (left)	—	—	43
AM F:18547	70	—	43
AM F:82008	—	68	—
AM F:82014	—	—	55
AM F:18833	92	50	41
AM F:57984	92	52[1]	39

[1] Estimated.

tal tarsals appear in the collections and there is no reason to think that *Meiolania* did not have the common chelonian number of four, but only two are known definitely. The fourth distal tarsal of *Meiolania* is the largest distal tarsal and is similar to that bone in other turtles. As in other turtles it fits into a con-

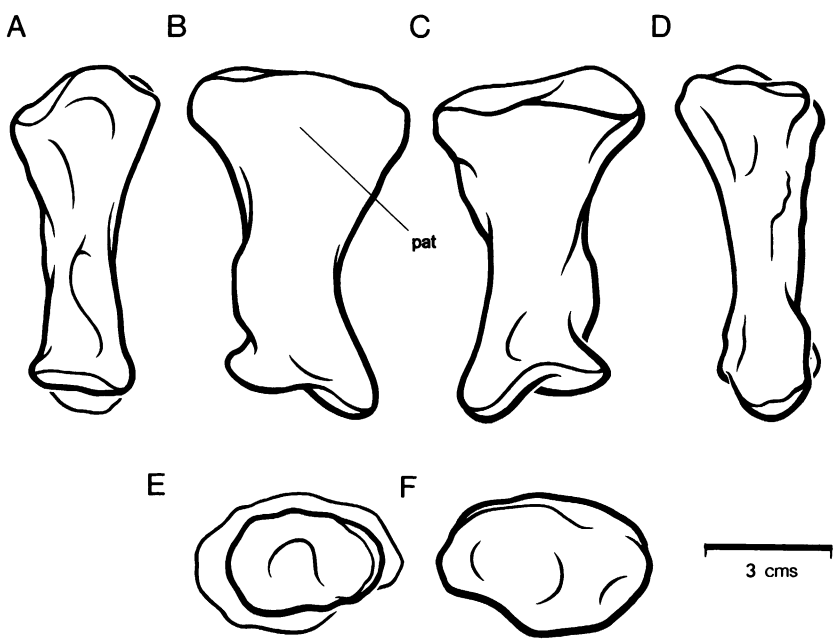


Fig. 46. *Meiolania platyceps*. Right tibia, AM F:57984 with some restoration from AM F:18833. **A**, Lateral; **B**, dorsal; **C**, ventral; **D**, medial; **E**, distal; **F**, proximal. Abbreviation: pat patellar tendon attachment.

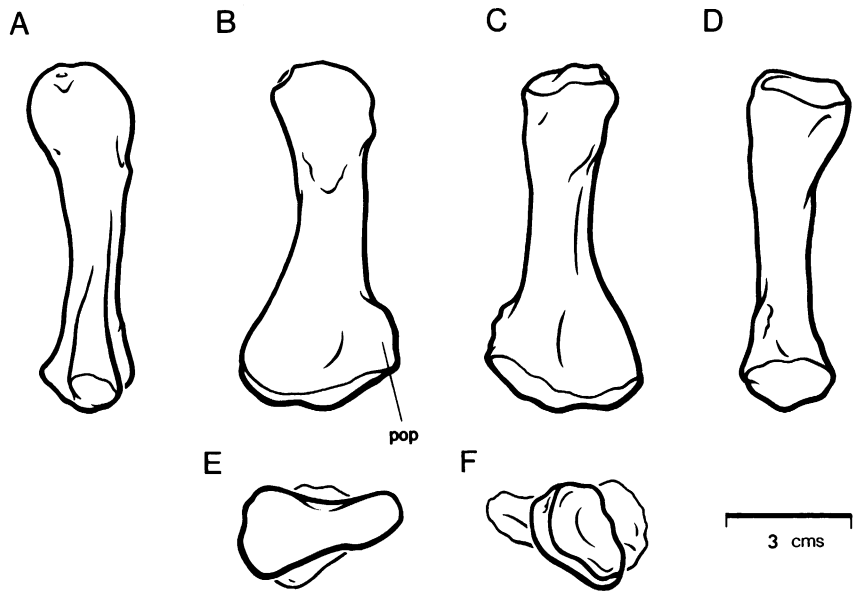


Fig. 47. *Meiolania platyceps.* Right fibula, composite of AM F:57984 and AM F:18833. **A,** Lateral; **B,** dorsal; **C,** ventral; **D,** medial; **E,** distal; **F,** proximal. Abbreviation: pop popliteus.

cavity on the astragalocalcaneum and loosely articulates with metatarsals four and five. The fourth distal tarsal in *Meiolania* is conical with the narrow end ventral. In contrast to the fourth distal tarsal of chelydrids, this bone in *Meiolania* fits more loosely in the tarsus and does not have tight-fitting articular surfaces with surrounding elements. The other distal tarsal articulated in AM F:49141 appears to be distal tarsal 2. It is an irregular ovoid nodule, slightly flatter where it contacts the astragalocalcaneum. It is similar to that bone in *Macroclemys.*

The metatarsals of *Meiolania* are known from a complete set in AM F:57984 (figs. 51, 52) and an articulated set lacking metatarsal 5 in AM F:49141 (fig. 48). The metatarsals of AM F:49141 are unusual because they are partially fused together as the result of a pathologic condition. Metatarsals II and III are completely fused along their adjacent margin and metatarsals I and II are partially fused. Metatarsal IV appears to be normal. Most of the phalanges for this foot are missing but digit I is preserved and the phalanx and ungual depart considerably from the normal configuration by bony growths, although the articulations are not fused. This may be the result of injury or arthritis.

The metatarsals of *Meiolania* are similar to those in other turtles. They have wide proximal bases that strongly overlap, as in chelydrids and baenids, and are relatively shorter than in *Proganochelys* and chelydrids. *Meiolania* metatarsals show strong serial differentiation to a greater extent than seen in *Proganochelys* and chelydrids. Metatarsal I is wider than long with a large proximal base that only overlaps slightly with metatarsal II. It is wider than any of the other metatarsals. Metatarsal II and III are more

TABLE 7
Fibula Measurements (mm)

Meiolania platyceps	Maximum length	Maximum proximal width	Maximum distal width
AM F:50638	100	34	45
AM F:18832	94	28	42
AM F:20513	85	29	35
AM F:20512	—	—	35
AM F:18832	91	30	43
AM F:57984	—	—	38

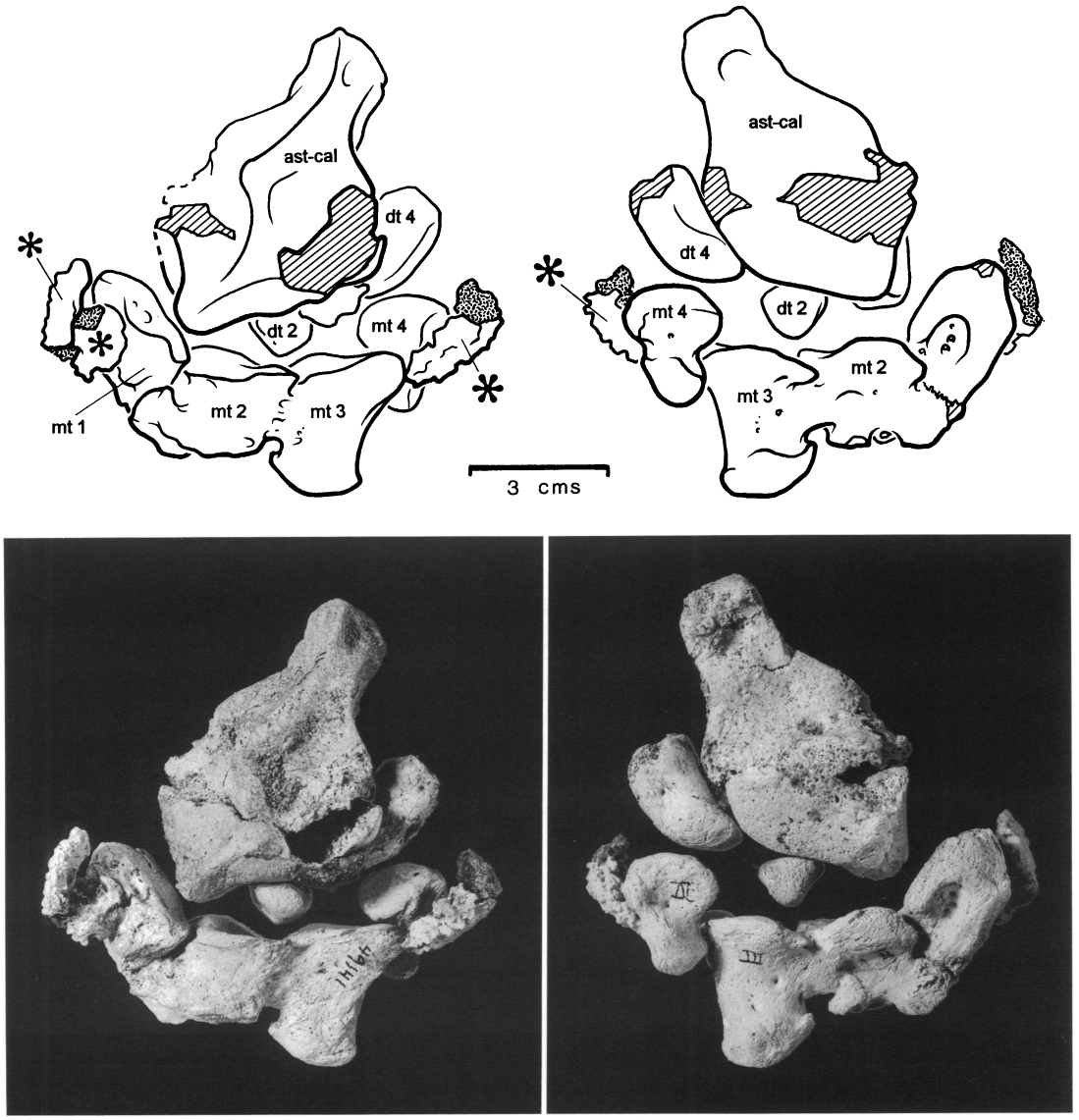


Fig. 48. *Meiolania platyceps,* AM F:49141, left tarsus and metatarsus associated in situ, dorsal views on left, ventral views on right. Abbreviations: ast-cal astragalocalcaneum, dt distal tarsal, mt metatarsal, * osteoderm.

"typical" in shape, with a narrow shaft, and wide bases that strongly overlap. They are longer than the other metatarsals with metatarsal II the longest. Metatarsals IV and V are short and stubby but significantly smaller than metatarsal I. Metatarsal V in *Meiolania* differs from most turtles, including *Proganochelys,* in not having a hooked shape. The metatarsal V of *Meiolania* is phalanx shaped although it does have the usual facet on its base for the articulation of the adjacent metatarsal. Metatarsal V differs from the other metatarsals in having a rugose distal surface rather than an articular surface as in the other metatarsals, because the fifth digit is absent in the *Meiolania* hind foot.

The hind foot phalangeal formula of *Meiolania* is interpreted here and in Gaffney (1990) as 2-2-2-2-0 (based primarily on AM F:57984 and AM F:18835), rather than 2-2-2-2-2 as

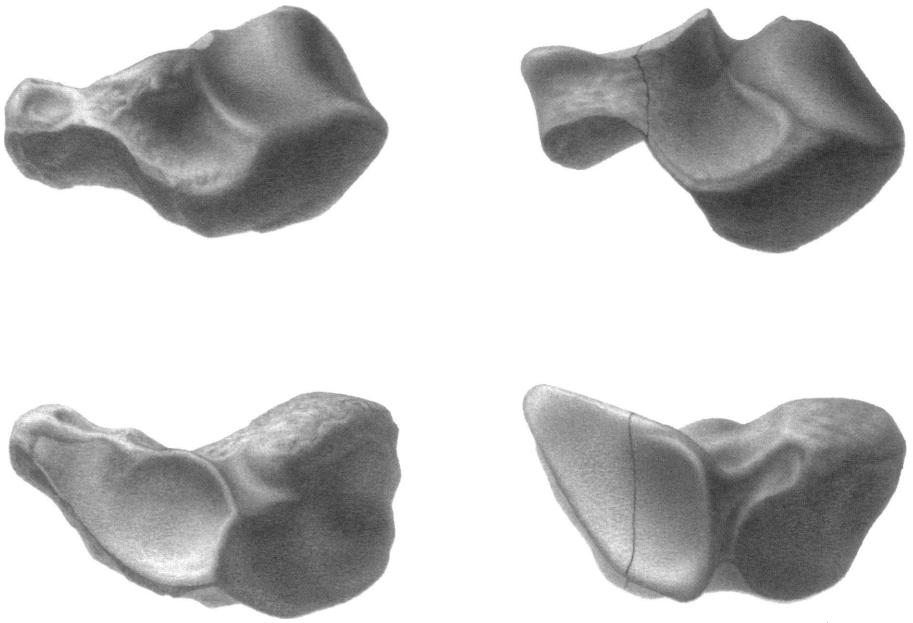


Fig. 49. Right astragalocalcaneum. See fig. 50.

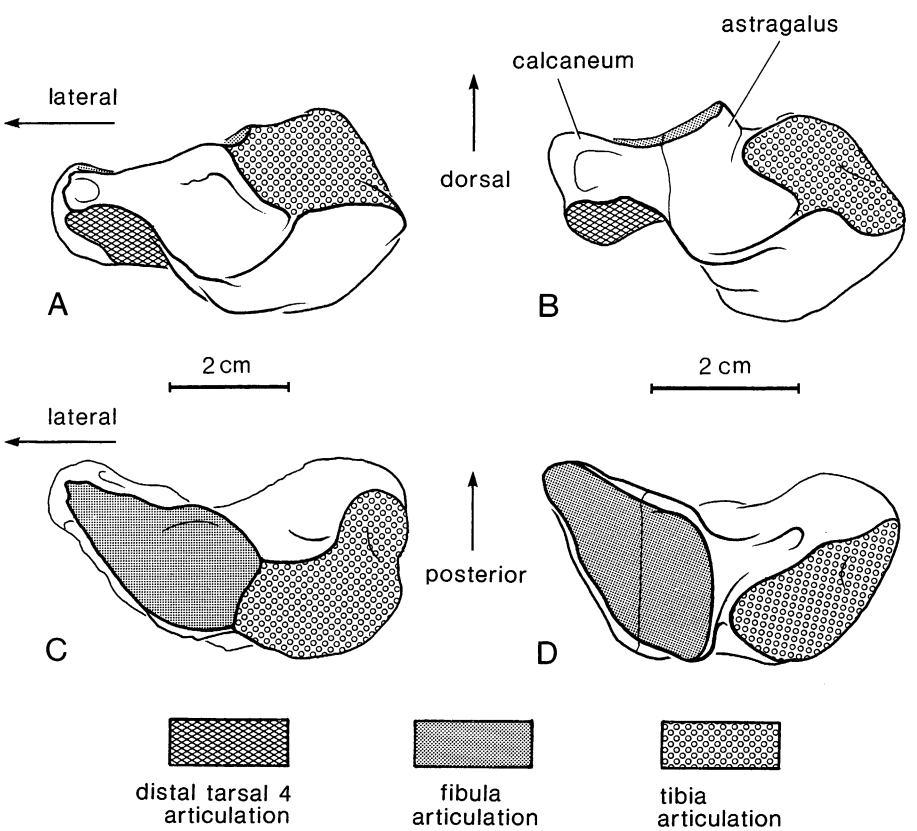


Fig. 50. Right astragalocalcaneum. **A, C,** *Meiolania platyceps,* AM F:57984; **B, D,** *Proganochelys quenstedti,* SMNS 17204 (left, reversed). Key to fig. 49. From Gaffney, 1990.

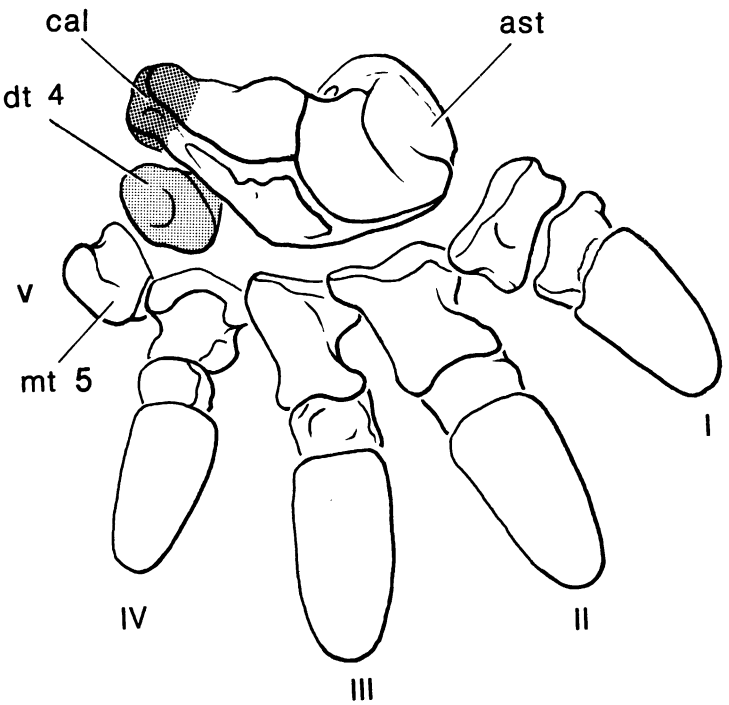


Fig. 51. *Meiolania platyceps,* AM F:57984, right pes in dorsal view, distal tarsals 1–3 not known in articulation. Abbreviations: ast astralgalus, cal calcaneum (in stipple), dt distal tarsal, mt metatarsal.

reported erroneously by Gaffney et al., (1992).

The proximal phalanx in the pes of *Meiolania* is broad in digit I but the other three are similar in size and shape. All the proximal phalanges are similar in both manus and pes. The proximal phalanges in *Meiolania* are short and blocklike, without a strong ventral flexor process as seen in *Proganochelys* and to a lesser extent in chelydrids.

The unguals of *Meiolania* are broad, flat, and not recurved, in contrast to *Proganochelys* and most primitive cryptodires. Unguals I and II are the largest with III and IV progressively smaller.

SKULL MORPHOLOGY (figs. 54–62)

Subsequent to the publication of the cranial morphology of *Meiolania platyceps* (Gaffney, 1983), three new skulls have become available and the sectioning of a braincase was completed. The high degree of variability in *Meiolania platyceps* increases the interest in new skulls of this species.

The three new skulls (figs. 54–57, table 10) are variably preserved. AM F:81965 is the least complete and is broken in many areas, but reveals much of the morphology of the internal surface of the skull roof and cheeks. AM F:64471 has suffered from breakage during collection by having two holes drilled through it, one through the right otic chamber and one through the base of the right B horn core. The left ventral margin of the cheek is missing. AM F:81965 lacks the braincase and palate but is otherwise nearly complete.

The conspicuous B horns are broken in AM F:82180 but they seem to match the longer horns seen in skulls like AM F:64471. The B horns of the new specimens do not extend the range of variation previously reported but

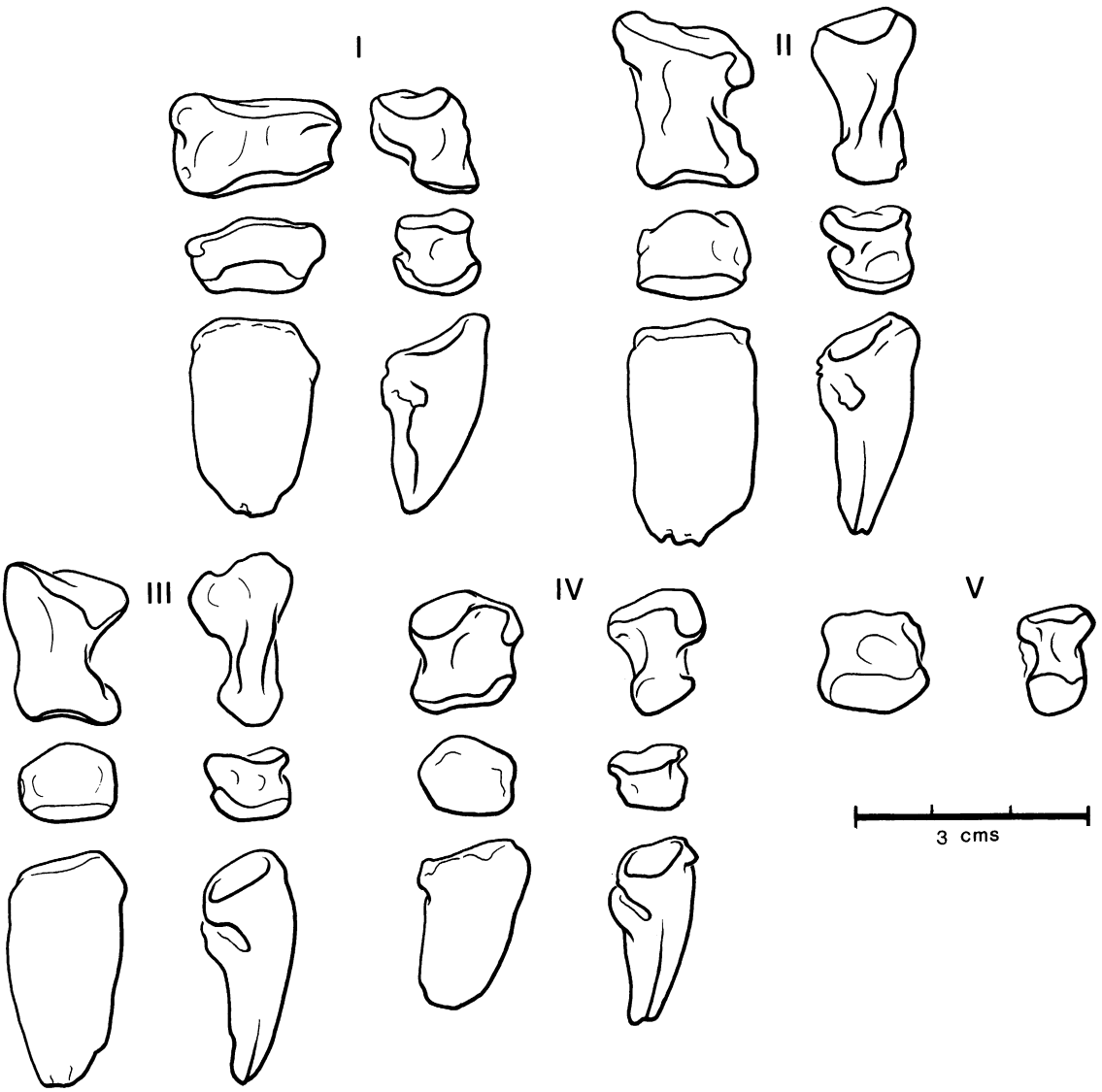


Fig. 52. *Meiolania platyceps,* AM F:57984, digits of right pes. Each digit is figured disarticulated in dorsal (left) and lateral (right) views. Proximal toward top of page.

they do provide more intermediates among the previously described skulls. AM F:81965 has B horns with a width/height ratio of 0.58, at the small end of the group reported in Gaffney (1983, table 1). The B horns of AM F:81965, however, are clearly longer than in AM F:43183 and approach those in AM F:61110. The B horns of the other new skull, AM F:64471, are long and narrow with a width/height ratio of 0.77, at the long end of the horn distribution.

SECTIONED BRAINCASE AM F:18668 (figs. 58–62)

The right ear region/basicranium of AM F:18668 (Gaffney, 1983: fig. 44) was removed

TABLE 8
Preserved Material of Tarsus and Pes

Meiolania platyceps	57984	49141	18833*	5542*
astragalocalcaneum	R	L	L	-
distal tarsal 1	-	-	-	-
distal tarsal 2	-	L?	-	-
distal tarsal 3	-	-	-	-
distal tarsal 4	R	L	L	L,R
metatarsal 1	R	L	L	L
metatarsal 2	R	L	L	L,R
metatarsal 3	R	L	L	-
metatarsal 4	R	L	-	-
metatarsal 5	R	-	L	-
phalanx I	R	L	L	-
phalanx II	R	-	L	-
phalanx III	R	-	L	-
phalanx IV	R	-	-	L
phalanx V	-	-	-	-
ungual I	R	L	-	L
ungual II	R	-	L	-
ungual III	R	-	-	L
ungual IV	R	-	-	L
ungual V	-	-	-	-

* Not in articulation—identification based on morphology only.

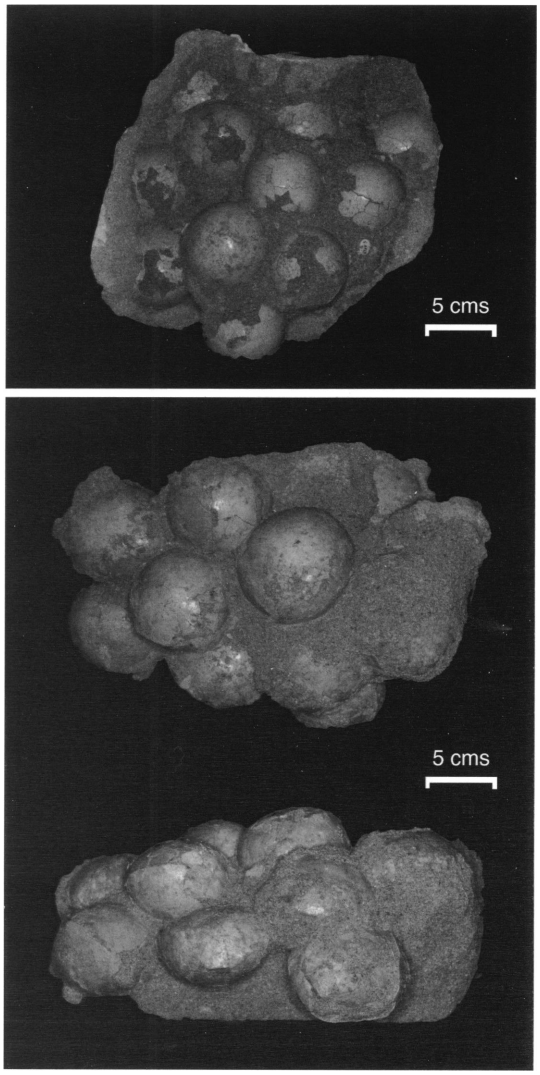


Fig. 53. Eggs presumed to belong to *Meiolania platyceps,* Ned's Beach Cliff (locality 5 in Gaffney, 1983), Lord Howe Island. **Top,** AM F:52080; **middle and bottom,** AM F:61401.

from the skull and sectioned transversely. These sections (figs. 58–62) allow tracing of some of the structures that make this area in *Meiolania* particularly complex. The braincase has been sectioned into four pieces (I–IV) by three cuts. In order to keep the parts of each section associated, the braincase was partially impregnated with wax. The sagittal contact with the other half of the skull was filled with plaster to further maintain stability. A cast of the sectioned braincase was made before sectioning and re-articulated with the rest of the skull. The cuts were made with a rock saw and they removed enough bone to make the opposing surfaces of each piece a bit different and informative. Therefore, each surface is illustrated. The pieces are arranged in order from posterior to anterior with the surface shown indicated by anterior or posterior labels. Thus III posterior is the posterior view (the surface facing posteriorly) of piece III. From back to front the arrangement is: I anterior, which is adjacent to II posterior, II anterior, which is adjacent to III posterior, and III anterior, which is adjacent to IV posterior. As the posterior surface of piece IV was not sectioned, it is not illustrated. Piece II and piece III, the only two pieces sectioned on both sides, are 6 mm and 8.5 mm thick respectively.

The sections are essentially supplements to the description and figures in Gaffney (1983: figs. 57–59) of the canalis caroticus internus

Fig. 54. *Meiolania platyceps.* Skull of AM F:82180, Old Settlement Beach (locality 1 in Gaffney, 1983), Lord Howe Island. **Upper left,** dorsal view; **upper right,** ventral view; **lower left,** left lateral view; **lower right,** anterior view.

and associated structures. This area of the skull is useful in obtaining characters relevant to cryptodire phylogeny, and it is particularly complex in *Meiolania.* Gaffney (1983: 447–449) described this region and should be consulted along with the sections shown here.

The sections have the sagittal midline as their medial margin (filled with plaster on this edge) and the foramen magnum/cavum cranii forms a quarter circle at the dorsomedial margin. The incisura columellae auris is seen in I anterior and II posterior and the edge of the cavum tympani forms the dorsolateral margin in the remaining sections. The processus interfenestralis is missing but would be visible in I anterior where the position of the fenestra ovalis is indicated by dashes. The processus would have formed the missing lower margin of the fenestra ovalis. Section I anterior shows the anterior surface of the posterior wall of the cavum acustico-jugulare.

The cavum labyrinthicum is in sections II posterior, II anterior, and III posterior. Its dorsal limits, including the semicircular canals, are largely missing and ventrally the bone has disintegrated in some places.

The most obvious canal extending anteroposteriorly through the sections is the canalis cavernosus. The canal is fully formed in sec-

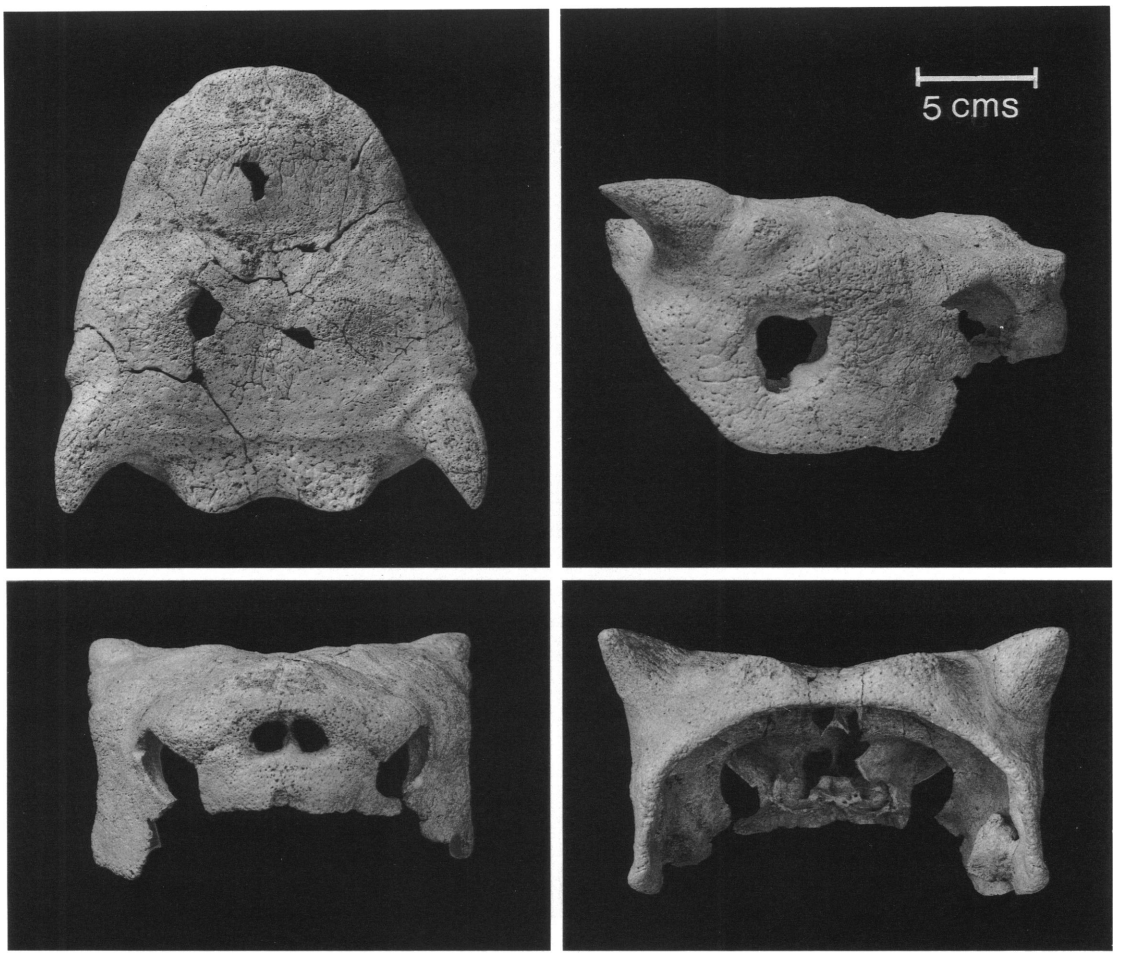


Fig. 55. *Meiolania platyceps.* Skull of AM F:81965, Ned's Beach Cliff (locality 5 in Gaffney, 1983), Lord Howe Island. **Upper left,** dorsal view; **upper right,** right lateral view; **lower left,** anterior view; **lower right,** occipital view.

tion II posterior and can be followed anteriorly through the sections to IV posterior. The separation of the stapedial artery is discernible in III posterior but the fully formed aditus canalis stapedio-temporalis is best seen in II anterior. The canalis stapedio-temporalis is almost completely separated from the canalis cavernosus in III posterior.

The path of the internal carotid artery begins posteriorly at the foramen posterius canalis carotici interni seen in II posterior. It can be followed anteriorly as the canalis caroticus internus in the remaining sections. In section III anterior the canalis lies very close to the pterygoid slit and in section IV posterior the canalis caroticus internus has a foramen, here identified as the foramen caroticum basisphenoidale, that communicates with the intrapterygoid slit (see Gaffney, 1983: figs. 58, 59). At this point the foramen pro ramo nervi vidiani extends ventrally from the canalis cavernosus to open near the foramen caroticum basisphenoidale. The position of this ventral opening of the foramen pro ramo nervi vidiani is more anterior and presumably more accurate than indicated in Gaffney (1983: fig. 59). The intrapterygoid slit is seen in III anterior and IV posterior.

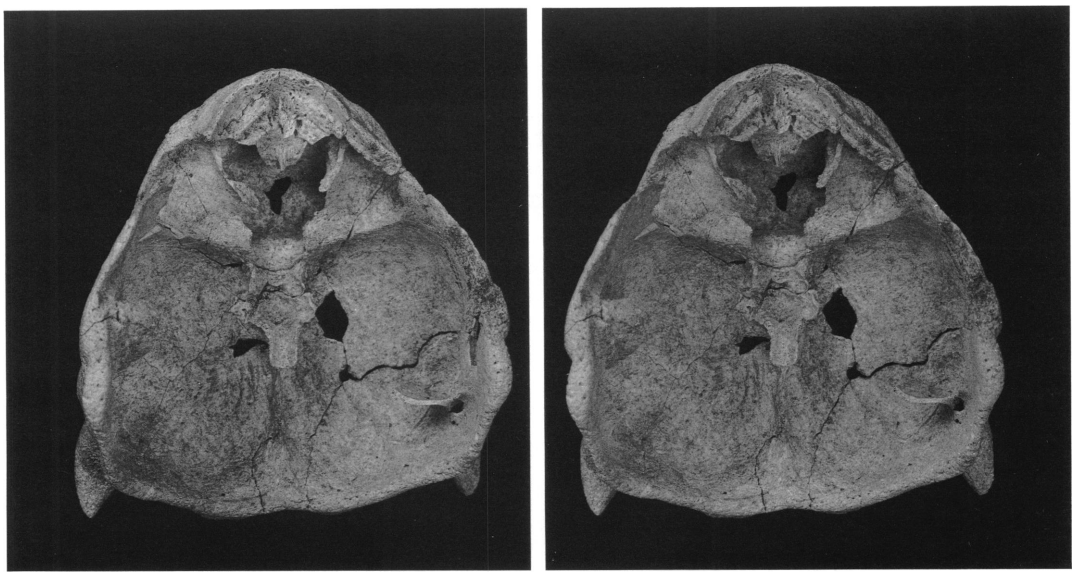


Fig. 56. *Meiolania platyceps,* AM F:81965, stereophotographs of ventral view of skull lacking braincase and palate.

One of the more puzzling questions in the *Meiolania* braincase is the path of the facial nerve. What is apparently the facial nerve has a posterior opening seen in II anterior and the adjacent III posterior. It extends anteriorly to open in the canalis cavernosus, visible in both III anterior and IV posterior, as described in Gaffney (1983: figs. 57, 59), although the actual relationships vary from the semi-diagrammatic reconstruction in figure 59 of that paper.

REVIEW OF THE FAMILY MEIOLANIIDAE

SYSTEMATICS

Order Testudines

Megaorder Cryptodira

Parvorder Eucryptodira

Suborder Meiolanoidea

Family Meiolaniidae

TYPE GENUS: *Meiolania* Owen, 1886b.

KNOWN DISTRIBUTION (figs. 88, 89): Eocene (possibly Cretaceous) of Argentina, Miocene to Pleistocene of mainland 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: Gaffney et al., 1984; Gaffney et al., 1992; Gaffney, 1985a, 1985b, 1992; Megirian, 1989, 1992; 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 posterolaterally 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 ex-

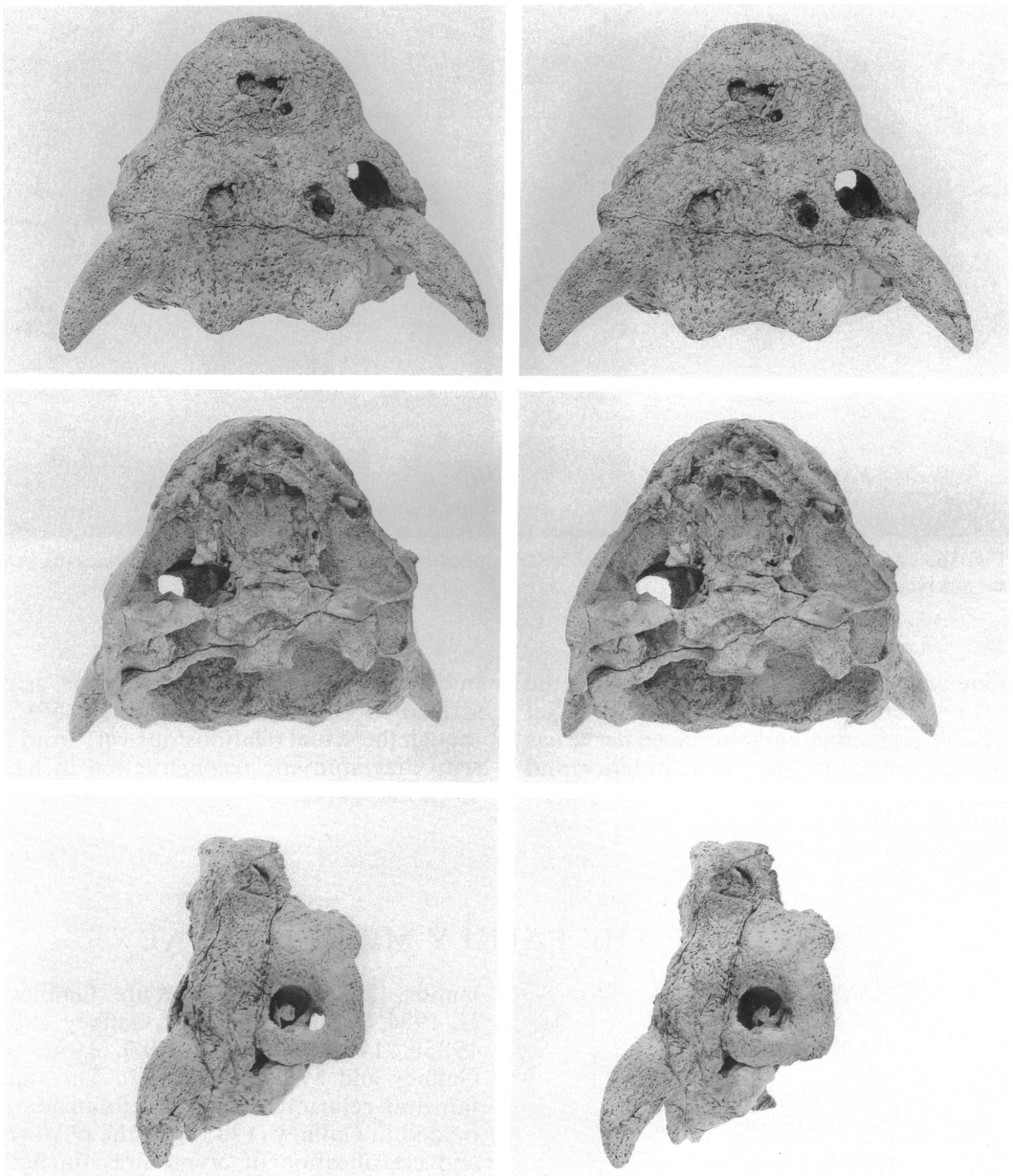


Fig. 57. *Meiolania platyceps*. Skull of AM F:64471, Ned's Beach tidal exposures (locality 4 in Gaffney, 1983), Lord Howe Island. Stereophotographs of dorsal view (upper), ventral view (middle), and right lateral view (lower).

tensive 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 turtles (determinable only in *Meiolania* and *Ninjemys*); broad squamosal/quadratojugal contact ventral to completely enclosed incisura

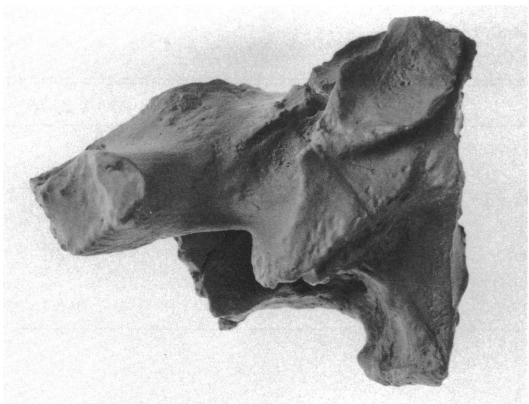
TABLE 9
Skull Measurements (cm)
(see table 2 in Gaffney, 1983)

Meiolania platyceps	AM F:82180	AM F:64471	AM F:81965
Length from anterior margin of premaxillae to posterior margin of occipital condyle	15.5	13.9	–
Length from anterior margin of nasals to posterior margin of skull roof	20.8	18.0	17.7
Skull width measured at base of "A" horn cores	21.0[1]	18.1	16.8
Skull width measured at lateral margin of area articularis mandibularis	19.0[1]	18.2	16.2
Skull height measured from skull roof to ventral margin of cheek at position of cavum tympani	11.0[1]	10.9	9.5

[1] Estimated.

TABLE 10
Comparison of Three Skulls of *Meiolania platyceps*
(see table 3 in Gaffney, 1983)

	AM F:82180	AM F:64471	AM F:81965
Locality	Old Settlement Beach (locality 1 of Gaffney, 1983)	Ned's Beach (locality 4 of Gaffney, 1983)	Ned's Beach Cliff (locality 5 of Gaffney, 1983)
Collector	Alex and Edith Ritchie, 1984	AMNH-AM party, June 1980	Mark Thompson, 1990
Figures and literature	None	None	None
Skull areas	Right cheek and most of braincase missing, left B horn broken	Nearly complete except for two holes drilled through it	Skull roof and cheeks complete, braincase and palate missing
Other elements preserved	Lower jaws, badly fractured shell	None	None
Sutures	Postorbital, jugal, quadratojugal, all others fused	Squamosal, supraoccipital, others fused	Nearly all fused
Bone thickness	Intermediate	Intermediate	Intermediate
Scale expression	Good	Not as distinct as AM F:57984	Very good
C horn	Distinct, as in AM F:61110	Very well developed as in AM F:57984	Distinct, as in AM F:61110
Bulge in D-scute area	Low, thin bone	Low, thin bone	Thick bone but not convex as in AM F:57984
Preorbital "boss" in scale area F	Well developed	Well developed	Well developed
B-horn	Curved postero-ventrally	Curved postero-ventrally	Curved postero-ventrally
B-horn length	55 mm as preserved, probably 70–80 mm originally	70 mm	45 mm
B-horn width	55 mm	41 mm	35 mm
Internarial septum	Complete	Complete	Complete
Nasal overhang	None	Slight	None
Choanal grooves on vomer and palatine	Indeterminate	Deepest anteriorly	Indeterminate
Labial ridge	Indeterminate	Intermediate	Indeterminate
Processus trochlearis oticum	Moderate	Indeterminate	Indeterminate
Processus interfenestralis of opisthotic	Ventral margin fused	Indeterminate	Indeterminate



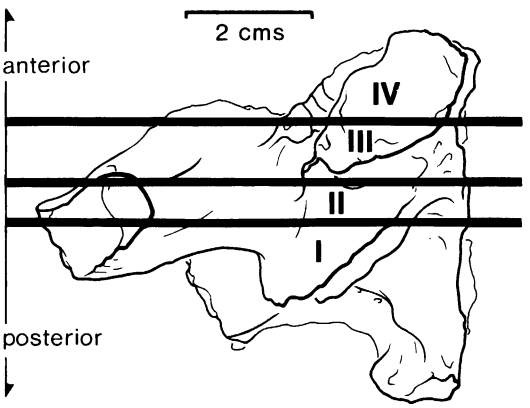
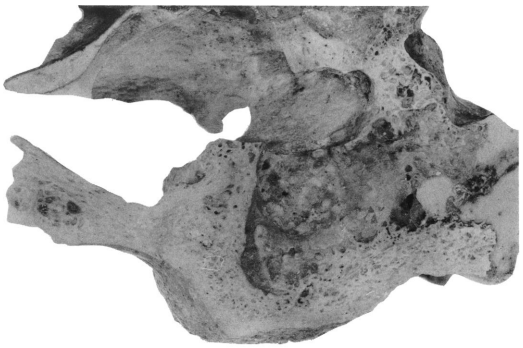
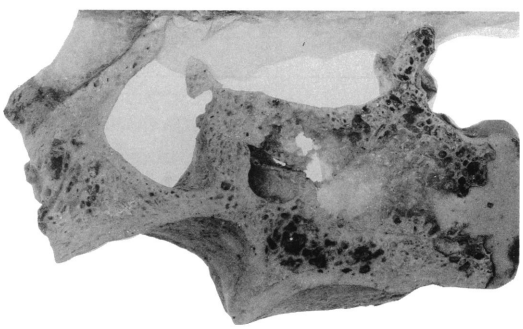


Fig. 58. *Meiolania platyceps,* AM F:18668, right half of basicranium in ventral view, showing positions of sections. Sectioned pieces are numbered, as indicated in following figures. See figures of complete skull in Gaffney (1983: fig. 44) for orientation.





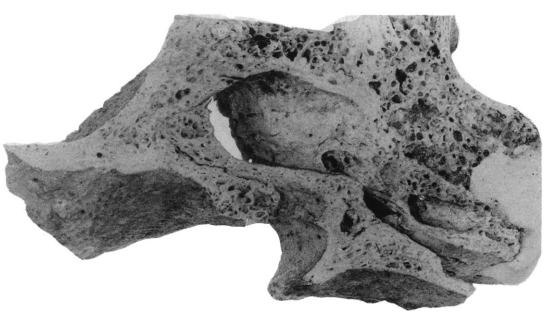


Fig. 59. *Meiolania platyceps,* AM F:18668. Anterior views of sectioned pieces; I (top), II (middle), III (bottom).

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 turtles; 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); 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 ligamentously attached to carapace;

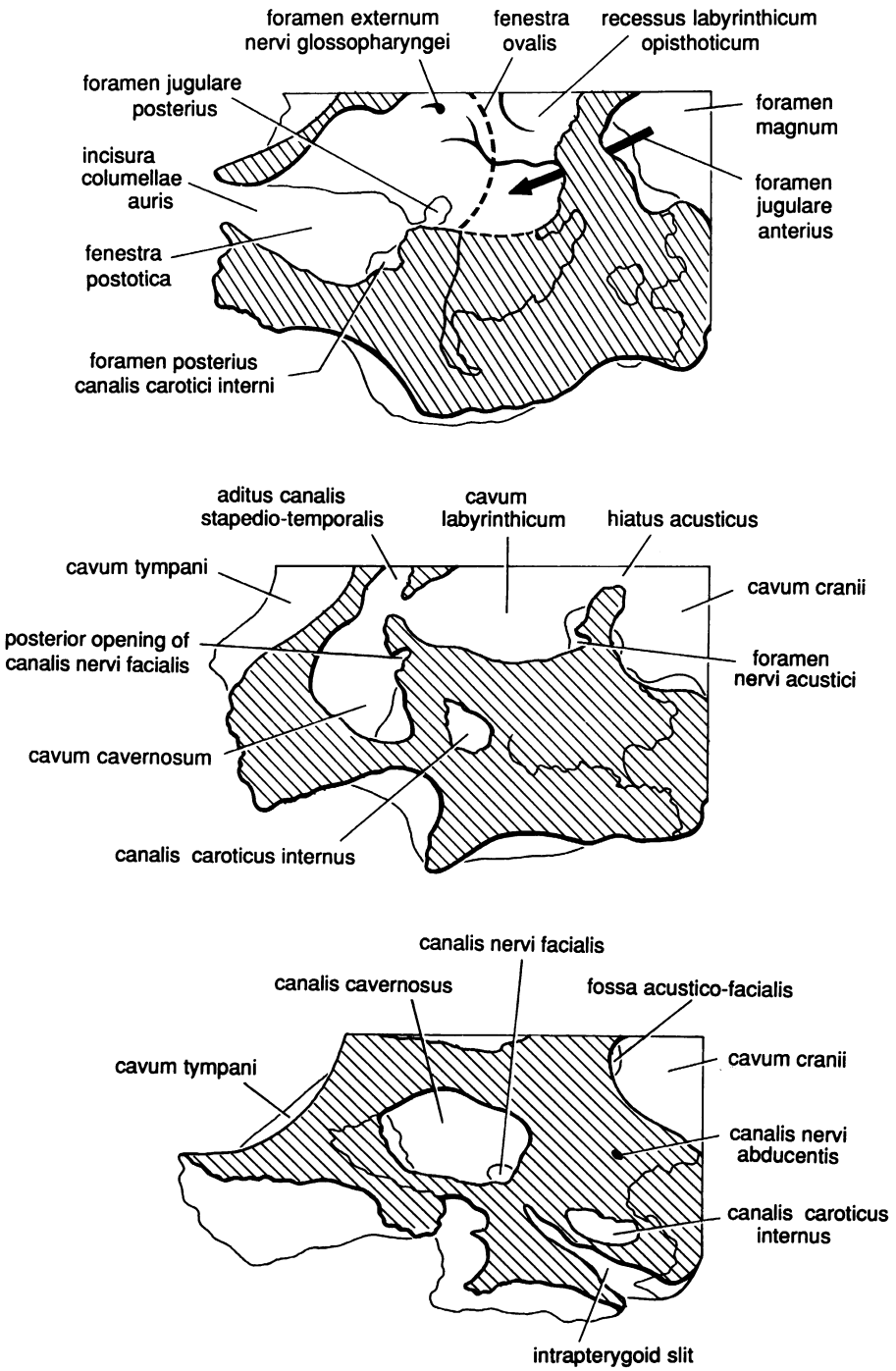


Fig. 60. *Meiolania platyceps,* AM F:18668, key to fig. 59. anterior views with midline on right, lateral on left.

axillary and inguinal buttresses do not extend onto costals; mesoplastra absent as in other eucryptodires; plastron with irregular fontanelles on midline; carapace with first thoracic vertebra facing anteriorly 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.

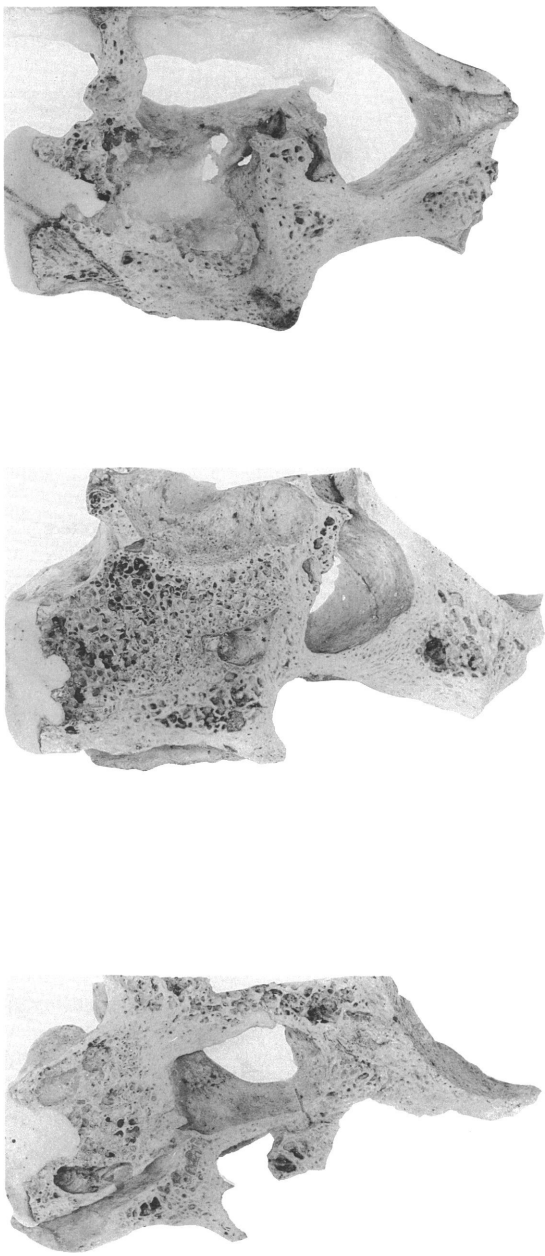


Fig. 61. *Meiolania platyceps,* AM F:18668. Posterior views of sectioned pieces; II (top), III (middle), IV (bottom).

Niolamia Ameghino, 1899

Crossochelys Simpson, 1937.

TYPE SPECIES: *Niolamia argentina* Ameghino, 1899.

ETYMOLOGY: None given.

KNOWN DISTRIBUTION: Eocene (and possibly earlier), Province of Chubut, Argentina (Simpson, 1938).

DIAGNOSIS: A meiolaniid known only from skull and tail ring, characterized by the unique possession of D scales separated by a large X scale, and A scales significantly larger than in any other meiolaniid; within meiolaniids the unique possession of an undivided apertura narium externa and only one accessory ridge on maxillary triturating surface; nasal bones not projecting beyond rest of skull; B scale projecting posterolaterally and not recurved as in *Meiolania,* D scale area relatively high in contrast to *Meiolania*; A, B, and C scales form a large shelf at back of skull as in *Ninjemys* but more extensive than in *Ninjemys*; intrapterygoid slit not covering foramen caroticum basisphenoidale; tail ring closed ventrally as in *Ninjemys.*

Niolamia argentina Ameghino

TYPE SPECIMEN: Neotype skull (fig. 63) designated by Simpson (1938: 242) is in La Plata Museum and was figured by Woodward (1901: pls. 15–17), Moreno (1899, fig. 2), and Ameghino (1906: figs. 14, 15).

TYPE LOCALITY AND HORIZON: In the type announcement of the name *Niolamia argentina,* Ameghino (1899: 10) refers to skull, shell, and dermal ossicles of this form coming from "formació guaranítica del Sehuen y del Chubut" (also quoted in Simpson 1938: 241). Florentino Ameghino considered *Niolamia argentina* as Cretaceous, but he included as Cretaceous faunas and horizons that are now

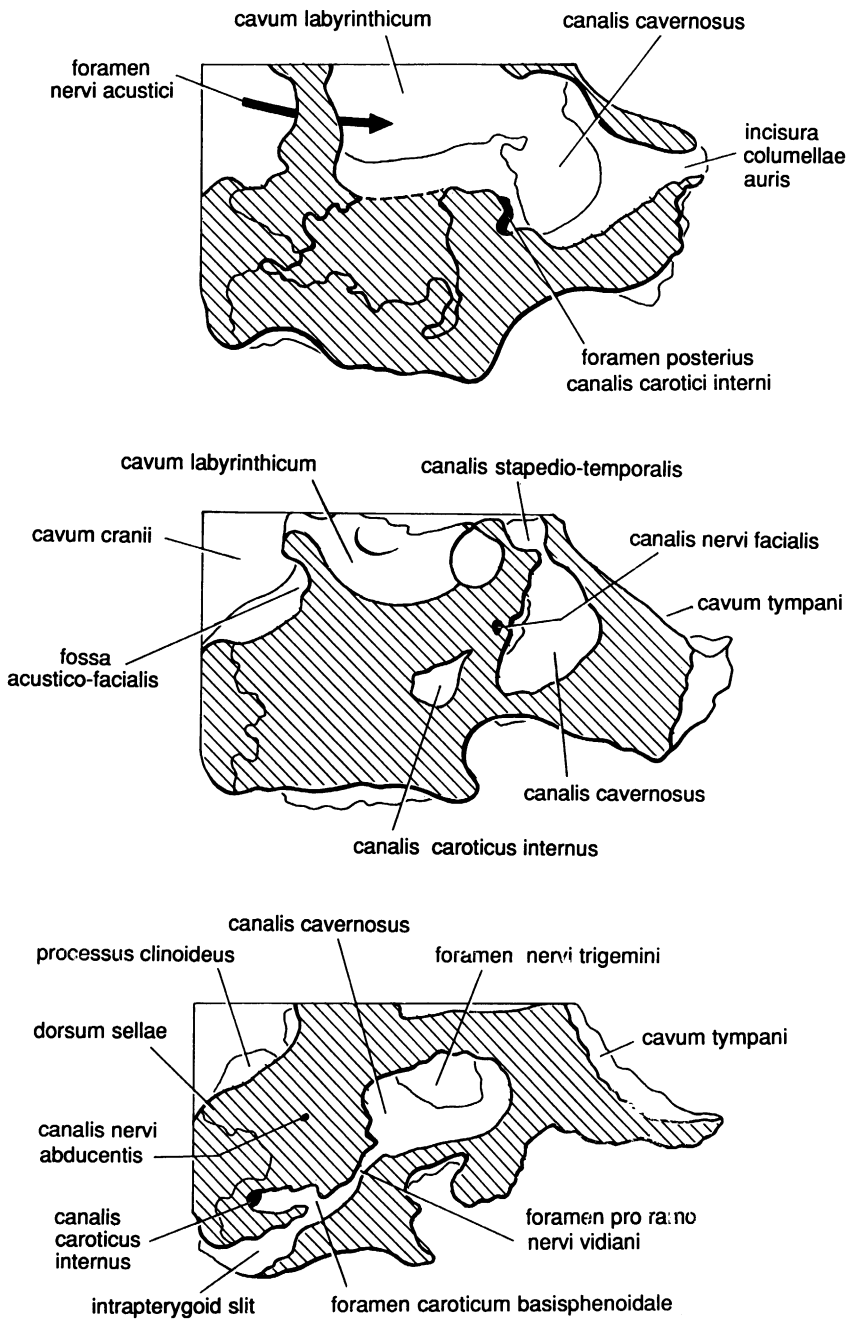


Fig. 62. *Meiolania platyceps,* AM F:18668, key to fig. 61. Posterior views with midline on left, lateral on right.

considered early Tertiary. Simpson (1938: 243) gave a review of this problem and concluded, "In fact it is still unknown whether [the material identified by Ameghino as] *Niolamia* really is from the Cretaceous, Eocene, or both, and again "*Niolamia* is either from

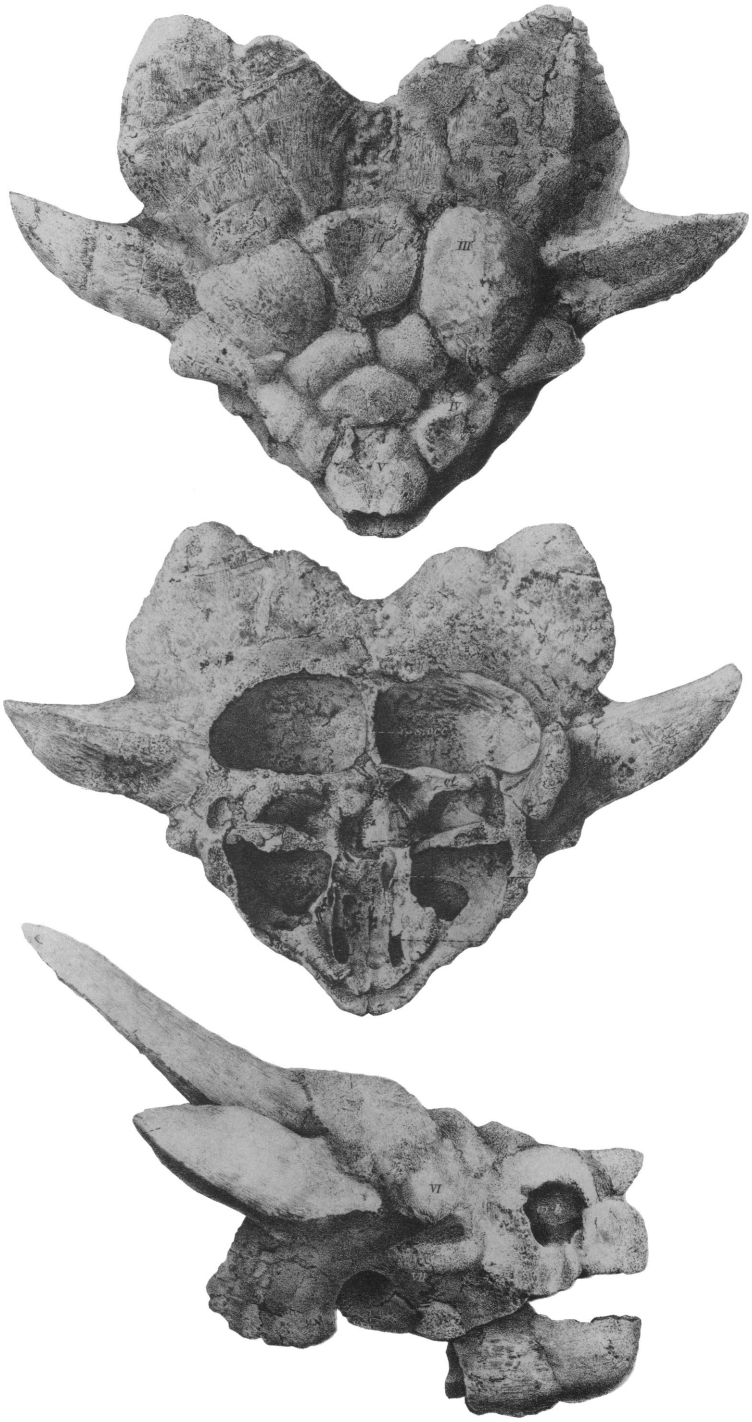


Fig. 63. *Niolamia argentina.* Skull of neotype specimen in Museo de la Plata. **Upper,** dorsal view; **middle,** ventral view; **lower,** right lateral view. From Woodward (1901).

the same beds [as *Crossochelys* i.e., the Eocene Casamayor] or from the Cretaceous—it is unlikely to be from the Paleocene, and almost surely not post-Eocene" (Simpson, 1938: 244). So the most precise age that can be given at present for the type skull of *Niolamia* is Cretaceous or Eocene, province of Chubut, Argentina.

REFERRED SPECIMENS: Although Ameghino (1899) and Moreno (1899) referred generally to other specimens besides the skull, only Woodward (1901) described more material. He described and figured a scapula fragment (Woodward, 1901: pl. 18, fig. 1) and described carapace fragments including a piece that has the ilium sutured to the costal bones. Woodward used this feature to substantiate the identification of *Niolamia* as a pleurodire in the debate then current about its affinities (see Gaffney, 1983: 395). Woodward also described the carapace as being serrated posteriorly, a feature that occurs in Australian meiolaniids. *Meiolania* is now known to have a typically cryptodiran free pelvis and the Meiolaniidae are best interpreted as cryptodires. Woodward was either mistaken or pleurodire fragments were mixed with the *Niolamia* specimens. Pleurodire shell fragments occur in Simpson's AMNH collections from Casamayor localities.

Also in the La Plata collections is a tail ring (fig. 65) figured by Woodward (1901: pl. 18, figs. 2, 2a). There is no specific locality or horizon stated for any of this material other than "red sandstone of Chubut." The tail ring adds to useful understanding of *Niolamia* but the scapula and other unfigured specimens have not been available for study.

REFERRED ON BASIS OF SYNONYMY: AMNH 3161, type of *Crossochelys corniger* Simpson, a disarticulated partial skull described by Simpson (1937, 1938).

HORIZON AND LOCALITY: "Casamayor Formation, in green bentonite with *Sebecus,* birds, etc., Cañadon Hondo near Paso Niemann south of the Rio Chico del Chubut, southern Chubut Territory (central Patagonia), Argentina" (Simpson, 1938: 222).

DISCUSSION: *Crossochelys* Simpson, 1937, is here interpreted as a young individual of *Niolamia,* an interpretation considered but rejected by Simpson. The skull of *Crossochelys,* as stated by Simpson (1938: 246) ". . . may not be fully grown," and some of the characters of *Crossochelys* might be the same as *Niolamia* in an adult. However, Simpson thought that there were some features differentiating the two taxa that could not be the result of ontogeny.

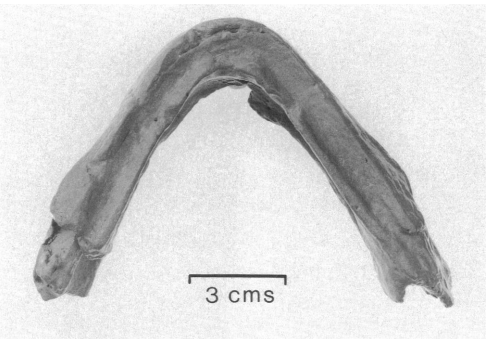


Fig. 64. *Niolamia argentina.* Cast of lower jaw of type specimen in Museo de la Plata. Dorsal view.

It should be stressed that since Woodward, no one (including the present author) working on meiolaniids has reexamined the type skull of *Niolamia argentina.* Simpson worked under the further handicap of using Anderson's skull reconstruction for comparative purposes and not actual specimens of *Meiolania platyceps.*

The size difference between the sole skull of *Crossochelys,* AMNH 3161, and the cast of *Niolamia* is hard to quantify because of the absence of sutures in *Niolamia* and the likely change in scale proportions during ontogeny. Nonetheless a best estimate of size comparisons indicates a difference of about 20%. Simpson did not consider this to be a diagnostic feature of *Crossochelys. Crossochelys* also has widely open sutures, probably the best indication of immaturity. Similarly, the temporal opening in the crest, as suggested by Simpson, could have reached closure with further growth.

The characters used by Simpson (1938) to differentiate *Crossochelys* and *Niolamia* are discussed below in the same order listed in table 11.

The nasal and orbital cavity features are based on comparisons Simpson made using

Fig. 65. *Niolamia argentina.* A scapula (left) and tail ring (right) ascribed to *Niolamia* by Woodward (1901). Tail ring: **Upper,** posterior view; **lower,** right lateral view. From Woodward (1901).

casts of *Niolamia* and *Meiolania platyceps,* the latter a cast of a reconstruction, not of an actual specimen. Both of these are inaccurate in the area of the nasal and orbital cavities. The bony limits of the fossa nasalis (character 1) are incorrect in the *Meiolania* reconstruction and almost certainly incorrect in the *Niolamia* cast. In fact, the *Crossochelys* type specimen is very similar to *Meiolania* as described in Gaffney (1983).

The "orbitosphenoid crest" (character 2) is the paired ridge forming the lateral margin of the sulcus olfactorius in Gaffney's terminology (1979b: 1983). Again the *Meiolania*

TABLE 11
Characters Used by Simpson (1938) to Differentiate *Crossochelys* and *Niolamia*
(see text for discussion)

Character	"*Crossochelys*"	Niolamia
(1) Nasal cavity completely separated from orbit	no	yes
(2) "Orbitospenoid crest"	"practically absent"	"probably present"
(3) Superior nasal recess	extends onto frontal	?
(4) Columellar notch	open	closed
(5) Intrapterygoid slit	less prominent	more prominent
(6) Squamosal (A, B) horns	smaller	larger
(7) Temporal fenestra	present	absent

cast is inaccurate and actual specimens of *Meiolania platyceps* (Gaffney, 1983) are quite similar to the *Crossochelys* skull. They both have a low but well-defined ridge. I would not characterize it as "absent" as Simpson has done. The internal areas of the *Niolamia* cast appear to be inaccurate and suggest a morphology that would be unusual in any turtle. The type skull of *Niolamia* has not been examined by the present author (Simpson also relied only on the cast) but it appears that some internal areas still contained matrix or were filled with some material to aid casting, which may explain the apparent inconsistencies in the morphology of the nasal and orbital areas.

The "superior nasal recess" (character 3) is a large concavity in the dorsal part of the fossa nasalis, again similar in *Crossochelys* and *Meiolania* and in my opinion, *Niolamia.* This feature is common in turtles.

The "columellar notch" or incisura columellae auris (character 4) appears to me the same in *Crossochelys, Niolamia,* and *Meiolania platyceps.* Gaffney (1983) showed that the closure of the notch is due to the squamosal in *Meiolania* and was very likely the same in *Crossochelys.*

Simpson (1938) described the intrapterygoid slit (character 5) as more prominent in *Niolamia* and less prominent in *Crossochelys.* The cast of *Niolamia* shows no sutures and very little detail of any kind in the basicranial area. The Woodward (1901) figures and what is visible in the cast seem quite consistent with the pterygoid preserved in *Crossochelys.* I have considered them to be consistent to the point of using both specimens to make a composite reconstruction of the basicranium (Gaffney, 1983: fig. 60).

The above characters are either the same in *Crossochelys* and *Niolamia* or are not determinable and unlikely to be different in *Niolamia.* The last two features (6 and 7 of Simpson), however, are obviously different in the two specimens. *Niolamia* clearly has larger A and B horn areas, a wider frill in general, and a more projecting B horn (character 6). The C scale area is not identical in shape in both and the X scale area ("a" of Simpson) also has a slightly different shape. The sample of *Meiolania platyceps* (Gaffney, 1983) indicates a much greater degree of individual variation than that between *Niolamia* and *Crossochelys* but one suspects that *Meiolania platyceps* is unusual even for meiolaniids. The differences in horn size between *Crossochelys* and *Niolamia* are what might be expected in a growth series. Similarly, the temporal fenestra (character 7) was suggested even by Simpson as a possible feature found in juveniles. However, Simpson (1938: 246) went on to conclude that "even though the unique specimen of *Crossochelys* may not be fully grown, it is probably essentially adult and synonymy with *Niolamia* seems extremely improbable." Although I conclude that, when examined from the perspective of a better understood *Meiolania,* it is best to interpret them as synonyms, study and preparation of the type skull of *Niolamia* may support Simpson's view. It is unfortunate that no new material of meiolaniids has been announced from South America since Simpson's discovery. Except for Lord Howe Island, everywhere meiolaniids are known they are rare.

The type skull of *Niolamia* was described and figured by Woodward (1901) and AMNH 3161 by Simpson (1938). Gaffney (1983) redescribed much of AMNH 3161 in comparisons with *Meiolania platyceps* and *Ninjemys* but did not refigure it.

Late Cretaceous meiolaniid fragments have been reported from the Los Alamitos fauna of Patagonia, Argentina (Broin, 1987). The basis of the identification is apparently that ". . . the fragments of shell of cf. *Niolamia* are similar to the corresponding parts of *Meiolania,*" and ". . . the humerus is also similar and very primitive, like in *Proganochelys. . .*" (Broin, 1987: 134). The specimens are also about the same size as the animal represented by the type skull of *Niolamia argentina.*

The shell fragments figured by Broin are not sufficiently complete to substantiate the identification. They could very well belong to a meiolaniid, but there are no characters shown that support this.

The figured humerus (Broin, 1987: pl. 1) is very similar to the humerus of *Meiolania platyceps.* Both humeri are relatively short and squat, with large medial processes, small lateral processes and closed ectepicondylar fossae. The intertubercular fossa is curved

and developed to a similar extent in both. However, all these features occur generally in primitive cryptodires, like *Kallokibotion,* baenids, and sinemydids. Despite the similarity in humeri, the characters only demonstrate the presence of a primitive cryptodire of large size. There should be Cretaceous South American meiolaniids, but positive identification of them awaits future discoveries.

Ninjemys Gaffney, 1992

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

TYPE SPECIES: *Meiolania oweni* (Woodward).

ETYMOLOGY: *Ninja,* in allusion to those totally rad, fearsome foursome who epitomize shelled success; *emys,* turtle.

KNOWN DISTRIBUTION: Pleistocene of southern Queensland, Australia.

DIAGNOSIS: A meiolaniid known only from skull and tail, characterized by the unique possession of laterally projecting B horns and the 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)

TYPE SPECIMEN: BMNH (Natural History Museum, London, formerly British Museum [Natural History]) R391, a nearly complete skull (figs. 66–69) 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 (fig. 69) 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 (fig. 66). Following this study, I can confirm not only the accuracy of Owen's original figures but the accuracy of the restoration as well. Except in the depth of the sagittal division between the A horn cores, all 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, and the restoration is accurate.

TYPE 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.

TYPE 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: pl. 64, pl. 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

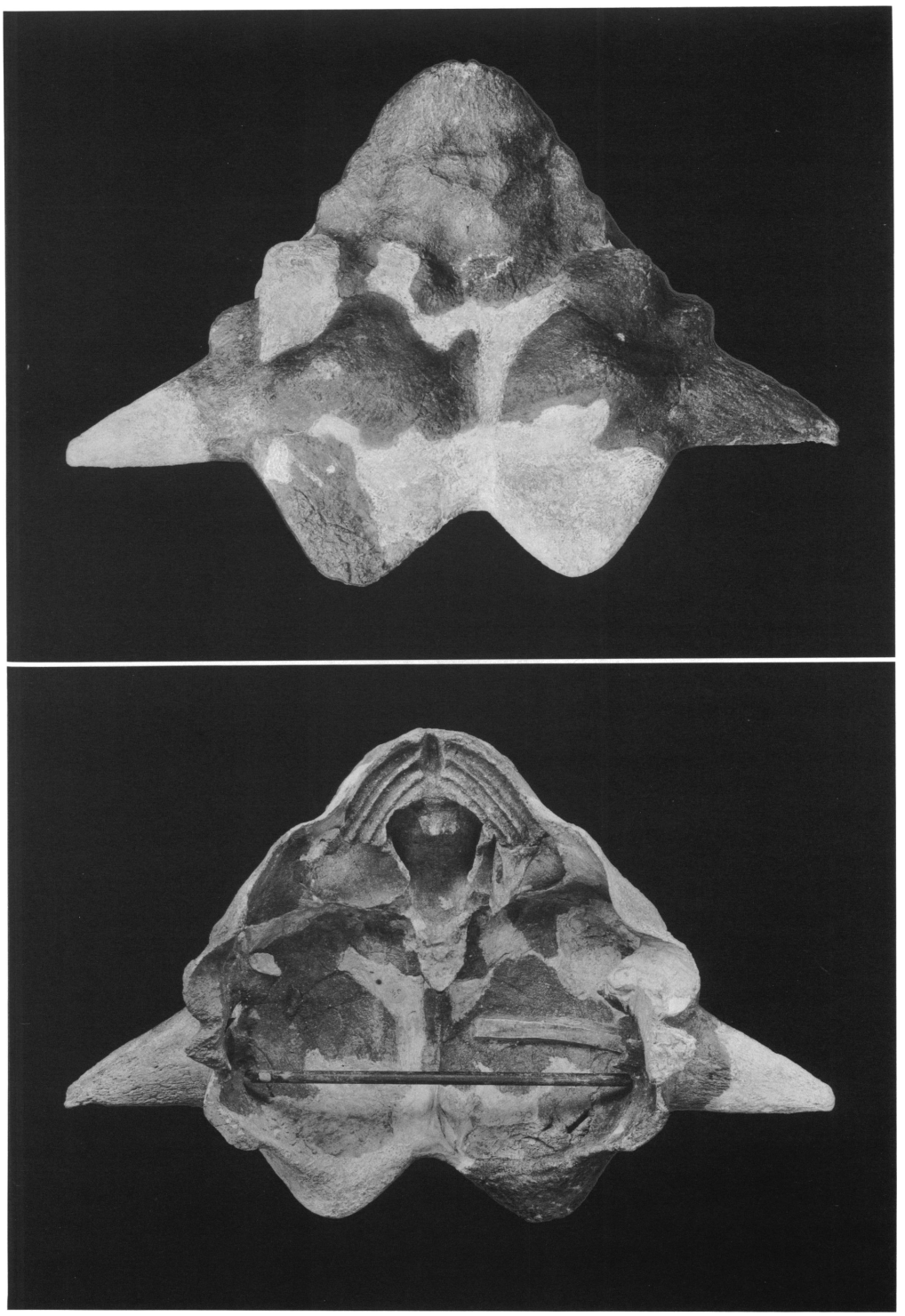


Fig. 66. *Ninjemys oweni.* Skull of type specimen, BMNH R391. **Upper,** dorsal view; **lower,** ventral view. Light areas restored in plaster. From Gaffney (1992).

Fig. 67. *Ninjemys oweni.* Skull of type specimen, BMNH R391. **Upper,** anterior view; **lower,** right lateral view. From Owen (1881).

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 (fig. 70) 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 also 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* (figs. 66–69) 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. Gaffney (1983) is primarily a description of *Meiolania platyceps* but extensive comparisons are also made with *"Meiolania" oweni* (= *Ninjemys oweni*) and *Niolamia argentina.*

DESCRIPTION: Although *Ninjemys oweni* is described in the literature, some discussion of the autapomorphies defining the species is appropriate. The nasal bones in *Ninjemys* (fig. 67) form an anteriorly projecting overhang that extends farther forward than the premaxillae, a condition 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 (fig. 68) 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 triturating 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. 90) projects primarily in a lateral direction, although there is a posterior component. The orientation of the B horn core in *Ninjemys*

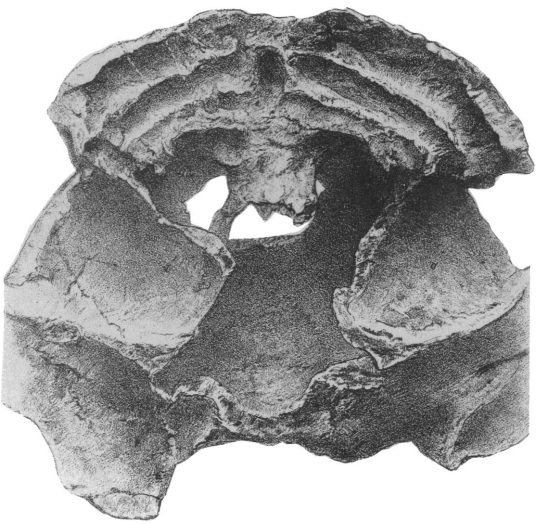


Fig. 68. *Ninjemys oweni.* Skull of type specimen, BMNH R391. Palatal view. From Owen (1881).

differs noticeably from *Niolamia,* but it is very different from the B horn core of *Meiolania.* In *Warkalania* 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 *Warkalania* 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.

cf. *Ninjemys oweni*

CONSISTS OF: AM F:1346a, two tail club bosses (fig. 70) presented by J. McMaster of Coolah (Etheridge, 1893).

HORIZON: (?) Pleistocene (see Gaffney, 1981).

LOCALITY: Oaky Creek, northwest of Coolah (Etheridge, 1893; see also Gaffney, 1981), New South Wales.

DISCUSSION: Described by Etheridge (1893). These tail club bosses are very similar to the tail club bosses of *Ninjemys oweni,* BMNH R392, from Queensland. They differ in that the New South Wales specimens have more

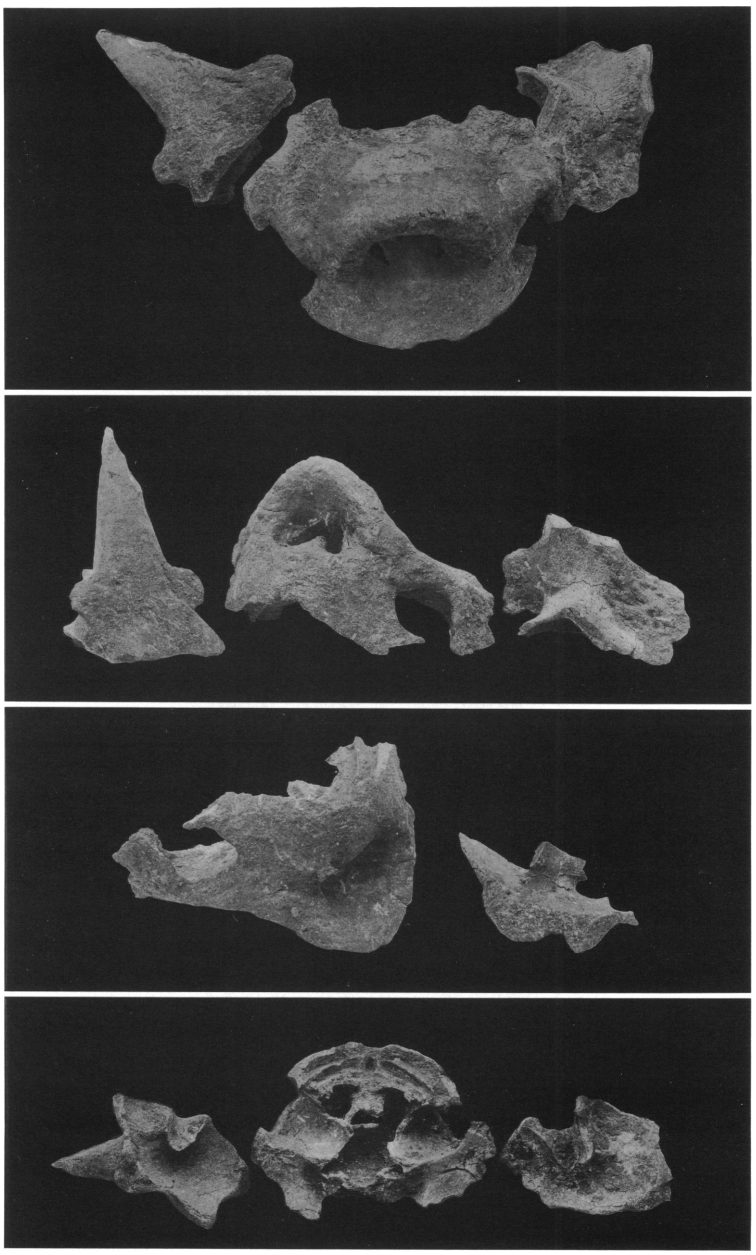


Fig. 69. *Ninjemys oweni.* Skull of type specimen, BMNH R391. Four views of skull elements as originally found, before reconstruction and restoration. Photos from Australian Museum archives, Sydney.

acuminate tips. Etheridge (1893) thought that they represented different species, Gaffney (1981) thought that they were the same species, and Gaffney (1992) quibbled identifying them as cf. *Ninjemys oweni.* The discovery of a second species of very a large meiolaniid, the Wyandotte species, which presumably had a large tail club like *Ninjemys oweni,* caused me to downgrade the identification to cf. *Ninjemys oweni.*

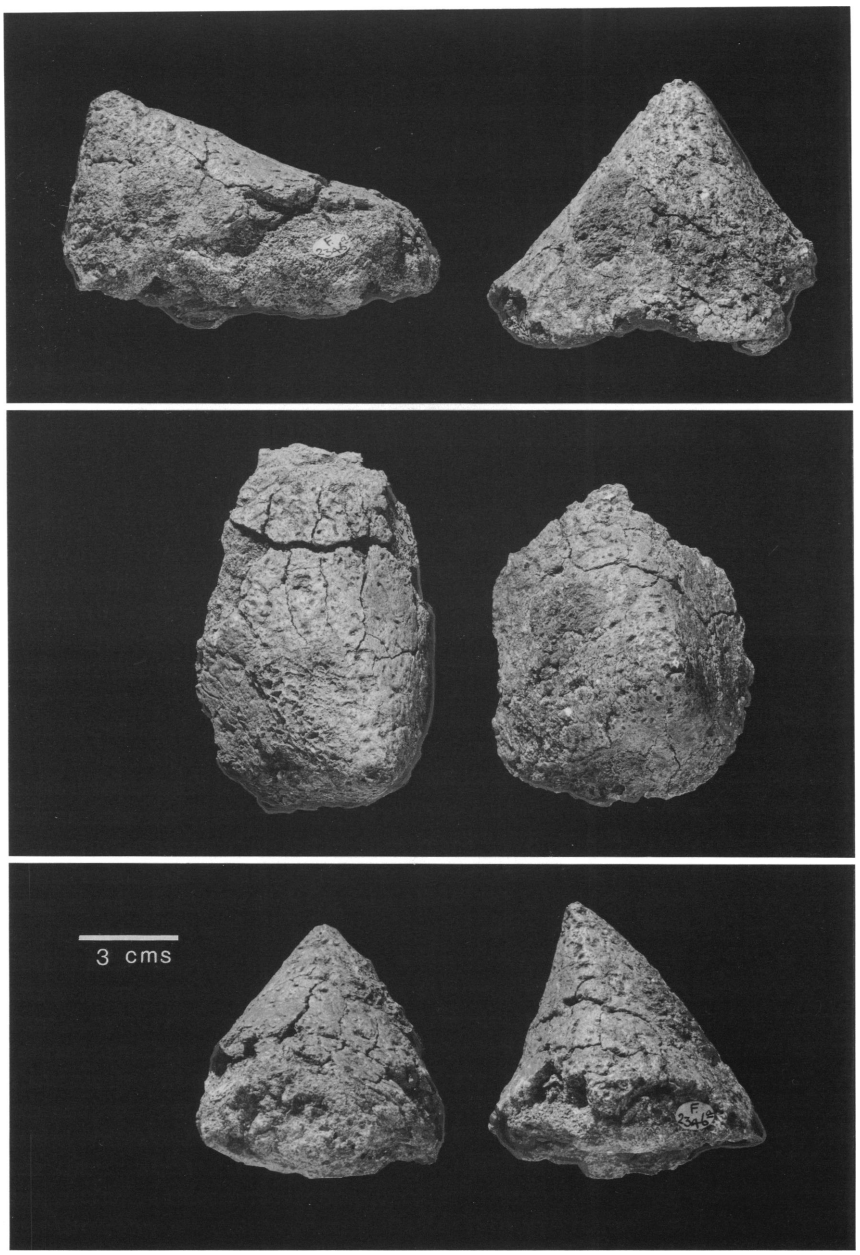


Fig. 70. Meiolaniid cf. *Ninjemys oweni.* Tail club fragments, AM F:1346a. The two fragments are shown in three views, orientation not known.

Warkalania Gaffney,
Archer, and White, 1992

TYPE SPECIES: *Warkalania carinaminor.*

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

KNOWN DISTRIBUTION: Mid-Tertiary, northwest Queensland.

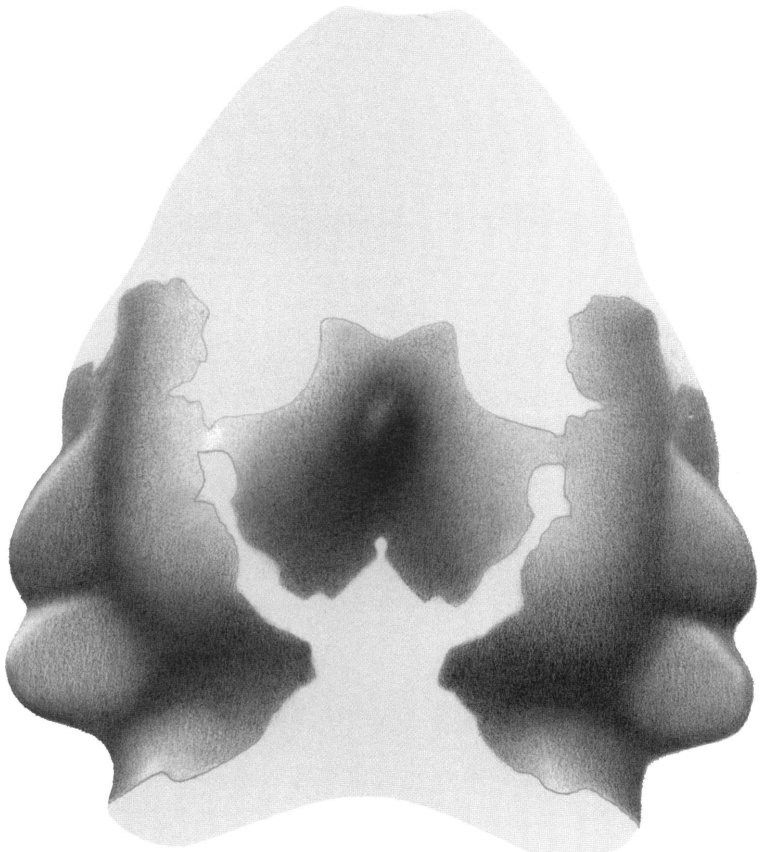


Fig. 71. *Warkalania carinaminor.* Dorsal view of restored skull based on QM F:22649, QM F:22650, and QM F:22651. Modified from Gaffney et al. (1992).

DIAGNOSIS: Meiolaniid with B scale area, a low, horizontal ridge, not a recurved horn as in *Meiolania* nor a large lateral projection as in *Niolamia* and *Ninjemys*; 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* but more protuberant than in *Meiolania*; X scale small, and D scales in midline contact as in *Ninjemys* and *Meiolania.*

Warkalania carinaminor Gaffney, Archer, and White 1992

TYPE SPECIMEN: QM F 22649, a right squamosal (fig. 74). 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 AM F:22650–22653 and 22682 belong to the same individual.

LOCALITY: Pancake Site, Riversleigh Station, northwest Queensland, see Archer et al. (1989).

HORIZON: "? late Oligocene to early Miocene," according to Archer et al. (1989: 64), but early Miocene *fide* Woodburne et al. (1993).

REFERRED SPECIMENS: QM F:22650 (fig. 73), a left squamosal with complete scale areas A, B, and C plus part of scale D. A fragment of the posterior wall of the antrum postoticum is preserved internally; QM F:22651 (fig. 71)—central section of right and left pa-

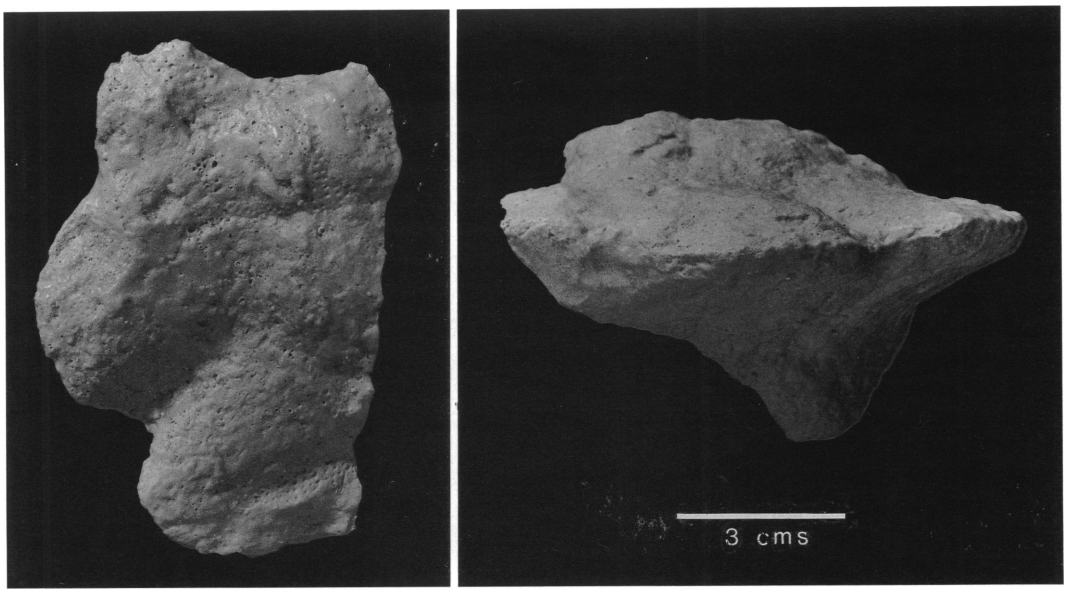


Fig. 72. *Warkalania carinaminor.* Left squamosal, QM F:22654. **Left,** dorsal view; **right,** lateral view.

rietals, bearing on its dorsal surface scale X and surrounding portions of scales G and D; QM F:22652 (fig. 75)—nearly complete right quadrate; QM F:22653 (fig. 75)—right exoccipital and basioccipital lacking ventral surface; QM F:22682—part of right supraoccipital containing semicircular canals, small portions of prootic and opisthotic; QM

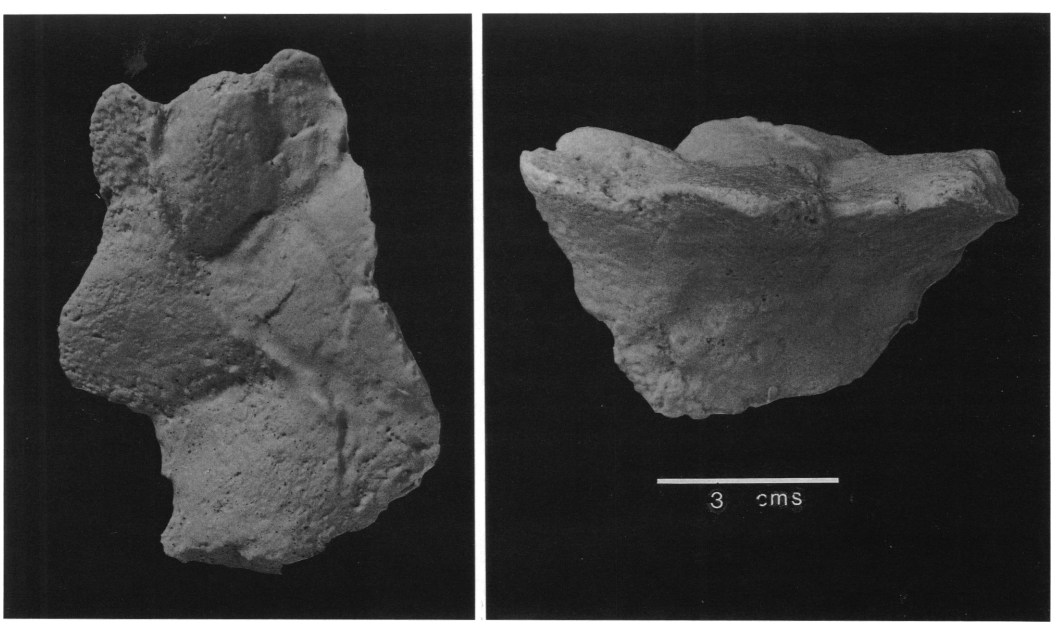


Fig. 73. *Warkalania carinaminor.* Left squamosal, QM F:22650. **Left,** dorsal view; **right,** lateral view.

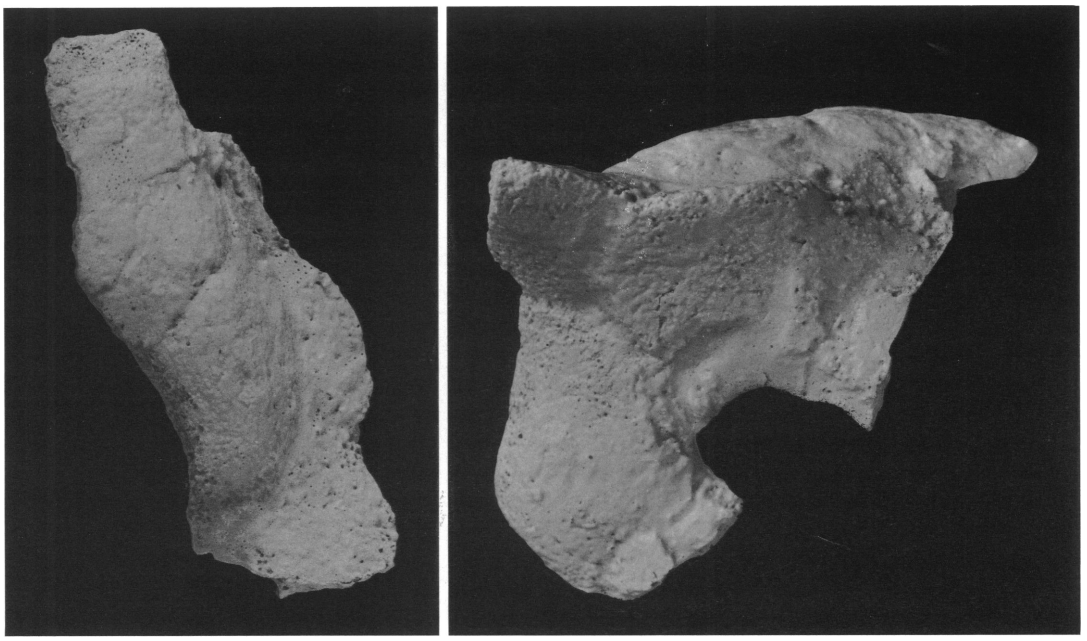


Fig. 74. *Warkalania carinaminor.* Right squamosal, QM F:22649, type specimen. **Left,** dorsal view; **right,** lateral view.

F:22654—left squamosal with scale areas B and C complete portions of scale areas A and K.

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.

DIAGNOSIS: Same as for genus.

DISCUSSION: It is apparent that at least two individuals are present in the available specimens because QM F:22650 and QM F:22654 consist of the same bone elements. The remaining fragments, QM F:22649, QM F:22650, QM F:22651, QM F:22652, QM F:22653, and QM F: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, QM F:22649 (fig. 74), has enough diagnostic characters so that it can stand alone as a new taxon of meiolaniid, even if the composite reconstruction (fig. 71) is in error due to the mixing of more than one individual and more than one species. QM F:22649 (fig. 74) 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 QM F:22649 differ significantly from all other meiolaniids. In all other meiolaniids the C horn is cone shaped or flat, but in *Warkalania* it is a horizontal ridge directed anteroposteriorly. The B scale of QM F:22649 is also a flattened ridge in strong contrast to the cowlike, recurved B horn core synapomorphic for *Meiolania.* The B horn cores of *Ninjemys* 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.

DESCRIPTION: (Most of this section is taken from Gaffney et al., 1992).

The areas preserved in *Warkalania* include only the posterior parts of the skull. The overall proportions and size of the *Warkalania* specimens are roughly the same as *Meiolania platyceps.* In most *Meiolania platyceps* skulls the scale areas are delimited by raised ridges,

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

The midline area of the skull in *Warkalania* is preserved in QM F: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 QM F:22651, and there are vague grooves that could be the sulci separating scales G and D from each other. However, if the sulci are present, they are poorly differentiated from other surface irregularities.

In *Ninjemys,* the X scale area is not well preserved, but it is smaller than in *Niolamia* and may be similar to *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* 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 meet in the midline in *Ninjemys.*

The ventral surface of QM F:22651 preserves a fragment of the dorsal 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, 1979b). This area is preserved in a number of specimens of *Meiolania platyceps* and in *Ninjemys* but not in *Niolamia.* Although this region is similar in all turtles, there are differences between *Ninjemys* and *Meiolania platyceps.* Unfortunately, not enough is preserved in QM F:22651 to determine which one it is most similar to. 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.* 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 QM F:22651. To the extent that it is preserved, it agrees with *Meiolania platyceps.*

The fragment of cranial roof, QM F: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* because AM F:57984 also lacks raised scale edges.

Scute D is a large, paired scale covering much of the posterior portion of the skull. This scale consists mostly of parietal and squamosal. Parts of scale D are preserved in QM F:22649, QM F:22650, QM F:22651, and QM F: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 QM F:22651 and the left anteromedial portion of QM F:22650. The two areas do not have a good contact but, when restored using QM F:22652 and QM F: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 QM F: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 present absence of the sulcus, rather than actual absence of this sulcus during life. 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* 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.* The C scale is a paired scale area on the posterolateral part of the skull,

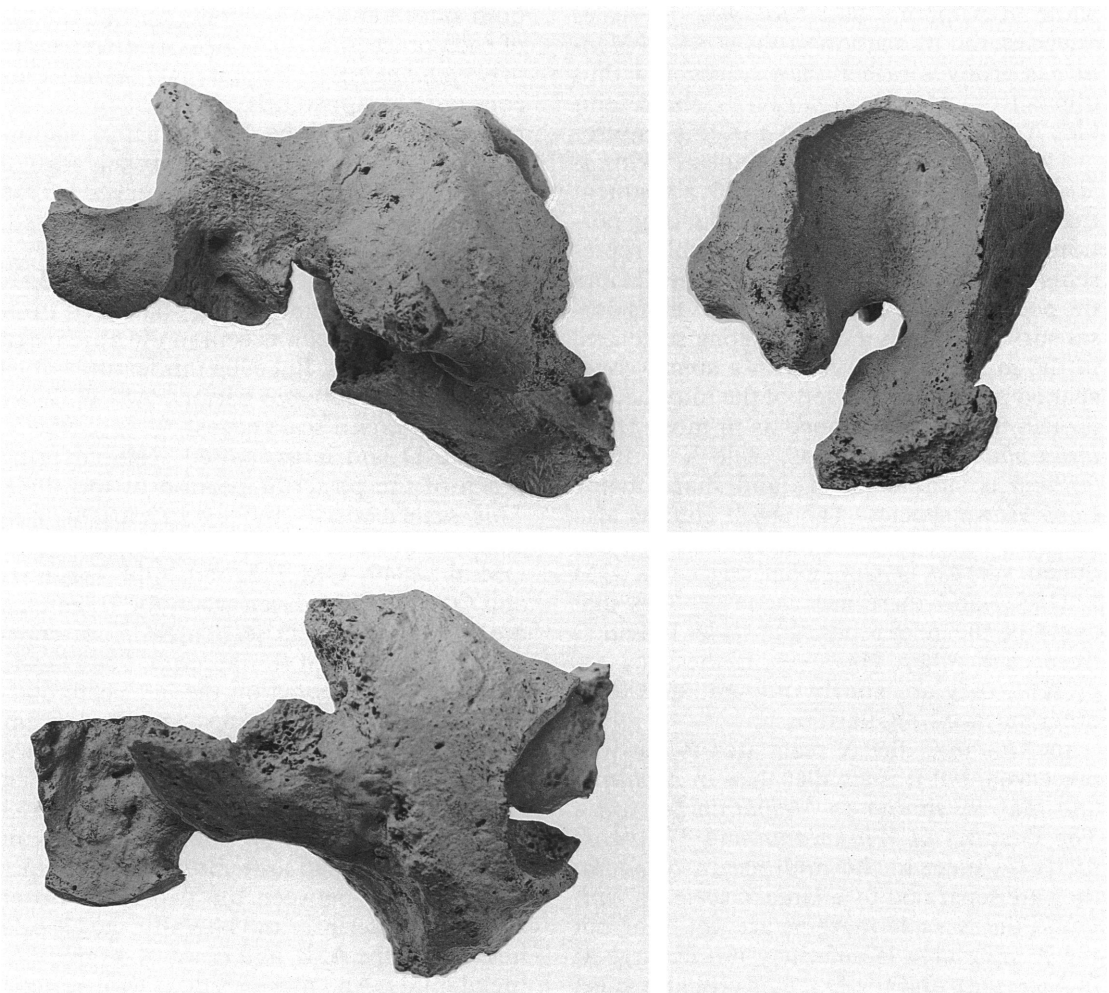


Fig. 75. *Warkalania carinaminor.* Partial braincase, QM F:22652 and QM F:22653. **Upper left,** occipital view; **lower left,** dorsal view; **upper right,** lateral view.

and is formed mostly by the squamosal bone. QM F:22649, QM F:22650, and QM F:22654, preserve 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 greater extent in QM F:22654. In *Meiolania platyceps, Ninjemys,* and *Niolamia* the C scale is more rounded and cone-shaped than in *Warkalania. Meiolania platyceps* varies from nearly flat in AM F:43183 to a well-developed cone in AM F:57984, but it is never a horizontal ridge as in *Warkalania.*

The B scale area is preserved completely in QM F:22650 and QM F:22654, and in QM F: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 QM F:22654 the B scale is thicker and has a blunter lateral edge than in QM F:22649 and QM F:22650. The most striking differences in skull morphology of meiolaniids can be found in the shapes of scale B. In *Ninjemys* 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

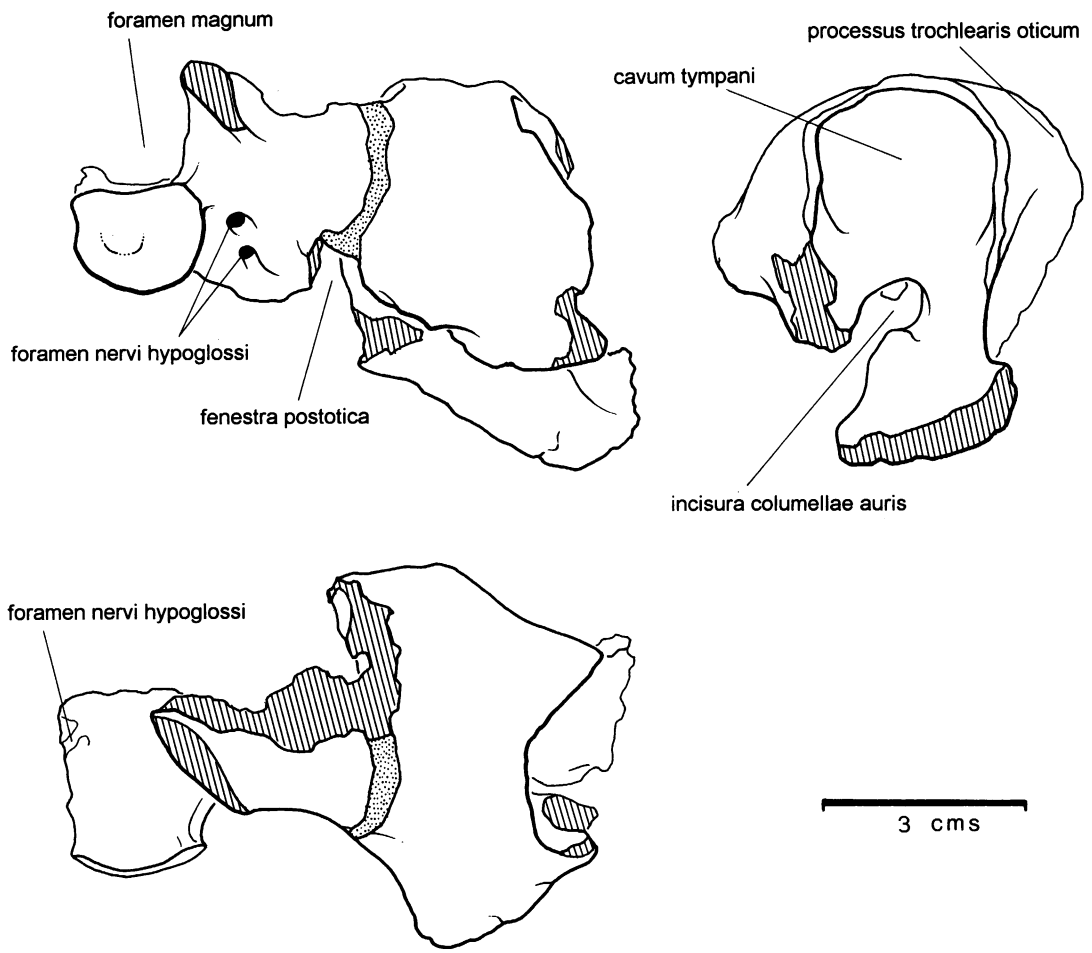


Fig. 76. *Warkalania carinaminor.* Key to fig. 75. QM F:22652 and QM F:22653.

also forms a projection but in this case it is the cowlike 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* or *Niolamia.* The B horn core of some individuals of *Meiolania platyceps* (e.g., AM F:43183 and AM F: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* 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. In *Meiolania platyceps* the A scale is formed mostly by the squamosal with smaller contribution from the supraoccipital. The A scale area in *Warkalania* is preserved in QM F:22650 and QM F:22654 but it is incomplete. Both specimens lack the posteromedial parts of the scale area that would allow the complete limits to be seen. The A scale area is restored by assuming that the tympanic opening in *Warkalania* parallels the midline as in all other meiolaniids (and almost all other turtles) and by filling in the missing region as conservatively as possible. The A scale of *Warkalania* is very similar in size and shape to the B scale. In QM F:22650 it has an acute edge but in QM F: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* 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 QM F:22649, QM F:22650, and QM F:22654. Of these, the most extensive and informative is QM F:22649. This specimen has the dorsal and ventral margins of the cavum tympani opening preserved. A small part of the posterior edge is also present in this specimen. 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* 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* have the entire limits of the squamosal preserved and only *Ninjemys* 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* being indeterminate. The K/J sulcus is preserved in QM F:22649 and it is more posterior to its position in *Meiolania platyceps,* but similar to the position in *Ninjemys* in which the J scale extends more posteriorly than in *Meiolania platyceps.* The area is not preserved in *Niolamia.*

The three braincase fragments, QM F:22652, QM F:22653, and QM F:22682, (figs. 75, 76) all belong to the right side and are probably 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.

QM F:22682 is the part of the right supraoccipital that contains the semicircular canals, plus some small portions of 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 stapediotemporale. The bone is similar to *Meiolania platyceps* and does not vary a great deal from other generalized cryptodires.

The internal portion of QM F:22682 contains the dorsal impression of the canalis semicircularis horizontalis (see Gaffney, 1979b, 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 AM F:57984, presumably a function of the smaller skull in *Warkalania.*

QM F: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 QM F:22682. The grooves do not appear to be part of the fossa acusticofacialis 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.

QM F:22652 is a right quadrate separated from the more medial part of the otic cham-

ber at roughly the position of the quadrate-opisthotic/pterygoid suture, exposing the canalis stapediotemporalis 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 QM F:22652 shows the canalis stapediotemporalis and the aditus canalis stapediotemporalis (see Gaffney, 1979b, fig. 10) but not the foramen stapediotemporale itself. The foramen would lie in the broken-off area. The supraoccipital fragment, QM F:22682, has the more medial groove leading to the foramen which would lie in the missing contact area between pieces F and D. The canalis cavernosus lies below the aditus canalis stapediotemporalis and its posterior length is preserved in QM F: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* 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 QM F: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 medially 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.

QM F: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 of the condylus 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 indeterminant 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* 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 open 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.

TABLE 12
Comparison of the Species of *Meiolania*

	platyceps	*brevicollis*	*mackayi*	*Wyandotte* sp.
B horn core projecting posteriorly in relation to skull	higher	lower	indet	indet
Width/height ratio of B horn core	0.47–1.31	0.32	0.42–0.69	0.40–0.48
A horn core	relatively large	relatively small	indet	indet
B horn core maximum height (cm)	9.6	13.2	8.3	21.0
Parasagittal ridge on premaxillary triturating surface	present	absent	indet	indet
Cervical vertebrae relatively short, high, and narrow	no	yes	indet	indet
Ventral keel on cervicals 5, 6	no	yes	indet	indet
Neural spine of axis relatively high and curved anteriorly	no	yes	indet	indet
Limb bones	more robust	more gracile	indet	indet
Estimated relative size (*Meiolania platyceps* = 1.0)	1.0	1.2	0.7	2.0+

In QM F: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 QM F: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, 1979b) are identifiable.

Meiolania Owen, 1886b

Megalania Owen, 1881 (in errore).
Ceratochelys Huxley, 1887.
Miolania Lydekker, 1889.

TYPE SPECIES: *Meiolania platyceps* Owen, 1886b.

ETYMOLOGY: None given, possibly referring to *meion,* Greek for "lesser" and *lanius,* Latin for "butcher" in contrast to *Megalania,* "great butcher."

KNOWN DISTRIBUTION: Miocene of western Queensland (Gaffney et al., 1992), Miocene of Northern Territory (Megirian, 1989, 1992), Pleistocene of northern Queensland (Gaffney and McNamara, 1990), Pleistocene of Walpole Island (Anderson, 1925) and Pleistocene of Lord Howe Island (Gaffney, 1983).

DIAGNOSIS: A meiolaniid genus known from the entire skeleton of the type species, differing from all other meiolaniid genera by the unique possession of posterolaterally projecting and recurved B horns and the absence of a continuous shelf formed by A, B, and C scale areas; D scale low and A scale relatively small as in *Warkalania* and in contrast to *Niolamia* and *Ninjemys*; second accessory ridge on maxillary triturating surface as in *Ninjemys*; D scales meet in midline, X scale small as in *Ninjemys* and *Warkalania*; Y and Z scales relatively large as in *Ninjemys*; X scale partially separates G scales as in *Ninjemys* and *Warkalania*; four tail ring segments incorporated into tail club rather than two as in *Ninjemys*; tail ring armor segments not enclosed ventrally in contrast to *Ninjemys* and *Niolamia.*

DISCUSSION: There are three named species (*platyceps, brevicollis, mackayi*) recognized in the genus *Meiolania* and a fourth probable as the Wyandotte species (table 12). However, only two of these, *platyceps* and *brevicollis,* can be diagnosed adequately and differentiated morphologically. The problem is that the other taxa are represented by horn cores, which provide a minimum of information at the species level. The recurved feature of the B horn is a good character for the genus *Meiolania* but the included taxa are differentiated primarily by geography, size, and B horn core thickness. The *Meiolania platyceps* sample of 50 B horns (Gaffney, 1983) demonstrated a wide range of variation

in horn core thickness in one presumed species. Measurements of the four compared taxa (table 12) show the thickness range among them. *Meiolania brevicollis* is clearly the narrowest, with *Meiolania mackayi* narrower than most *Meiolania platyceps* but nonetheless overlapping with both *Meiolania platyceps* and the Wyandotte species.

Even reliance on B horn thickness is not well founded. There is a certain amount of variation between measurements of the same cores by different workers (compare Megirian, 1992, and Gaffney and McNamara, 1990) because it is so difficult to determine homologous positions on variably broken specimens. The results generally agree, but using more sophisticated analytic techniques on horn core measurements would be pushing the basically subjective nature of the measurements too far.

Meiolania platyceps Owen, 1886b

Meiolania minor Owen, 1886b
Ceratochelys sthenurus Huxley, 1887

TYPE SPECIMEN: BMNH R675, figured in Owen (1886b: pl. 30, fig. 1; pl. 31, fig. 1) and Gaffney (1983: fig. 9). Huxley (1887, fig. 3) also illustrated this specimen, comparing it with *Chelydra.*

TYPE LOCALITY: Lord Howe Island, New South Wales, Australia (Owen, 1886b). Collector not definitely known, obtained by Robert Fitzgerald, well known Australian botanist, in 1884 and sent to Owen in 1885. It was collected possibly on the 1882 *Thetis* expedition to Lord Howe Island. It is known that H. Wilkinson, New South Wales geologist, collected *Meiolania* bones on this trip but the actual specimens have not been identified as such (see Gaffney, 1983, for a history of *Meiolania* collecting on Lord Howe Island). The source of the type specimen on Lord Howe Island is also not known. The type specimen is in heavily indurated calcarenite which is more typical of exposures in the Old Settlement Beach area rather than Ned's Beach, but indurated fossil-bearing calcarenite can be found throughout the Ned's Beach Calcarenite. Nonetheless, all of the early collections seem to have come from the lagoon side of the island (see Gaffney, 1983, for geologic map and distribution of *Meiolania* localities).

HORIZON: Ned's Beach Calcarenite, Pleistocene. The exact age of the Ned's Beach Calcarenite and the *Meiolania* fossils included in it is unknown, but Gaffney (1983, see for discussion and further references) suggested that the fossils might be 100,000–120,000 years old.

REFERRED SPECIMENS: Gaffney (1983) provided appendices with lists of *Meiolania platyceps* specimens in the Australian Museum, Sydney (the largest and most important collection), the Mining and Geological Museum in Sydney, the Museum of Natural History in London, and the American Museum of Natural History. There are now hundreds of individual bones of *Meiolania platyceps* known from Lord Howe Island along with a few articulated specimens.

DIAGNOSIS: Differs from other species of *Meiolania* in having a B horn core that is usually relatively wider, however, the height/width ratio of *Meiolania platyceps* varies a great deal and does overlap with *Meiolania mackayi* and the Wyandotte species; B horn core projects posteriorly at a higher angle than in *Meiolania brevicollis*; A horn core larger than in *Meiolania brevicollis*; parasagittal ridge on premaxillary triturating surface present; cervical vertebrae relatively longer, lower, and wider than in *Meiolania brevicollis*; no ventral keel on cervicals five and six; neural spine of axis relatively low and flat in contrast to *Meiolania brevicollis*; limb bones relatively robust in comparison to *Meiolania mackayi*; estimated relative size 30% larger than *Meiolania mackayi,* about 20% smaller than *Meiolania brevicollis* and about 50% smaller than the Wyandotte species.

DESCRIPTION: *Meiolania platyceps* is known from nearly every part of the skeleton and is represented by hundreds of specimens from Lord Howe Island. Older literature references can be found in Gaffney (1983) which is a description of the skull while the vertebral column is described in Gaffney (1985a). The remaining postcranials are described here.

DISCUSSION: *Meiolania platyceps* is by far the most completely known member of the family Meiolaniidae and is the basis for most comparisons with other higher taxa of turtles. Nonetheless, the relatively wide range of

morphologic variation seen in the skull and shell of the Lord Howe Island specimens shows that there are significant problems in understanding the alpha-level systematics of the various meiolaniid taxa.

Meiolania mackayi Anderson, 1925

TYPE SPECIMEN: AM F:17720, left A horn core, figured in Anderson (1925: pl. 32, figs. 5, 6).

TYPE LOCALITY: Walpole Island, about 100 miles southeast of New Caledonia.

HORIZON: Specimens occur in phosphatic guano deposits in coral rock. I am not aware of any dating of any rocks from Walpole Island but the guano is generally presumed to be Pleistocene or Holocene.

REFERRED SPECIMENS: The following B horn cores (fig. 77)—AM F:17654 (right), AM F:17655 (left), AM F:17656 (left), AM F:17721 (left), AM F:17722 (right), and AM F:7723 (right); AM F:17719 humerus (Anderson, 1925, pl. 38, fig. 6), AM F:17658 humerus, AM F:17657 humerus, AM F:18832 tibia, AM F:17760 tibia, AM F:17662 tibia, AM F:17663 tibia, and AM F:17661 radius.

DIAGNOSIS: B horn core characterized by being narrower than most *Meiolania platyceps* and wider than *Meiolania brevicollis*; limb bones more gracile than in *Meiolania platyceps*; estimated relative size at least 30% smaller than *Meiolania platyceps* and *Meiolania brevicollis* and more than 50% smaller than the Wyandotte species.

DESCRIPTION: The horn core description of *Meiolania mackayi* in Anderson (1925) is brief but accurate. There are seven Walpole Island horn cores (fig. 77, table 13) and they are clearly smaller and more slender, but otherwise nearly identical, to *Meiolania platyceps*. Subjectively, the *Meiolania mackayi* cores are curved to about the same degree seen in most *Meiolania platyceps,* but they are a bit more curved than in *Meiolania brevicollis* and straighter than in the Wyandotte *Meiolania*. Two of the *Meiolania mackayi* B horns, AM F:17655 and AM F:17720, have the complete base preserved along with some of the contiguous squamosal bone forming the skull proper. These pieces show the dorsal edge of the cavum tympani and the C-shaped ridge on the internal surface that defines the antrum postoticum. They are nearly identical to similar specimens of *Meiolania platyceps* and differ only in being smaller and having thinner bone.

The humerus in *Meiolania mackayi* is represented by four specimens: AM F:17719, a left humerus lacking the distal end and the radial process (figured by Anderson, 1925: pl. 38, fig. 6); AM F:17658, the central shaft of a left humerus lacking both ends; AM F:17657, the distal end of a right humerus lacking part of the ectepicondylar surface (figured by Anderson, 1925: pl. 38 figs. 7, 8); and AM F:17659, the distal end of a left humerus. Although mentioned by Anderson (1925), none has been described in detail. The best specimen, AM F:17719, lacks the radial process, the distal end, and has some damage to parts of the articular surface. The preserved areas agree closely with humeri of *Meiolania platyceps,* and, other than size, I can find no morphologic differences between them. The ulnar process in AM F:17719 is slightly smaller than in AM F:18750 and the groove entering the ectepicondylar foramen is barely more distinct in AM F:17719, AM F:17657, and AM F:17659. The two *Meiolania mackayi* humeri that lack distal ends are both damaged in the area of the ectepicondylar process, revealing the position and shape of the ectepicondylar foramen. This structure and the foramen agree closely with *Meiolania platyceps*. AM F:17658, the central shaft of a humerus, seems to have a slightly deeper bicipital fossa than AM F:17719, but otherwise agrees closely in size and shape.

The figures in Anderson (1925) comparing *Meiolania platyceps* and *Meiolania mackayi* humeri are misleading in that they show more differences than are really present. This is mostly due to slight differences in orienta-

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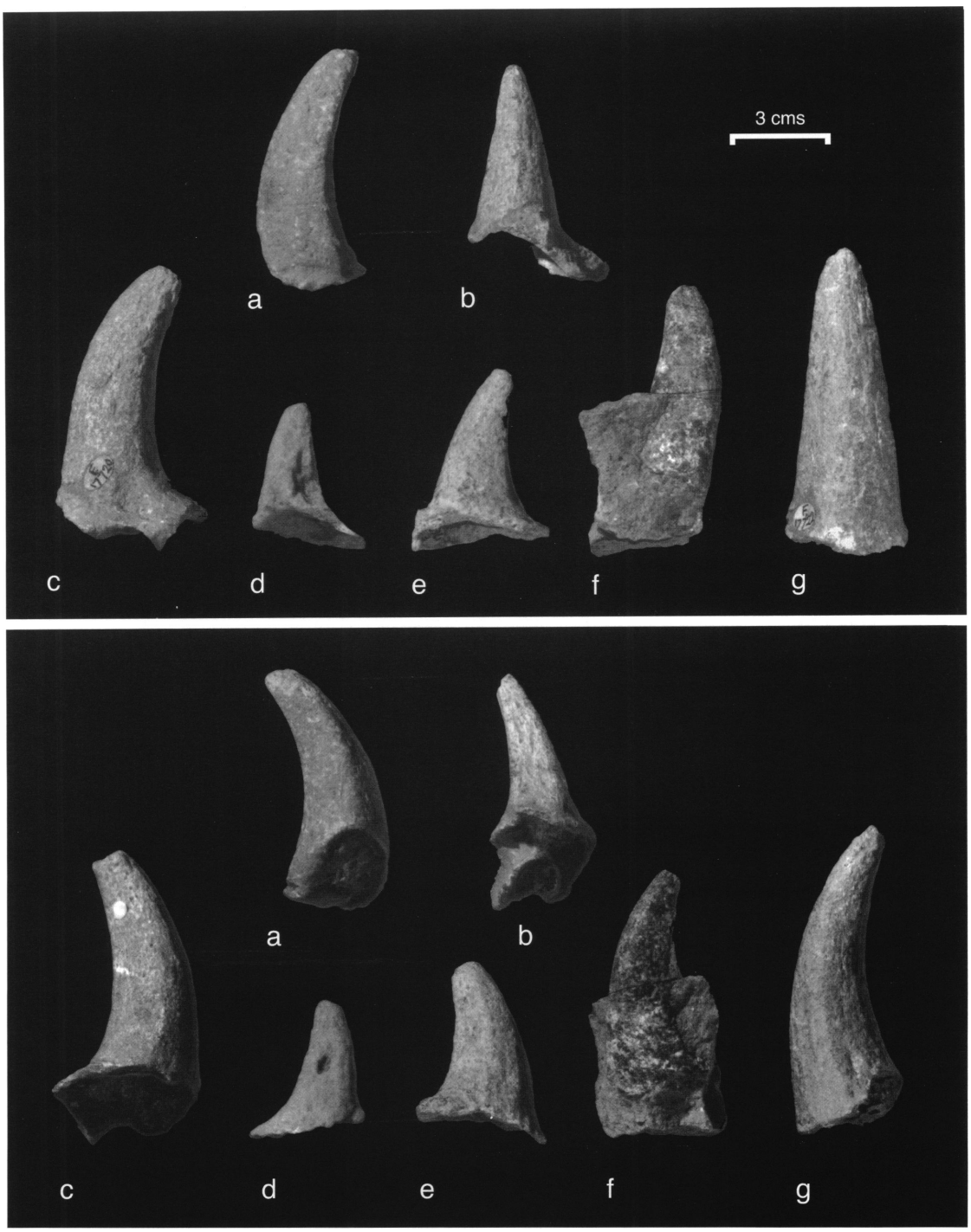
Fig. 77. *Meiolania mackayi,* Walpole Island, New Caledonia, Pleistocene. All are B horn cores. **Upper figure: a,** AM F:17721, left, lateral view. **b,** AM F:17655, left, anterior view. **c,** AM F:17720 (type specimen), left, lateral view. **d,** AM F:17654, right, medial view. **e,** AM F:17656, left, lateral view. **f,**



AM F:17723, right, anterior view. **g,** AM F:17722, right, anterior view. **Lower figure: a,** AM F:17721, left, medial view. **b,** AM F:17655. **c,** AM F:17720 (type specimen), left, medial view. **d,** AM F:17654, right, lateral view. **e,** AM F:17656, left, medial view. **f,** AM F:17723, right, medial view. **g,** AM F:17722, right, medial view.

TABLE 13
Measurements of B Horn Cores in *Meiolania mackayi* (cm)

	Width	Height	Width/ Height
AM F:17655	2.5	4.7	0.53
AM F:17654	2.3	3.3	0.69
AM F:17656	3.0	4.5	0.66
AM F:17720 (type)	3.4	6.6	0.51
AM F:17723	3.2[1]	6.6	0.48
AM F:17721	3.3	7.5	0.44
AM F:17722	3.6	8.4	0.42

[1] Estimated.

tion, treatment of damaged areas the same as well-preserved areas, and different illustration methods (lined versus halftone) among the figures.

AM F:17661 is a left radius of *Meiolania mackayi* with a nearly complete proximal end, but a partially missing distal end. AM F:17661 agrees closely in shape and size with a right *Meiolania platyceps* radius, AM F:20510. The most distal part of the *Meiolania mackayi* articulation surface is broken off and the more proximal area of that articulation surface is damaged.

A right femur of *Meiolania mackayi* lacking the distal end, part of the trochanter major, and some of the edges of the head was figured by Anderson (1925: pl. 30, fig. 3). The figure (as all of Anderson's hatched line/Bailey figures) is not a good representation of the specimen. A lump of matrix (since removed) on the trochanter minor was figured as part of the bone. The *Meiolania mackayi* femur appears to be identical to *Meiolania platyceps* femora except in size. The intertrochanteric fossa lacks the web of bone seen in a few *Meiolania platyceps,* but this may be a factor of size.

There are three tibias for *Meiolania mackayi,* all nearly complete. The figured tibia (Anderson, 1925: pl. 30, fig. 4) is a right tibia that is the best preserved and is lacking only some of the edges around the articular areas. AM F:17663 is a left tibia that is thinner and more gracile than AM F:17660, although they are both the same length. AM F:17662 is a right tibia that is shorter and even more gracile than the other two. Comparing AM F:17662 with a well-developed *Meiolania platyceps* tibia like AM F:18832 shows some difference in proportions. The other features of the tibia of *Meiolania mackayi* agree very closely with *Meiolania platyceps.* The muscle/ligament attachment sites in *Meiolania platyceps* are more rugose and a bit larger than in *Meiolania mackayi* but this differs a great deal among the known *Meiolania platyceps* tibias, and within species of living turtles represented by good samples.

DISCUSSION: The material representing *Meiolania mackayi* is inadequate to substantiate the differentiation of this taxon from *Meiolania platyceps.* If it had not already been named I would not support it as a new species. It probably is a different "biologic" species (whatever that is) because it's from an isolated island, but the few morphologic features available give only a hint of distinctness. The *Meiolania mackayi* situation is closely comparable to the *Meiolania* sp. from Wyandotte, Queensland, (Gaffney and McNamara, 1990) which is only represented by horn cores and a caudal vertebra. *Meiolania mackayi,* however, provides a name for the Walpole Island material that is useful in discussion. Basically the more commonly found B horn cores of *Meiolania* do not provide enough characters to objectively differentiate these taxa in the absence of other characters.

Meiolania mackayi has B horn cores that when measured for width and height (less than completely objective at best, see above) yield width/height ratios of 0.42–0.69 with the more complete cores averaging about 0.53 (total average is also 0.53). This is relatively narrower than most B horns of *Meiolania platyceps* but within its range of 0.47–1.31. *Meiolania brevicollis* is clearly narrower at 0.32 but the Wyandotte species is very close at 0.40–0.48. Only *Meiolania platyceps* has a large sample of cores, however, and as Anderson warned in 1925, ". . . it is barely possible that a larger series would show a gradation and enable the two to be united under the name *Meiolania platyceps*" (p. 240). So *Meiolania mackayi* can be differentiated at present only by its small size and fairly narrow B horn cores.

Meiolania brevicollis Megirian, 1992

TYPE SPECIMEN: NTM P87103-2, partial right squamosal consisting of A and B scale areas.

LOCALITY: "Blast Site," Camfield Station, Northern Territory.

HORIZON: Bullock Creek Local Fauna, probably Middle to Late Miocene (Megirian, 1992).

REFERRED SPECIMENS: From the "Blast Site," NTM P8695-93, second cervical vertebra; NTM P87103-4, fifth cervical vertebra; NTM P894-1, sixth cervical vertebra; NTM P894-2, rostrum fragment composed of the nasal and left cheek regions; NTM P87103-8, partial right hypoplastron with the anterior extremity of the xiphiplastron; NTM P87103-7, carapace fragment; NTM P87103-29, distal first costal with part of the first thoracic rib; NTM P87103-6, osteoderm; NTM P87103-3, base of a left B horn-core with part of the cavum tympani. From "Top Site," NTM P87114-3, isolated A horn core; NTM P87114-2, left cranial cheek region with part of the orbit preserved.

DIAGNOSIS: Differs from all other species of *Meiolania* in having a very narrow B horn core; B horn core projects posteriorly at a lower angle than in *Meiolania platyceps*; A horn core small in comparison to *Meiolania platyceps*; parasagittal ridge on premaxillary triturating surface absent; cervical vertebrae relatively shorter, higher, and narrower than in *Meiolania platyceps*; ventral keel on cervicals five and six present; neural spine of axis relatively high and curved anteriorly in contrast to *Meiolania platyceps*; estimated relative size 20% larger than *Meiolania platyceps,* +50% larger than *Meiolania mackayi,* and roughly 40% smaller than the Wyandotte species.

DESCRIPTION: *Meiolania brevicollis* is known from a partial skull, various skull fragments, cervical vertebrae, and other elements. Descriptions and figures of this material are in Megirian (1989, 1992).

DISCUSSION: This species and *Meiolania platyceps* are the only adequately diagnosed *Meiolania* species. Although *Meiolania brevicollis* is known from sparse material compared to *Meiolania platyceps,* the specimens do allow comparison of more characters besides the thickness of the B horn core.

Meiolania cf. *platyceps*

CONSISTS OF: NMV P183195 (fig. 78), a left B horn core; NMV P183196 (fig. 78), a right B horn core; NMV P183197, a left B horn core and surrounding areas of skull roof; NMV P183198, a posterior caudal vertebra. The horn cores are also figured in Gaffney and McNamara (1990: figs. 1, 2).

LOCALITY: Wyandotte Creek, northern Queensland (see McNamara, 1990).

HORIZON: Unit A, Wyandotte Formation, Late Pleistocene, between 45,000 and 200,000 years before present (Gaffney and McNamara, 1990).

DESCRIPTION: For ease of comparison, this description is in the form of a diagnosis:

Differs from all other *Meiolania* species in relatively large size, estimated body size at least 70% larger than any other *Meiolania*; B horn core relatively wide as in most *Meiolania platyceps* and *Meiolania mackayi* and distinctly wider than in *Meiolania brevicollis.*

Gaffney and McNamara (1990) provided figures and descriptions of the Wyandotte specimens. See also tables 14 and 15.

MEIOLANIIDAE INDETERMINATE TO GENUS

CONSISTS OF: A large number of fragments in the Mining Museum, Sydney, including four figured by Etheridge (1889). One of these, a cranial horn core, MM F:13841, is described here along with two other skull fragments, a right quadrate, MM F:13855, and a lower jaw, MM F:13898 (fig. 79).

HORIZON: Probably Early Miocene (see Gaffney, 1981, for references and discussion).

LOCALITY: Canadian Lead, four and a half miles from Gulgong, New South Wales.

DESCRIPTION: *B horn core* (fig. 79). The Gulgong horn core MM F:13841 is clearly identifiable as a B scale area and is most comparable to B horn cores of the genus *Meiolania.* The Gulgong specimen exhibits recurving which is limited to that genus in the presently adopted systematic scheme. The natural rugosity of the bone surface seems to

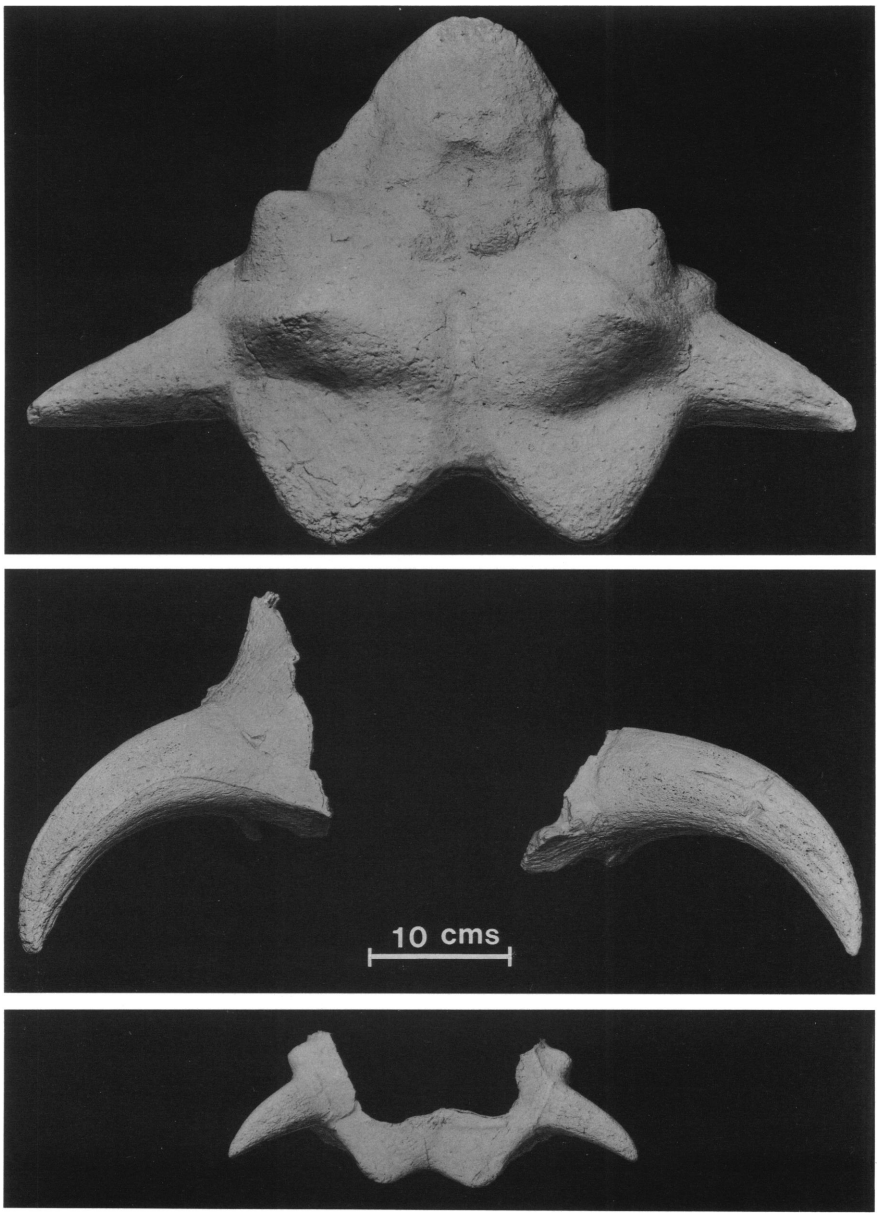


Fig. 78. Dorsal views of meiolaniids for comparison with Wyandotte horn cores. All photographs to same scale. **Upper,** *Ninjemys oweni,* cast of BMNH R391, Darling Downs, Queensland. **Middle,** cf. *Meiolania platyceps,* Wyandotte Station, Queensland, B horn cores, NMV P183195 (left) and NMV P183196 (right). **Lower,** *Meiolania platyceps,* Lord Howe Island, AM F:16866. All specimens are casts of originals. From Gaffney and McNamara (1990).

have been exaggerated by erosion and weathering but I am assuming that the original shape has not been significantly altered. There is no indication of scale margins or sulci.

The Gulgong B horn core seems to be from the right side but this is not certain. The inner surface is not well-enough preserved to show the antrum postoticum and the outer surface

TABLE 14
Comparison of Horn Cores

	Width	Height	Width/ Height
Meiolania platyceps (Lord Howe Island)			
AM F:1209 (left)	4.7	9.6	0.48
AM F:1209 (right)	4.9	9.3	0.52
AM F:47544 (right)	4.5	7.5	0.60
AM F:16866 (left)	4.5	8.3	0.54
AM F:16866 (right)	4.5	8.4	0.53
Meiolania cf. *platyceps* (Wyandotte)			
NMV 183195 (left)	8.5	20.5	0.41
NMV 183196 (right)	8.5	21.0	0.40
NMV 183197 (left)	9.0	18.5	0.48

TABLE 15
Meiolaniid Caudal Measurements (cm)

	Probable caudal number	Length	Length of same caudal in *M. platyceps*
NMV P183198	7	11.2	4.8 (AM F:18715)
QM F:9034	3	7.2	4.5 (AM F:18704)
QM F:32155	7	9.9	4.8 (AM F:18715)

lacks any natural edges. The horn, however, is curved asymmetrically in the same way that most *Meiolania platyceps* B horns are curved, and this is the basis for the determination of it as a right horn core.

The Gulgong horn core is much smaller than nearly all of the known *Meiolania* cores with the exception of a few *Meiolania platyceps* specimens. The sample of this species is large and shows a great deal of variability in scale area development (Gaffney, 1983). From the other Gulgong specimens it is likely that the Gulgong species is smaller than the Lord Howe species and the small horns are a reflection of this rather than of unusually small horn cores as is the case in some *Meiolania platyceps* (e.g., AM F:43183). The height of the Gulgong horn is measured as 2.6 cm but the tip is broken and the horn was presumably closer to 3.0 cm. The width is harder to measure because the Gulgong horn is flattened rather than circular in cross section as in all other currently recognized *Meiolania* species. The narrowest dimension is about 2.2 cm and the broadest dimension is about 2.5 cm. The width/height ratios would vary from 0.73 to 0.96 for the Gulgong core, but the one most comparable to the ratios generated for *Meiolania platyceps* (Gaffney, 1983) and *Meiolania brevicollis* (Megirian, 1992) would be 0.73. This one falls at one end of the *Meiolania platyceps* samples but certainly within the group. The entire spread of the Gulgong ratios, 0.73 to 0.96, falls outside the *Meiolania brevicollis, Meiolania mackayi,* and the Wyandotte *Meiolania* species.

However, a more significant distinction between the Gulgong horn and other *Meiolania* horns is the flattening seen in cross section. All the other known meiolaniid B horns that are recurved are also nearly circular in cross section without significant flattening. The Gulgong horn is flattened more or less dorsoventrally as seen in *Niolamia* (fig. 63) and *Warkalania* (fig. 71). Furthermore the flattening is asymmetrical with a low ridge extending posteromedially from the shaft of the horn. This is comparable to the form of asymmetrical flattening seen in *Warkalania* (Gaffney et al., 1992). This feature suggests a more primitive condition for the B horn core in the Gulgong species, although it would seem that the distinct recurved shape still places it in or near the genus *Meiolania.*

Quadrate (fig. 79). A partial right quadrate *MM F:13855* from Gulgong is identifiable as meiolaniid, on the basis of its large size (compared with possible alternative turtle groups in the Australian fauna) and its clearly cryptodiran features. Comparison of the quadrate is primarily with *Meiolania platyceps* due to the lack of good material from the other taxa. A disarticulated left quadrate of *Meiolania platyceps,* AMNH 20921, has made this comparison easier.

The Gulgong quadrate preserves the anterior surface of the cavum tympani that is continuous with the incisura columellae auris. The opening of the incisura is only partially preserved but appears to be slightly larger than in *Meiolania platyceps.* The lateral wall of the cavum acustico-jugulare is similar to *Meiolania platyceps* but the wall itself, formed by the cavum tympani laterally and the cavum acustico-jugulare medially is much thicker in the Gulgong quadrate than

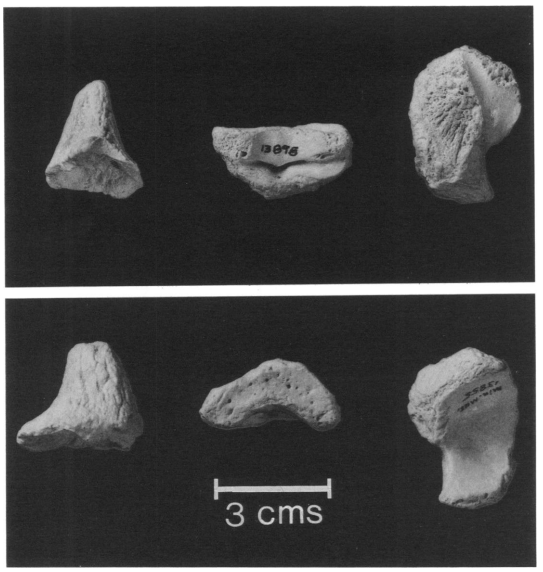


Fig. 79. Meiolaniidae indeterminate, Gulgong, New South Wales, Miocene. Two views of three fragments. **Upper left,** posterior view of right squamosal B horn core MMF:13841. **Upper center,** posterior view of lower jaw symphysis MMF: 13898. **Upper right,** medial view of right quadrate MMF:13855. **Lower left,** lateral view of right squamosal B horn core MMF:13841. **Lower center,** dorsal view of lower jaw symphysis MMF:13898. **Lower right,** lateral view of right quadrate MMF: 13855.

in *Meiolania platyceps.* This probably indicates that in *Meiolania platyceps* the cavum tympani is more extensive medially than in the Gulgong species. The aditus canalis stapediotemporalis and the canalis stapediotemporalis can be seen in the Gulgong quadrate. They are very similar to those canals in *Meiolania platyceps* as seen in AMNH 20921. The processus articularis is missing in the Gulgong quadrate. The less extensive cavum tympani in the Gulgong species is probably a more primitive condition than the more extensive one seen in *Meiolania platyceps.*

Lower jaw (fig. 79). The lower jaw fragment is described along with the Riversleigh lower jaw in that section.

Meiolaniidae indeterminate

CONSISTS OF: UCMP 61018, an associated but not articulated group of fragments, presumed to represent a single individual; cervical rib, articular region of lower jaw, elements of manus and pes (figs. 81, 82), caudal vertebrae, shell fragments.

HORIZON: Etadunna Formation, Ngapakaldi Fauna, Late Oligocene; (Woodburne et al., 1993).

LOCALITY: UCMP V5857, Lake Pitikanta (fig. 80), South Australia (Stirton et al., 1961, fig. 2, for map).

DESCRIPTION: *Limb elements.* These elements, five unguals, right metacarpal I and phalanx I, right metatarsals I, II, and III, are identified solely on the basis of comparison with Lord Howe Island *Meiolania platyceps*; there was no original articulation. The South Australian foot bones are quite similar to those of *Meiolania platyceps* but differ in being more lightly built.

The metacarpal I of UCMP 61018 is very similar to the same bone in AM F:57984 (figs. 81, 82). They both have the same blocklike shape with the proximal articulation beveled for the first distal carpal, so that the medial edge is shorter than the lateral edge. The dorsal surface of both is slightly depressed with a distinct tuberosity on the lateral edge. The distal articulation surface for the phalanx is relatively flat in AM F:57984 but UCMP 61018 has a dorsoventral channel dividing the surface. This is the only apparent difference between the two bones. Ventrally both have a large process on the proximal edge for the flexor attachment.

The phalanx of the first digit in UCMP 61018 was identified on the basis of the closeness of its fit to the metacarpal I. It has a dorsoventral ridge on its proximal articulation surface where it fits against metacarpal I. This ridge-and-channel form is seen commonly throughout turtles and its absence in *Meiolania platyceps* appears to be a derived feature of this form. The first digit phalanx is a relatively small, irregular block that has a better-defined flexor process in UCMP 61018 than in AM F:57984 and a better-formed distal articulation. In AM F:57984 the first digit differs from the others in having a much smaller ungual that just sits on the phalanx as a cap. The better formed articulation in UCMP 61018 suggests that in this Miocene form the ungual was more like the other unguals and less derived than in *Meio-*

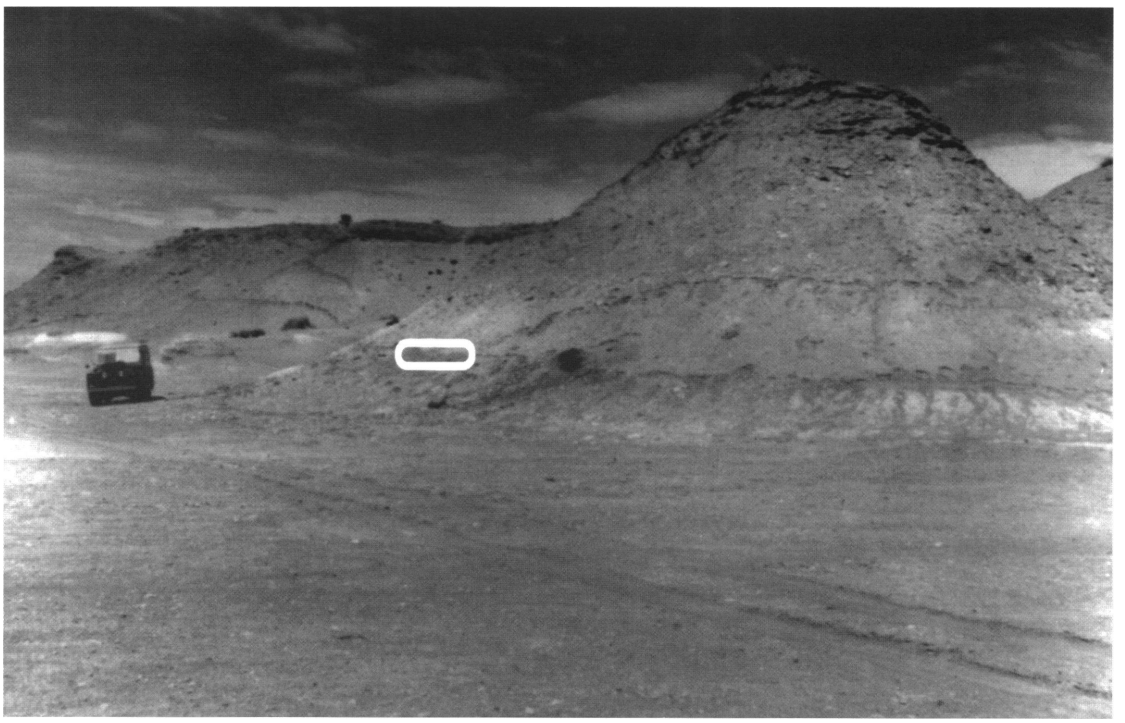


Fig. 80. Lake Pitikanta, South Australia, UCMP locality V5857. The white enclosed area is the spot in the Oligocene Etadunna Formation where the meiolaniid, UCMP 61018, was discovered. Photo by Dr. R. Tedford, 1958.

lania platyceps. One or more of the UCMP 61018 unguals could have belonged to digit I and articulated with the first phalanx but the rather general nature of the joint articulations prevents a reasonable identification.

The other metapodials are from the right hindfoot. Metatarsal I in *Meiolania platyceps* is very distinctive, very short and broad with no pinching along the main body. The South Australian metatarsal I is also short and broad in comparison to the more lateral metatarsals but not quite as short and broad as in AM F:57984. UCMP 61018 also has a slight indication of a narrower main body. The distal articulation surface in AM F:57984 is relatively flat, while in UCMP 61018 there is a dorsoventral channel or groove dividing the surface. This groove is commonly found in other turtles.

Metatarsal II is also heavier and thicker in *Meiolania platyceps* than in the South Australian form. UCMP 61018 has a slimmer shape with a narrower pinching along the shaft. The distal articulation surface of AM F:57984 has a vestige of the dorsoventral channel that is well developed in UCMP 61018.

Metatarsal III differs from metatarsal II in being narrower and slightly smaller. As in metatarsal II, the metatarsal III of the two meiolaniids differ in degree of robustness. UCMP 61018 is thinner and has a more pronounced pinching on the shaft than AM F:57984. The distal articulations are both similar, however, UCMP with a slightly more pronounced dorsoventral channel and AM F:57984 with a less pronounced but still distinct dorsoventral channel.

The unguals of the manus and pes in *Meiolania platyceps* are hardly distinguishable so there is no basis for identifying the unguals in UCMP 61018 as to position. However, the South Australian unguals are not as flattened as in the Lord Howe species. Otherwise they are very similar to each other.

A right radius lacking the distal articula-

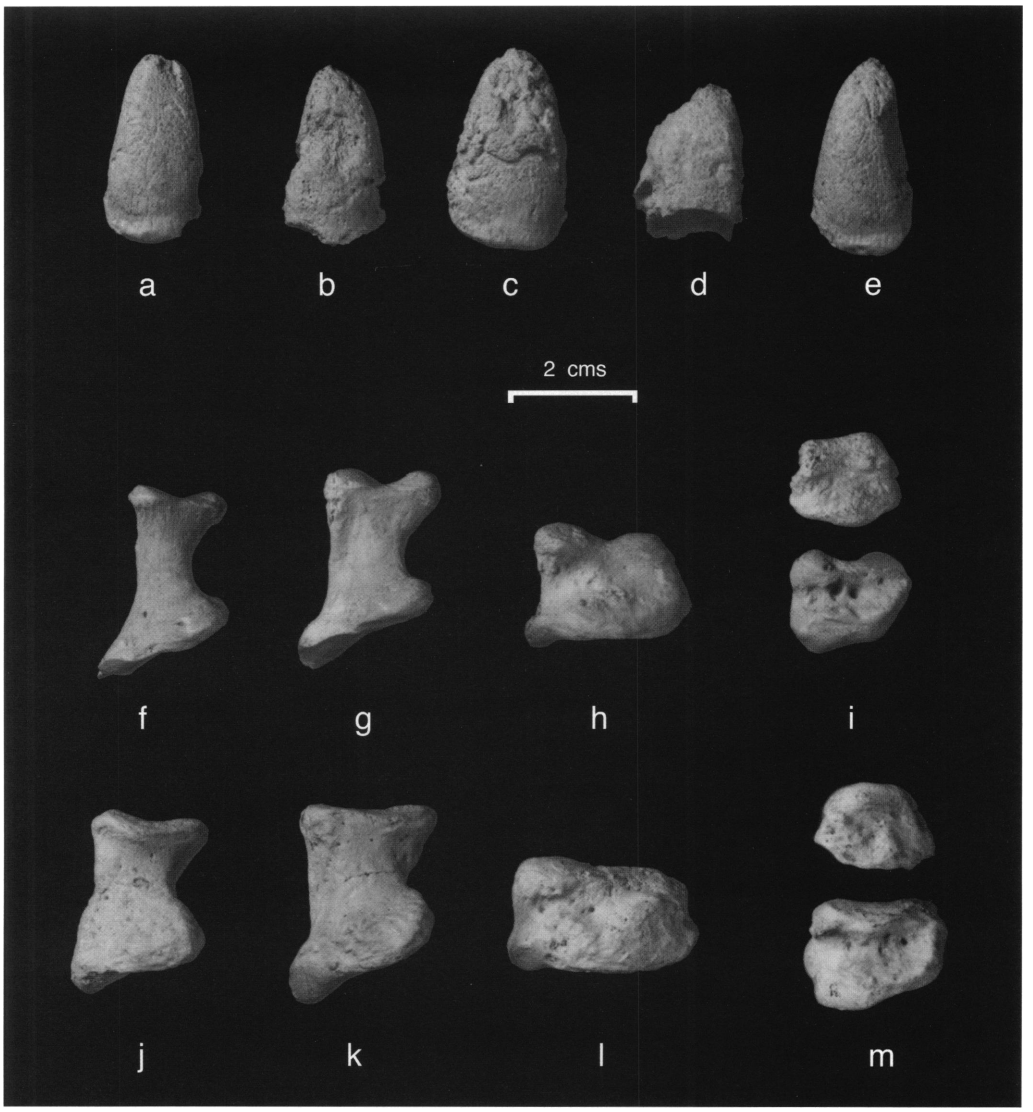


Fig. 81. Meiolaniidae indeterminate, Lake Pitikanta, South Australia, Etadunna Formation, Oligocene. Elements of manus and pes in dorsal view in upper two rows. Lower row shows same elements in *Meiolania platyceps* for comparison. **a–e,** Manus and/or pes unguals UCMP 61018. **f,** Right metatarsal III, UCMP 61018. **g,** Right metatarsal III, UCMP 61018. **h,** Right metatarsal I, UCMP 61018. **i,** Right carpal phalange I and right metacarpal I, UCMP 61018. **j,** Right metatarsal III, AM F:57984. **k,** Right metatarsal II, AM F:57984. **l,** Right metatarsal I, AM F:57984. **m,** Right carpal phalange I and right metacarpal I, AM F:57984.

tion agrees closely with *Meiolania platyceps.* This radius is smaller than AM F:49141 and about the same size as AM F:5527, both of *Meiolania platyceps.* The proximal articulation surface in UCMP 61018 is more circular than in AM F:5527 but otherwise they are almost the same.

Caudal vertebrae. A nearly complete vertebra in UCMP 61018 appears to be a first caudal on the basis of comparison with *Meiolania platyceps* (Gaffney, 1985a, fig. 14). It has the anteriorly curving transverse processes and inclined central axis characteristic of this vertebra. The South Australian form

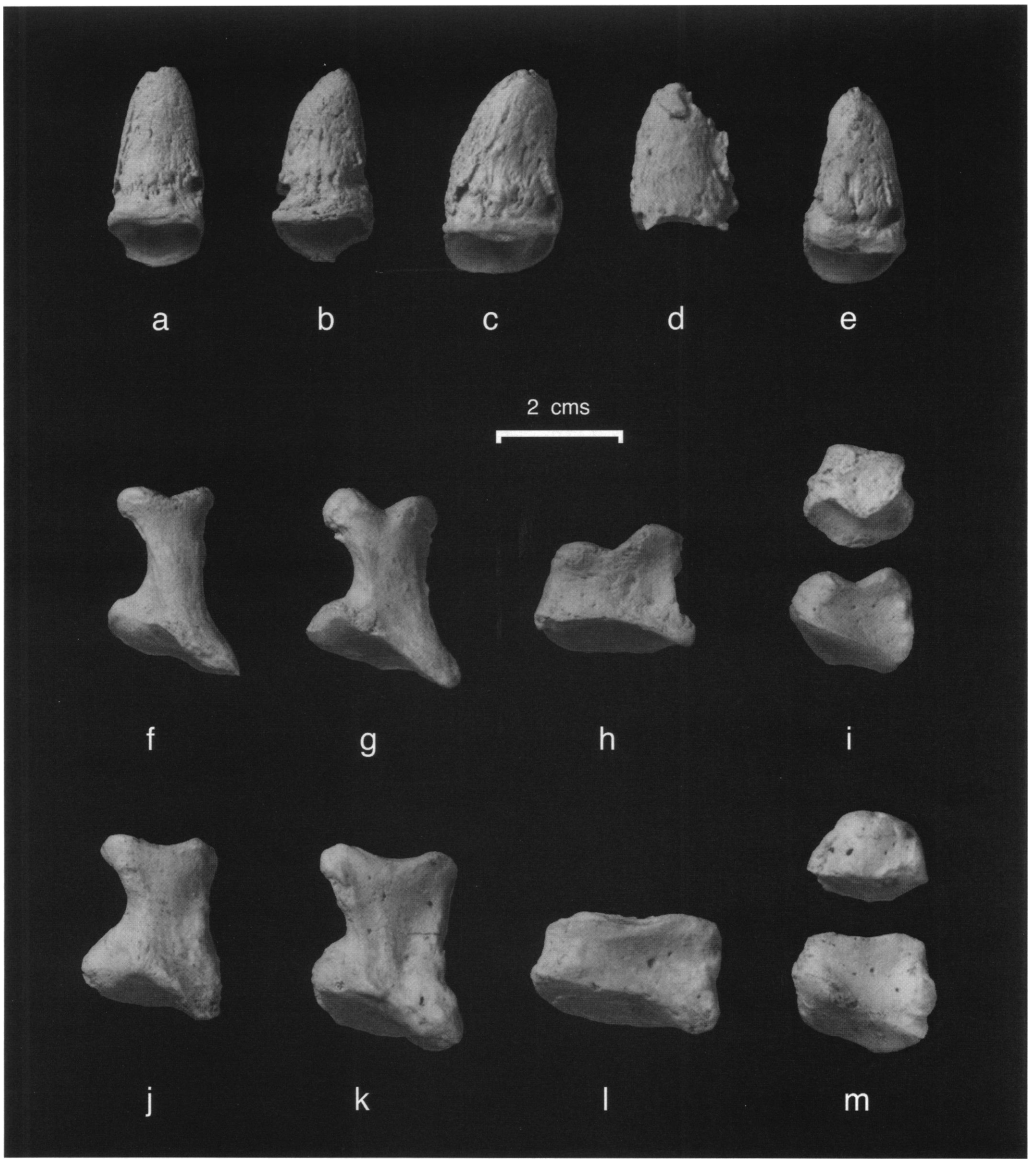


Fig. 82. Meiolaniidae indeterminate, Lake Pitikanta, South Australia, Etadunna Formation, Oligocene. Elements of manus and pes in ventral view in upper two rows. Lower row shows same elements in *Meiolania platyceps* for comparison. **a–e,** Manus and/or pes unguals UCMP 61018. **f,** Right metatarsal III, UCMP 61018. **g,** Right metatarsal III, UCMP 61018. **h,** Right metatarsal I, UCMP 61018. **i,** Right carpal phalange I and right metacarpal I, UCMP 61018. **j,** Right metatarsal III, AM F:57984. **k,** Right metatarsal II, AM F:57984. **l,** Right metatarsal I, AM F:57984. **m,** Right carpal phalange I and right metacarpal I, AM F:57984.

is very similar to AM F:61409 from Lord Howe except in the form of the anterior central articulation. In AM F:61409 the articulation surface is a low convexity while in UCMP 61018 the articulation is a concavity. The surface in both is wider than high in contrast to the posterior central articulation which is equidimensional in both. Also in both the posterior articulation is concave.

Another caudal in UCMP 61018 is com-

plete except for the neural arch and spine, and seems to be from the anterior region of the caudal series. It is probably around fourth or fifth on the series being particularly similar to the caudal figured in Gaffney (1985a: fig. 15B) as the fourth. It is slightly longer and a little deeper suggesting a more posterior position. It should be kept in mind, however, that an articulated tail is not known from *Meiolania platyceps* and the series assignations in Gaffney (1985a) are based on morphology. UCMP 61018 also includes two other more posterior caudal centra and many fragments.

Cervical ribs. UCMP 61018 includes a single (right) cervical rib that is similar to but not identical with those in *Meiolania platyceps* (Gaffney, 1985a: fig. 11). The ribs of *Meiolania platyceps* change shape between the fourth and fifth cervicals because the intercentral articulation pattern changes (see ibid.). In cervicals 2 and 3 the intercentra are fused to the posterior edge of the centrum. Cervical 4 has no intercentra fused to it, and cervicals 5 through 8 have the intercentra fused to the anterior edge of the centra. The cervical ribs articulating with centra 2 through 4 have the two heads about the same length but the ribs articulating with centra 5 and 6 have the capitulum (ventral head) distinctly longer than the tuberculum (dorsal head). Centra 7 and 8 either lack or have very small ribs in *Meiolania platyceps.* The cervical rib found with UCMP 61018 is one of the more posterior ribs, with a long capitulum and is therefore associated with a cervical posterior to cervical 4. However, it is larger than the ribs of cervicals 5 and 6 preserved in *Meiolania platyceps.* It is likely that the rib in UCMP 61018 represents a more primitive condition of the serial morphology of cervical ribs than those in *Meiolania* platyceps. *Meiolania platyceps* has the unusual condition of the anterior ribs being largest and the ribs becoming smaller posteriorly. In UCMP 61018 the larger posterior rib suggests that this process was not as developed in this species as it was in *Meiolania platyceps.* The cervical rib from another individual, UCMP 84682, from Lake Ngapakaldi, supports this idea. If UCMP 61018 is a fifth cervical rib then UCMP 84682 could be a sixth rib because it is smaller yet not as small as comparable posterior ribs of *Meiolania platyceps.* Both UCMP 61018 and UCMP 84682 ribs differ from *Meiolania platyceps* in having the tuberculum better defined and set off from the main shaft to a greater extent. It could be argued that the South Australian ribs are closer to a primitive condition than those in *Meiolania platyceps* because of their better-defined articulations, a condition seen in *Proganochelys* (Gaffney, 1990). *Proganochelys,* as well as primitive tetrapods generally, has the cervical ribs approximately equal in size along the series in contrast to *Meiolania platyceps* which has a strong reduction in rib size posteriorly in the series. It could be argued that the South Australian form has this condition but not as extreme as in *Meiolania platyceps.* If UCMP 61018 and UCMP 84682 are from the same species and similar-sized individuals and if the above identifications are correct, then the more posterior ribs do show a reduction in size but not to the degree seen in *Meiolania platyceps.* In any case, it is likely that these ribs are from a different species than *Meiolania platyceps.* In the absence of any cervical ribs associated with any other meiolaniid, further comparisons are impossible.

Right atlantal neural arch. A right neural arch from the atlas is preserved in UCMP 61018. It is very similar to one from *Meiolania platyceps,* AM F:57984, figured in Gaffney (1985a: fig. 2, left, and fig. 5). UCMP 61018 differs from AM F:57984 in being slightly narrower anteroposteriorly but UCMP 61018 is wider than the atlantal neural arch of AM F:61105 (Gaffney, 1985a: fig. 1).

Left lower jaw fragment. A portion of the left prearticular, angular, and articular in UCMP 61018 is very similar to those bones in *Meiolania platyceps,* AM F:57984, as figured in Gaffney (1983: figs. 61, 62). The part of the angular forming the ventral margin of the foramen intermandibularis caudalis is present and is very similar to *Meiolania platyceps.* The foramen posterius chorda tympani lies on the dorsal surface of the area articularis mandibularis as in *Meiolania platyceps.* The area articularis mandibularis in UCMP 61018 is slightly smaller than in AM F:57984 but this is the only difference.

Shell fragments. There are a number of shell

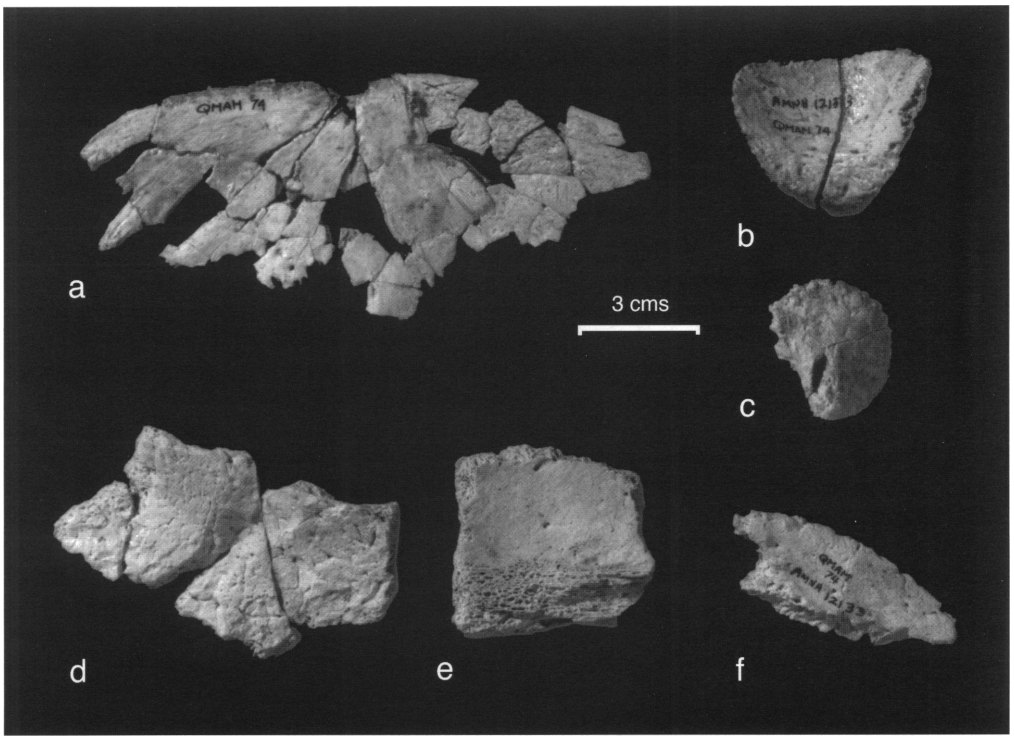


Fig. 83. Meiolaniidae indeterminate, Lake Pinpa, South Australia, Namba Fromation, Oligocene, AMNH 12133. **a,** Dorsal (internal) view of a left xiphiplastron, anterior to the right, medial toward bottom of page. **b,** Osteoderm in internal view. **c,** Osteoderm in external view. **d,** Costal fragment in external view. **e,** Costal fragment in internal view showing rib trace along lower edge. **f,** Unidentified bone.

fragments associated with UCMP 61018 and these are the typically meiolaniid thin bones with a dorsal surface of irregular pits and short channels. One peripheral fragment has a marginal sulcus and does not show a serration as in *Meiolania platyceps.* However, this could be from an anterior peripheral and only the posterior peripherals of *Meiolania platyceps* are serrated.

Meiolaniidae indeterminate

CONSISTS OF: AMNH 12133 (figs. 83, 84), an associated group of fragments, some in articulation presumed to represent a single individual; two caudal vertebrae, left ilium, left xiphiplastron, costal fragments, osteoderms, and an unidentified bone.

HORIZON: Namba Formation, Pinpa Fauna, Late Oligocene (Woodburne et al., 1993).

LOCALITY: Lake Pinpa, Site D, South Australia (see Tedford et al., 1977, for map). Collector: R. Tedford, 1971.

DESCRIPTION: *Caudal vertebrae* (fig. 84). Two caudal vertebra with this specimen are very similar to caudals of *Meiolania platyceps* described by Gaffney (1985a: fig. 15). They are particularly close to AM F:18715 (ibid., fig. 15C) which is identified as caudal seven in the reconstruction of the tail in *Meiolania platyceps.*

Left ilium (fig. 84). Associated with the other elements of AMNH 12133, is a left ilium, which is similar to ilia of *Meiolania platyceps.* The acetabular portion bears the usual one-third of the articulation, but the articular surface faces more posteriorly than in specimens of *Meiolania platyceps.* The internal surface of the dorsal process which articulates with the sacral ribs, is eroded in AMNH 12133,

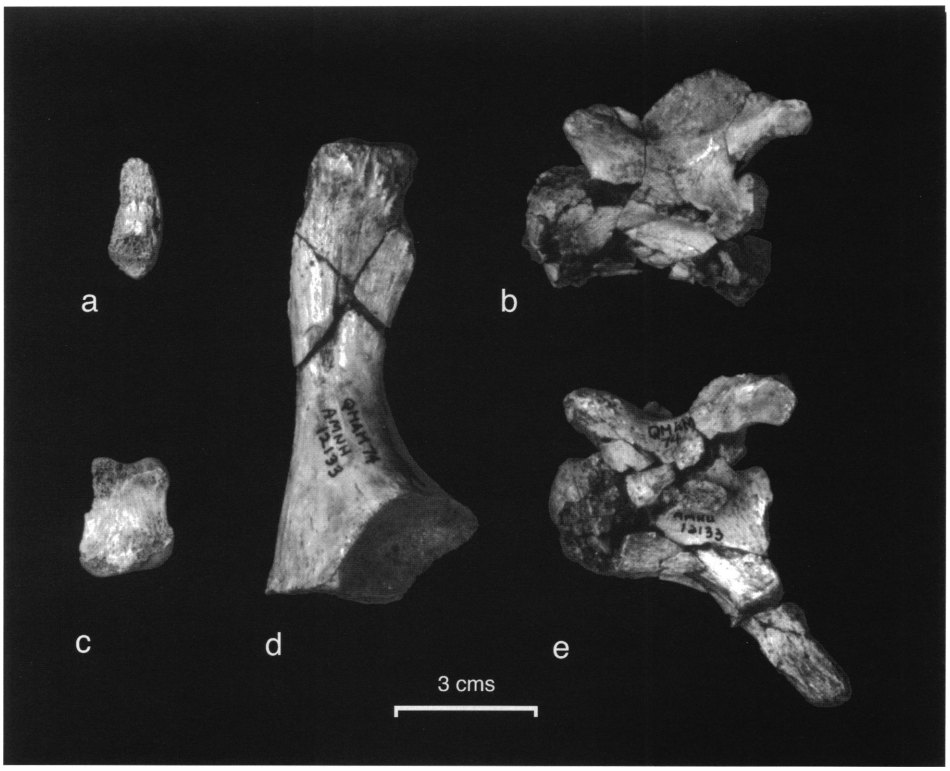


Fig. 84. Meiolaniidae indeterminate, Lake Pinpa, South Australia, Namba Formation, Miocene. **a,** AMNH 12134, ventral view of manus or pes ungual. **b,** AMNH 12133, posterior caudal. **c,** AMNH 12185, metatarsal/metacarpal. **d,** AMNH 12133, left ilium in lateral view. **e,** AMNH 12133, posterior caudal with hemal arch.

and its original shape is not completely preserved. However, instead of flaring dorsally as in *Meiolania platyceps,* AMNH 12133 is narrower and seems to have less room for sacral articulations. Although the shape of the dorsal process of the ilium in AMNH 12133 definitely differs from that in *Meiolania platyceps,* the extent and systematic significance of this difference is not clear.

Left xiphiplastron (fig. 83). Associated with the other elements of AMNH 12133 is a flat bone (fig. 83a) that, thanks to Dr. Peter Meylan, is best identified as a left xiphiplastron. The bone is similar to the right xiphiplastron of AM F:18775 but smaller and not as well ossified. AMNH 12133 has a relatively smooth internal (dorsal) surface and a more rugose external (ventral) surface. There is no sign of a sulcus on the external surface. The xiphiplastron is thick along its lateral edge and thins medially to a series of digitate projections, similar to xiphiplastra of *Meiolania platyceps.* Also as in *Meiolania platyceps,* there seem to be midline fontanelles. One fairly large fontanelle is at the anteromedial edge, with one or two smaller ones more posteriorly. The AMNH 12133 xiphiplastron is roughly 20% smaller than AM F:18775, which is consistent with the other elements thought to belong to the individual represented by AMNH 12133. In addition to size, the xiphiplastron of AMNH 12133 differs from that in *Meiolania platyceps* in being less ossified; the medially directed processes are longer and the fontanelles larger.

Costal fragments (fig. 83). Carapace fragments of costal bones showing rib traces are associated with the other elements of AMNH 12133. These bones show the typical external surface texture of irregular pits and short channels and grooves (fig. 83d, e).

Osteoderms (fig. 83). AMNH 12133 includes teardrop-shaped conical bones that are associated with limbs in *Meiolania platyceps*

and found with a number of meiolaniid specimens (see previous section on manus). These bones form spurs or projections covered with a scale and exposed on the outer surface of the limb. They are similar to those seen in living testudinids. A second, larger ossification type also seems to be embedded in the skin with one surface exposed. This osteoderm is broadly curved and has a thickened edge. Similarly shaped osteoderms also occur in the Gulgong collections, but do not occur in the extensive *Meiolania platyceps* collections from Lord Howe Island. It is possible that these larger, curved osteoderms are part of tail sheaths.

DISCUSSION: AMNH 12133, the Pinpa meiolaniid, is similar to *Meiolania platyceps* but is 20%–30% smaller and has minor differences in some elements. Unfortunately key diagnostic areas, like horn cores, tail club, or lower jaws, were not found with the specimen. Nonetheless, it is unlikely to be the same species as *Meiolania platyceps* but could represent another species of *Meiolania* or a different taxon such as *Warkalania.*

Unidentified bone. A small, triangular bone was found associated with the other elements of AMNH 12133. The bone is most similar to an epiplastron but, although well preserved, there is no sign of any scale sulci. The broad end has an unusual, semicircular margin. All of the margins appear unbroken. The convex, curved margin appears to be a free edge while the more irregular margins appear to be sutures. It is totally different from the epiplastra of *Meiolania platyceps* which have well-developed gular projections and obvious scale areas. The bone looks like it should be part of a turtle shell, but I am unable to identify it further.

Meiolaniidae indeterminate

CONSISTS OF: UCMP 84682, cervical rib.

HORIZON: Wipajiri Formation, Middle Miocene (Woodburne et al., 1985, 1993).

LOCALITY: UCMP V6213, Leaf Locality, Lake Ngapakaldi (see Stirton et al., 1967, for maps).

DESCRIPTION: See UCMP 61018.

Meiolaniidae indeterminate

CONSISTS OF: QM F:22655, an A horn core (fig. 85); QM F:22656, lower jaws (fig. 87); QM F:22657, caudal vertebra; QM F:22658—QM F:22660, tail rings (fig. 86); QM F:22661, tibia; QM F:22662, osteoderm; QM AR1667, postorbital; QM AR 9949, quadrate (fig. 85).

HORIZON: Carl Creek Limestone, early Miocene (Woodburne et al., 1993; see also Archer et al., 1989).

LOCALITY: Riversleigh Station, Queensland. See Archer et al. (1989).

DESCRIPTION: (Much of this section is from Gaffney, et al., 1992.) *"A" scale area* (fig. 85). QM F: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, in the internal surface there is one continuous sheet of finished bone with no indications of a depression for each scale area as in *Warkalania.* QM F:22655 does differ from *Meiolania platyceps* in having more acute posterior edges, rounded in *Meiolania platyceps.* The A horn of *Meiolania brevicollis* (Megirian, 1989, 1992) is lower than in either *Meiolania platyceps* or QM F: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 (fig. 87). A lower jaw of a meiolaniid from Riversleigh is QM F:22656 (Camel Sputum). 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 (table 16) are known for *Niolamia* (Woodward, 1901; see also fig. 64) and for an unnamed meiolaniid known from very fragmentary material from Gulgong, New South Wales (MM F:13898, see fig. 79). All the jaws

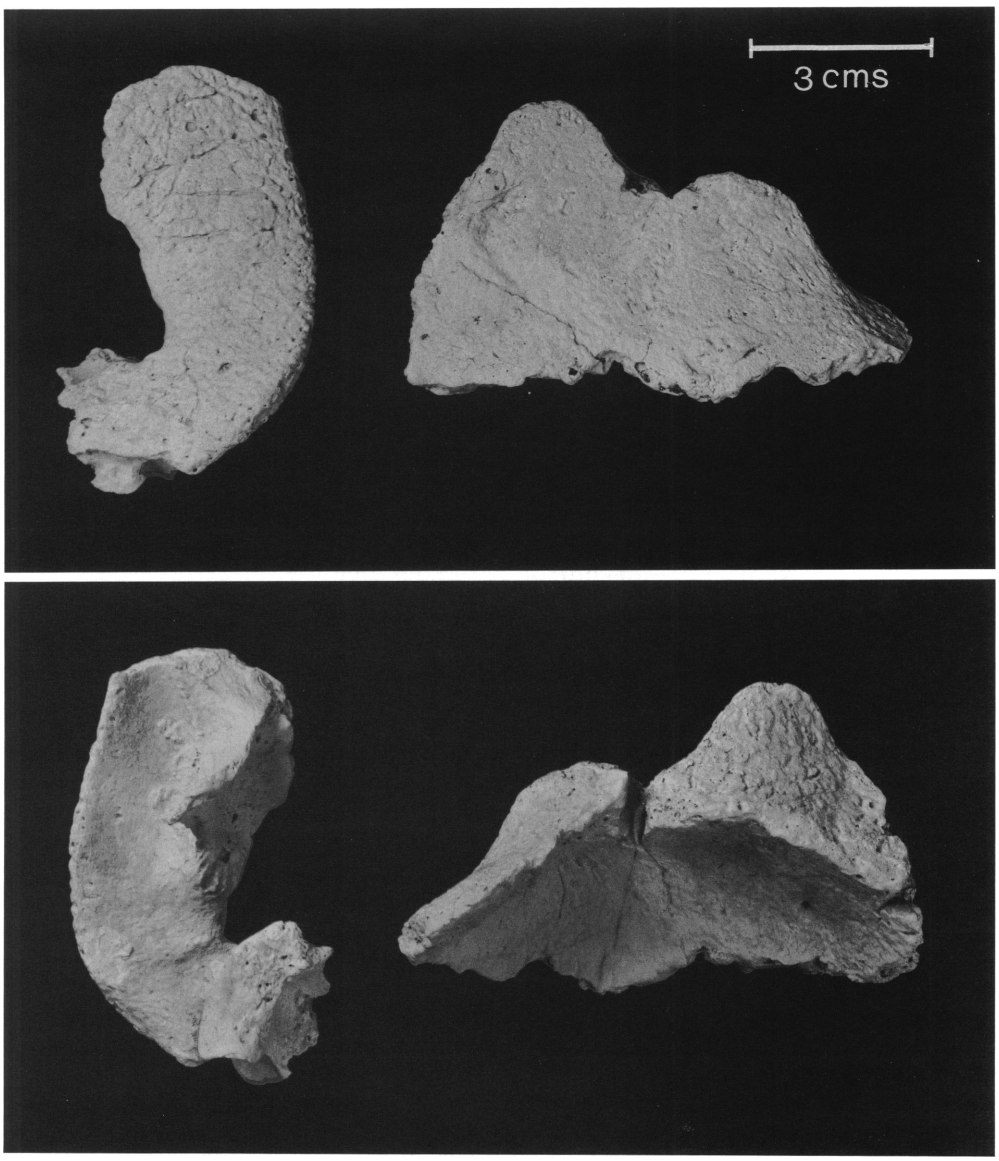


Fig. 85. Meiolaniidae indeterminate, Riversleigh Station, Queensland, Miocene. **Left,** QM AR 9949, portion of left quadrate, quadratojugal, and squamosal in lateral view (upper) and medial view (lower). **Right,** QM F:22655, left A scale area in dorsal view (upper) and ventral view (lower).

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 QM F:22656 the ridges are sharp and well defined and a medial cusp is present (Gaffney, 1983: 449). The lingual (inner) ridge is distinctly higher than the labial (outer) ridge in *Meiolania platyceps* and QM F:22656 in contrast to the ridges being even in *Niolamia* and the Gulgong fragment. The Riversleigh jaws, however, differ significantly from *Meiolania platyceps.* The lingual ridge in *Meiolania pla-*

TABLE 16
Meiolaniid Lower Jaws

	Niolamia argentina	Meiolaniid indet.	*Meiolania platyceps*	Meiolaniid indet, Riversleigh
Basis of comparison	AMNH cast + Woodward, 1901	MM F:13898	AM F:57984	QM AR 17101
Portion preserved	most of dentary	symphyseal area of dentary	entire lower jaw	most of dentary
Lingual ridge higher than labial ridge	no	no	yes	yes
Symphyseal cusp	absent	absent	present	present
Accessory ridge present adjacent to lingual ridge	no	no	yes	no
Anterior edge of lower jaw at symphysis	sloping	sloping	vertical	vertical
Triturating ridges	low	very low	high	high

tyceps is accompanied by an equally well-developed accessory ridge, absent in QM F: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* and *Meiolania brevicollis* (both of which lack lower jaws but presumably would have accessory ridges on them). It is unlikely that QM F:22656 belongs to the genus *Meiolania.* It is possible that they belong to *Warkalania,* although there is no real evidence for this.

Caudal vertebra. QM F:22657 (Camel Sputum) 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.* QM F:22657 is similar to AM F:18715, figured in Gaffney (1985a: fig. 15C). The neural spine is a bit shorter and more like AM F:57984 (ibid., fig. 15B) which is a more anterior caudal.

Tail rings (fig. 86). 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 roughly determine relative positions of tail rings and to categorize serial differentiation (Gaffney, 1985a: 26). Using criteria developed from *Meiolania platyceps,* the most anterior tail ring is QM F:22660 (Camel Sputum), with more posterior rings being QM F:22658 (Ringtail Site), and QM F:22659 (Sticky Beak). The anterior ring, QM F: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 QM F: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 QM F:22658 (the specimen originally identified by Alex Ritchie of the Australian Museum), which is the only Riversleigh tail ring to be essentially complete (fig. 86). It is similar to AM F:50635, figured in Gaffney (1985a: fig. 21), but the projections are lower in QM F:22658. Again, however, this is probably due to QM F:22658 being more anterior than AM F: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. QM F:22659 is similar to but less complete than QM F:22658. Both seem to be from the posterior part of the tail although QM F:22659 has a smaller diameter and may be more posterior than QM F:22658.

Both *Niolamia* (Woodward, 1901: pl. 18, fig. 2) and *Ninjemys* (Owen, 1881: pl. 65, figs. 1–4) have posterior tail rings preserved. As noted by Gaffney (1985a: 27) the only ap-

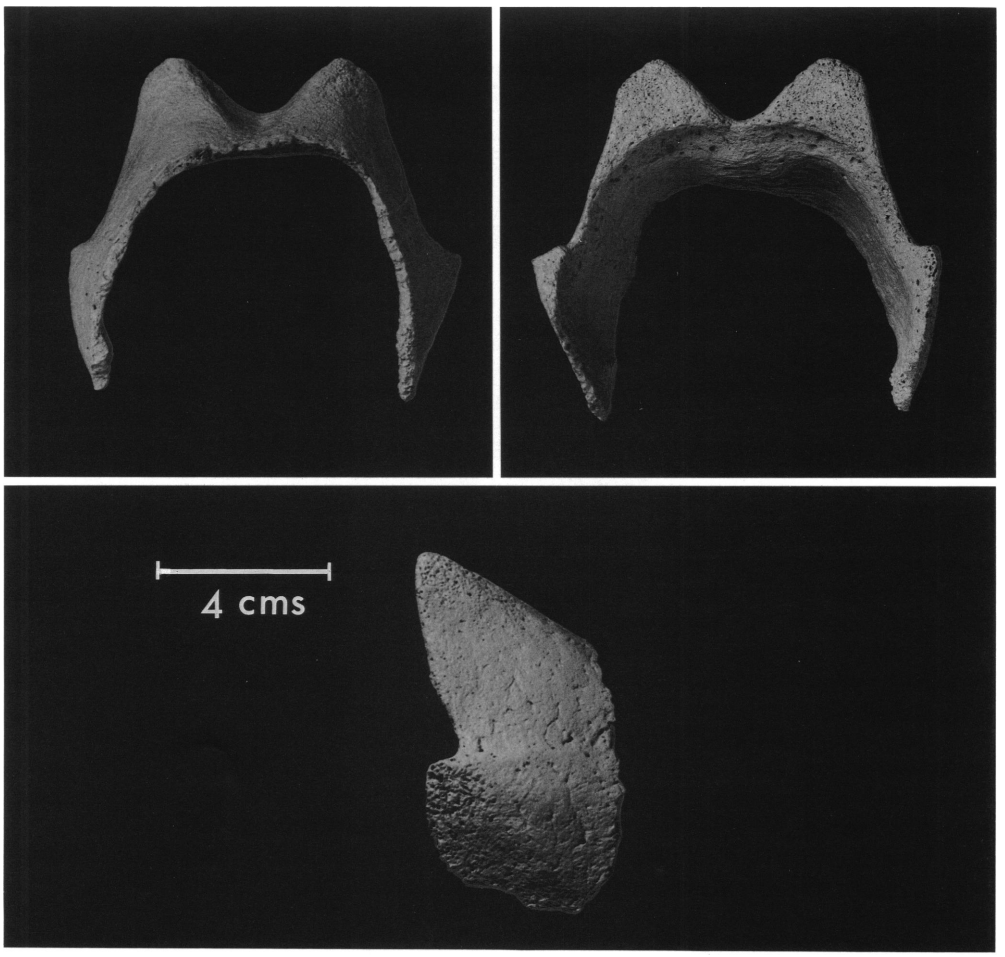


Fig. 86. Meiolaniidae indeterminate, Riversleigh Station, Queensland, Miocene. Tail ring, QM F:22658. **Upper left,** anterior view; **upper right,** posterior view; **lower,** lateral view.

parent systematic difference among the tail rings of meiolaniids is that the posterior rings of *Niolamia* and *Ninjemys* are complete circles, while in *Meiolania platyceps* the posterior rings are incomplete ventrally. QM F:22658 is well-enough preserved to show that it is incomplete ventrally and nearly indistinguishable from *Meiolania platyceps.*

Tibia. A partial right tibia, QM F:22661 (Camel Sputum), 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. QM F:22662 (Camel Sputum) 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). Similar osteoderms occur at Gulgong and Lake Pinpa.

Left postorbital. A left postorbital (QM AR16677) shows close similarities to *Meiolania platyceps.* The bone preserves the posterior orbital margin, the thickened transverse ridge on the internal surface behind the fossa orbitalis, and much of the temporal roof-

ing area of the postorbital. However, due to breakage a sutural edge is preserved only along the anterior and anteromedial margins.

The Riversleigh postorbital differs from that bone in *Meiolania platyceps* principally in the presence of sulci as grooves rather than raised ridges. The sulci defining the circumorbital F scale are present in about the same place in both species. However, medially the F–H sulcus divides into two sulci to form a scale pattern that is not strictly identical to *Meiolania platyceps.* The scale so defined is probably a large G scale that is more prominent in *Ninjemys* and *Niolamia* than in *Meiolania.* This area is not preserved in *Warkalania,* and it is not possible to exclude that genus. The bone probably does not belong to *Meiolania.*

Left ear fragment (fig. 85). A portion of the quadrate, squamosal, and quadratojugal (QM AR9949) from the left posteroventral part of the skull is very similar to this region of *Meiolania platyceps.* The external part of the skull preserved consists of the ventral process of the squamosal that forms the region between the posterior edge of the skull and the tympanic ring. The quadratojugal area that forms the ventral part of the cheek below the tympanic ring and attaches to the squamosal is also present. This external part of the skull is very similar to *Meiolania platyceps* except that the dorsal edge of the posterior margin seems to rise more vertically in the Riversleigh fragment than in *Meiolania platyceps.*

Medially the articular surface of the quadrate and the ventral portion of the processus articularis are preserved internal to the quadratojugal. More dorsally a medial sheet of thin bone that forms the posterodorsal part of the cavum tympani is present.

DISCUSSION: The fragments from Riversleigh could all belong to *Warkalania,* with the exception of the A scale area, QM F:22655. This fragment differs from *Warkalania* and could belong to a *Meiolania* species or a new taxon. At Riversleigh, then, there are at least two species of meiolaniids.

Meiolaniidae indeterminate

CONSISTS OF: QM F:9034, caudal vertebra.

HORIZON: Probably Chinchilla Sands, Pliocene, on basis of locality.

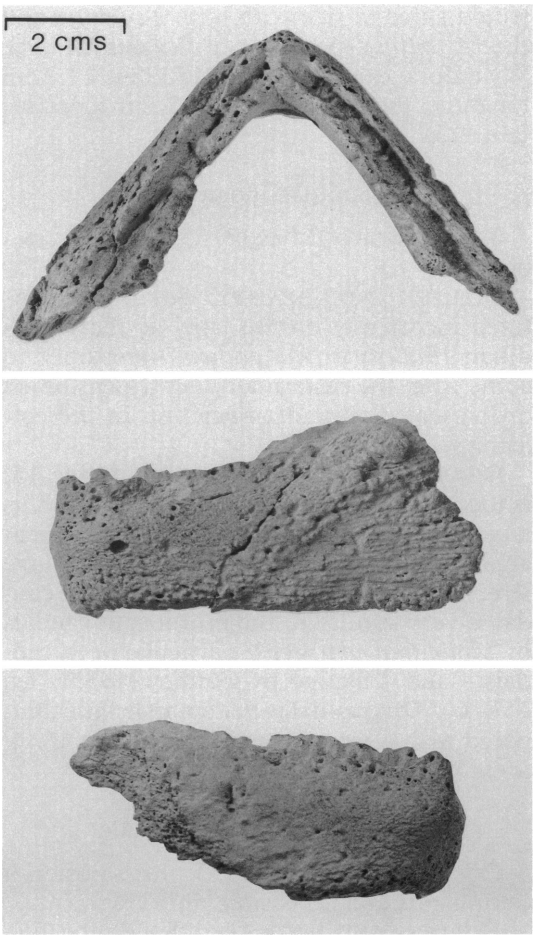


Fig. 87. Meiolaniidae indeterminate, Riversleigh Station, Queensland, Miocene. Lower jaws, QM F:22656. **Upper,** dorsal view; **middle,** left lateral view; **lower,** right lateral view.

LOCALITY: "Armour" Station, Condamine River, Macalister, Queensland. Collected G. Ross May 23, 1963 (label, *fide* Gaffney, 1981: 19).

DESCRIPTION: The stout well-developed haemal arch, procoelus centrum, and large size is diagnostic for meiolaniids in Australia. The caudal is nearly identical in morphology to the described caudals of *Meiolania platyceps* (Gaffney, 1985a) and particularly to one identified by Gaffney as the third (ibid., fig. 15A). It is not possible at present to distinguish separate meiolaniid taxa on the basis of caudals except for size. This specimen

would agree in size with both *Ninjemys* and the *Meiolania* species from Wyandotte. The Wyandotte caudal, NMV P18398 is 11.2 cm long and the QM 9034 is 7.2 cm long (see table 15).

Meiolaniidae indeterminate

CONSISTS OF: QM F:32155, caudal vertebra.

HORIZON AND LOCALITY: Unknown, identified incorrectly on the label as the crocodilian "*Pallimnarchus pollens,*" presumed to come from the eastern Darling Downs based on preservation and association in the collection.

DESCRIPTION: This large caudal (table 15) is identified as meiolaniid on the basis of its large hemal arch (broken off but attachment areas remain), procoelus centrum, and large size. Although eroded to some extent the caudal is very similar to the mid-length caudals of *Meiolania platyceps,* particularly to caudals 4 and 7 figured by Gaffney (1985a: fig. 15B, C). This caudal is 9.9 cm in length compared with 4.8 cm for caudal seven in *Meiolania platyceps* (AM F:18715).

Meiolaniidae indeterminate

CONSISTS OF: QM F:2553, three posterior peripherals and a possible limb fragment.

HORIZON AND LOCALITY: "Sandhurst Ck., 3 mls. N.E. from Fernlees Rlwy Stn., at a broken mill; don: J. M. Garvey, 9-8-1937" (label as quoted in Gaffney, 1981: 19). Queensland.

DESCRIPTION: These peripherals are about two to three times larger than similar peripherals of *Meiolania platyceps,* putting them in the size range of *Ninjemys* and the Wyandotte *Meiolania* species. The Lord Howe Island *Meiolania platyceps* has a well-developed serration pattern on the posterior peripherals which is similar to the morphology of the Sandhurst Creek peripherals and this provides the basis of the identification. The Queensland peripherals differ primarily in their large size and greater bone thickness, suggesting an animal at least twice the size of *Meiolania platyceps.*

Meiolaniidae indeterminate

CONSISTS OF: Museum National d'Histoire Naturelle NCP 05, a nearly complete seventh cervical.

LOCALITY: Main Pindai Cave, Nepoui Peninsula, New Caledonia.

HORIZON: Found in mixed cave deposits with Holocene as well as Pleistocene fossils (see Gaffney et al., 1984).

DISCUSSION: This specimen is described and figured in Gaffney et al. (1984) and compared with *Meiolania platyceps.* The New Caledonian cervical exhibits some differences from *Meiolania platyceps* but it is inadequate to provide the basis for a new taxon. Megirian (1989, 1992) also discusses the Tiga Island cervical with reference to *Meiolania brevicollis* and species within the genus *Meiolania.* Unfortunately, at present, it is very difficult to use vertebrae for meiolaniid systematics because cervicals are known only for *Meiolania platyceps* and *Meiolania brevicollis.*

Meiolaniidae indeterminate

CONSISTS OF: Museum National d'Histoire Naturelle NCT 01, a fragmentary centrum of a posterior cervical, probably the seventh.

LOCALITY: Tiga Island, in the Loyalty Group, New Caledonia.

HORIZON: Phosphates, presumed to be Pleistocene, deposited in karstified calcarenites (see Gaffney et al., 1984).

DISCUSSION: This cervical is described and figured in Gaffney et al. (1984). The centrum fragment is very similar to *Meiolania platyceps.*

RELATIONSHIPS OF TAXA WITHIN THE MEIOLANIIDAE

Monophyly of the Meiolaniidae is well tested by six characters, listed in table 18 and discussed below. Relationships of the taxa within the group is hampered by poor preservation of some taxa and the absence of an outgroup that would allow polarization of the

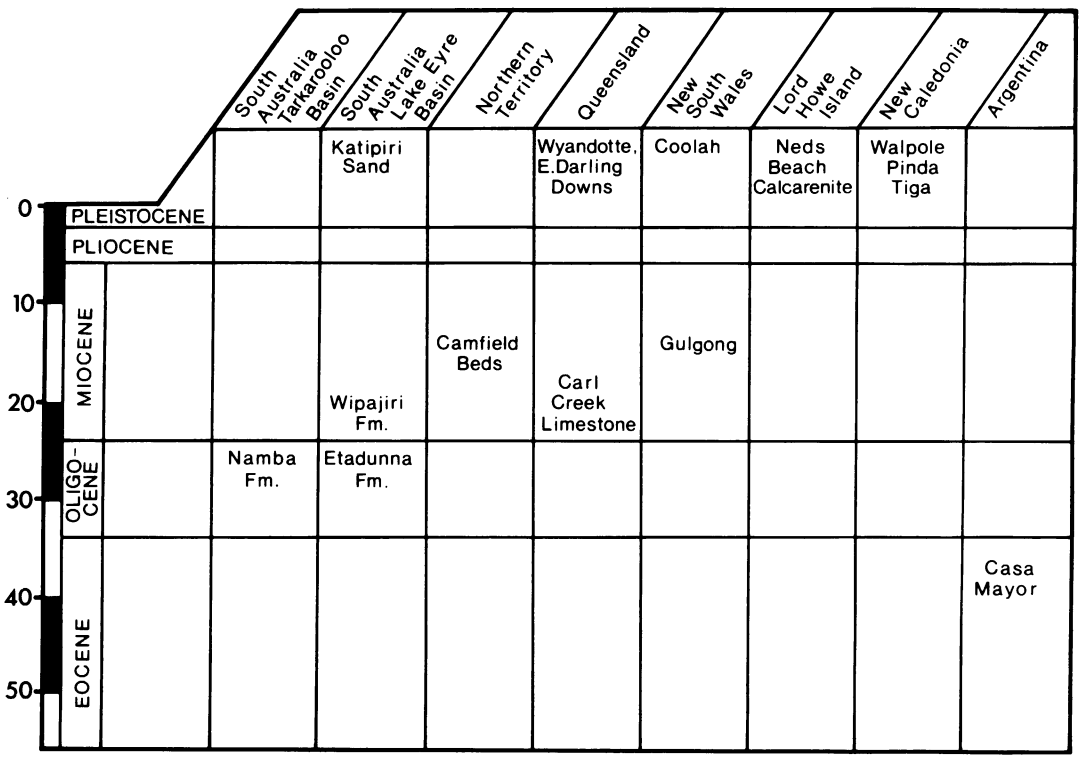


Fig. 88. Stratigraphic distribution of meiolaniids. Time scale and correlation based on Woodburne et al. (1993).

cranial scale characters. The analysis presented here is weakened by missing data for poorly represented taxa.

The fully roofed skull of meiolaniids is covered by a series of well-defined scales that often form processes or horns. The scale areas differ systematically among the meiolaniid taxa and provide the most useful source of characters defining taxa within the family. However, the scale characters cannot be polarized by reference to a cryptodiran outgroup because the very presence of these consistently recognizable scale areas on the completely roofed skull is a meiolaniid synapomorphy. Cranial scale areas are not very consistent in turtles and I have been unable to find likely homologues outside meiolaniids. The scale characters can be polarized within meiolaniids by accepting the argument that *Niolamia* is the sister taxon to the other meiolaniids. This argument was advanced by Gaffney (1983) and is based on a basicranial character (character **14**) that can be polarized by outgroup comparison, and an accessory triturating ridge, character **17**. Gaffney (1983: 431–435) argued that *Niolamia* ("*Crossochelys*") has an intrapterygoid slit that is primitive with respect to the intrapterygoid slit of *Meiolania platyceps* (ibid., fig. 60). The newly described specimens of sinemydids and other primitive eucryptodires (Brinkman and Peng, 1993a, 1993b; Gaffney and Ye, 1992) support this argument because they show a basicranial morphology closer to *Niolamia* than to *Meiolania*. Similarly, new material of primitive eucryptodires show the complete absence of an accessory triturating ridge (character **17**), further supporting *Niolamia* as the sister group to other meiolaniids.

The cladogram obtained from an analysis of 22 characters is shown in figure 92. The PAUP analysis fully resolves the eight taxa into a single tree with a consistency index of 1.0. However, this CI is a spurious indication of confidence in this tree. As discussed above,

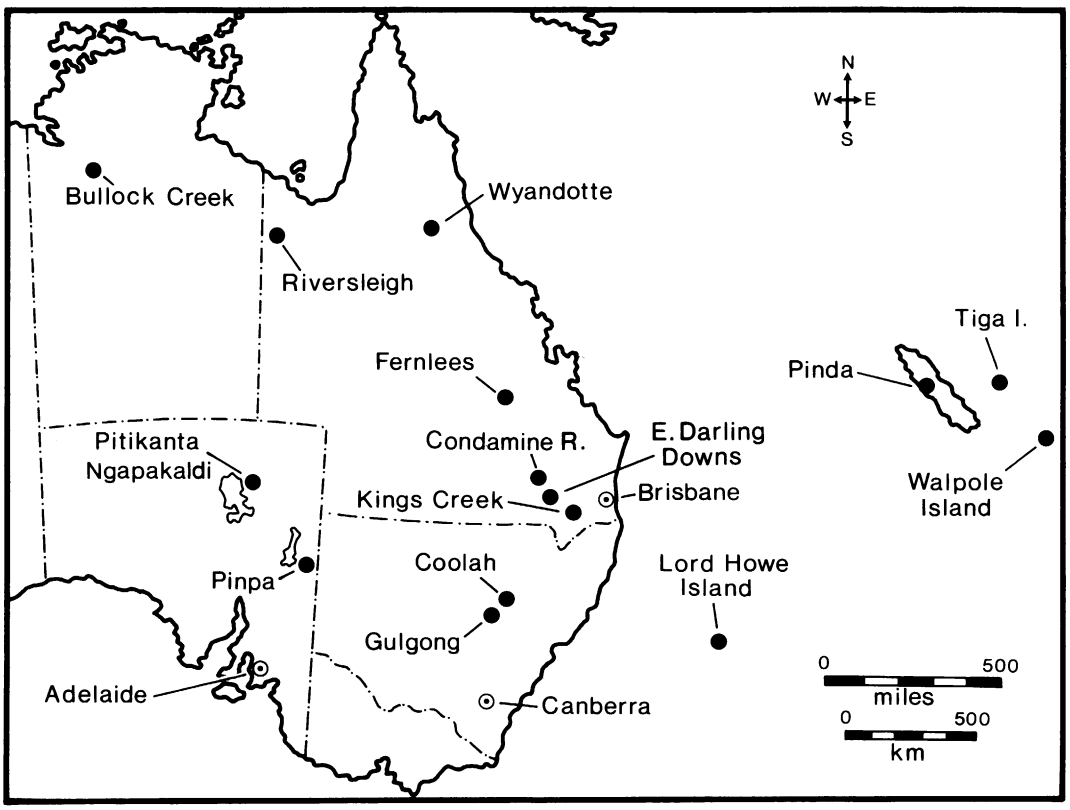


Fig. 89. Geographic distribution of meiolaniids in Australasia.

most of the characters involve the cranial scale areas, and other features unique to meiolaniids, with no comparable outgroup to polarize the characters with more confidence.

The taxa in the cladogram and table 18 follow the terminology of Gaffney (1992) and Gaffney et al. (1992). Some of the groups are better tested than others. I think there is good reason to accept *Niolamia* as the sister group of the remaining taxa even though many of the characters uniting Group II are ambiguous at that level resulting from missing data for many of the taxa. *Ninjemys* as the sister group to *Warkalania* plus *Meiolania* is relatively well supported (Group III) but it must be kept in mind that *Warkalania* consists only of a restored partial skull that is limited to information on the posterior cranial scales. New material of *Warkalania* could alter this resolution of *Warkalania* + *Ninjemys* + *Meiolania.* However, even if *Warkalania* were deleted from the analysis, *Meiolania* plus *Ninjemys* as the sister group to *Niolamia,* would be well supported.

Meiolania really has only two reasonably diagnosed species: *platyceps* and *brevicollis.* The other two taxa are based on essentially B horn cores. The resolution of four possible taxa in *Meiolania* is based solely on narrowness of the B horn core, and this is very weak, virtually speculative. Because of the limited material available for some of these taxa, it doesn't seem worthwhile trying to find other measurements that reflect B horn core shape.

1. D scales meet in midline: no = 0; yes = 1.

Morphology: The cranial scales of meiolaniids are described in Gaffney (1983) and Gaffney et al. (1992), see also figures presented here (figs. 90, 91).

Primitive condition: Polarizing the D scale morphology is based on accepting *Niolamia* as having the primitive condition.

Homoplasy: None known.

Discussion: The D scales are incompletely preserved in *Ninjemys* and *Warkalania* but there is enough preserved to demonstrate that the D scales had some midline contact.

2. X scale much smaller than D scale: no = 0; yes = 1.

Morphology: The cranial scales of meiolaniids are described in Gaffney (1983), see also figures presented here (figs. 90, 91).

Primitive condition: Polarizing the X scale morphology is based on accepting *Niolamia* as having the primitive condition.

Homoplasy: None known.

Discussion: The median X scale is only partially preserved in *Ninjemys* but the other scales show that the X scale must have been small. The close relationship of the X and D scales could argue that this and character **1** should be treated as one character. Doing so does not change the cladogram, however.

3. A, B, C scales form a continuous posterolateral shelf: yes = 0; no = 1.

Morphology: The relatively smaller A, B, C scales of *Meiolania* are described in Gaffney (1983) while the primitive condition of a shelf with A, B, C scales on it is described in Gaffney et al. (1992) for *Warkalania.* See also figures 90, 91.

Primitive condition: Polarizing the cranial scale morphology is based on accepting *Niolamia* as having the primitive condition.

Homoplasy: None known.

Discussion: The morphology of the A, B, C scale area is the basis for the most consistent comparisons among the meiolaniids. The continuous posterolateral shelf seen in *Niolamia, Ninjemys,* and *Warkalania* is in contrast to the more helmet-like *Meiolania.*

4. D scale: high = 0; low = 1.

Morphology: Meiolaniid cranial scale areas are described in Gaffney (1983) and figured here (figs. 90, 91). Original sources include Owen (1881) for *Ninjemys,* Gaffney et al. (1992) for *Warkalania,* and Woodward (1901) for *Niolamia.*

Primitive condition: Polarizing the cranial scale morphology is based on accepting *Niolamia* as having the primitive condition.

Homoplasy: None known.

Discussion: The high, protuberant central area of the D scale can be seen in *Niolamia* and *Ninjemys.* This character is useful because it is also preserved in the poorly known *Warkalania.* In *Warkalania, Meiolania brevicollis,* and *Meiolania platyceps* the scale area is relatively low and not protuberant as in *Niolamia* and *Ninjemys.*

5. B scale a recurved horn: no = 0; yes = 1.

Morphology: Meiolaniid cranial scale areas are described in Gaffney (1983), Gaffney et al. (1992) and figured here (figs. 90, 91).

Primitive condition: Polarizing the cranial scale morphology is based on accepting *Niolamia* as having the primitive condition, a straight, flattened B horn core.

Homoplasy: None known, except with cows (*Bos taurus*).

Discussion: The recurved B horn core has been accepted as the principal synapomorphy of a restricted *Meiolania* (Gaffney, 1983; Megirian, 1989, 1992).

6. Recurved B horn core narrow: not recurved, or width/length ratio greater than 0.6 = 0; recurved, width/length ratio between 0.6 and 0.48 = 1; recurved, width/length ratio less than 0.48 = 2.

Morphology: The B horn core of *Meiolania* is described in Gaffney (1983), Gaffney and McNamara (1990), and Megirian (1992). The use of width/length ratios as a relatively crude basis for horn core comparison was initiated by Gaffney (1983) and followed by Gaffney and McNamara (1990) and Megirian (1992).

Primitive condition: Using *Niolamia, Ninjemys,* and *Warkalania* as outgroups, the short, squat B horn core would be primitive in contrast to a long, slender B horn core.

Homoplasy: Strictly speaking, none known, however, the systematic use of B horn core shape must be considered to be very tenuous and unsupported by any other characters. Two of the four "taxa," *Meiolania mackayi* and the unnamed Wyandotte species, are only barely diagnosable at all and probably should not be named. The horn core shape is the only basis for any comparison (other than body size, which does differentiate these two taxa). The measurements made by Gaffney (1983) show a width/height range for *Meiolania platyceps* from 0.46 to 1.31. This is a very wide range which cautions against using the small samples of *Meiolania brevicollis* (1 specimen), *Meiolania mackayi* (6 specimens), and Wyandotte species (3 specimens). With ratio overlaps between *Meiolania mackayi* and *Meiolania platyceps,* and be-

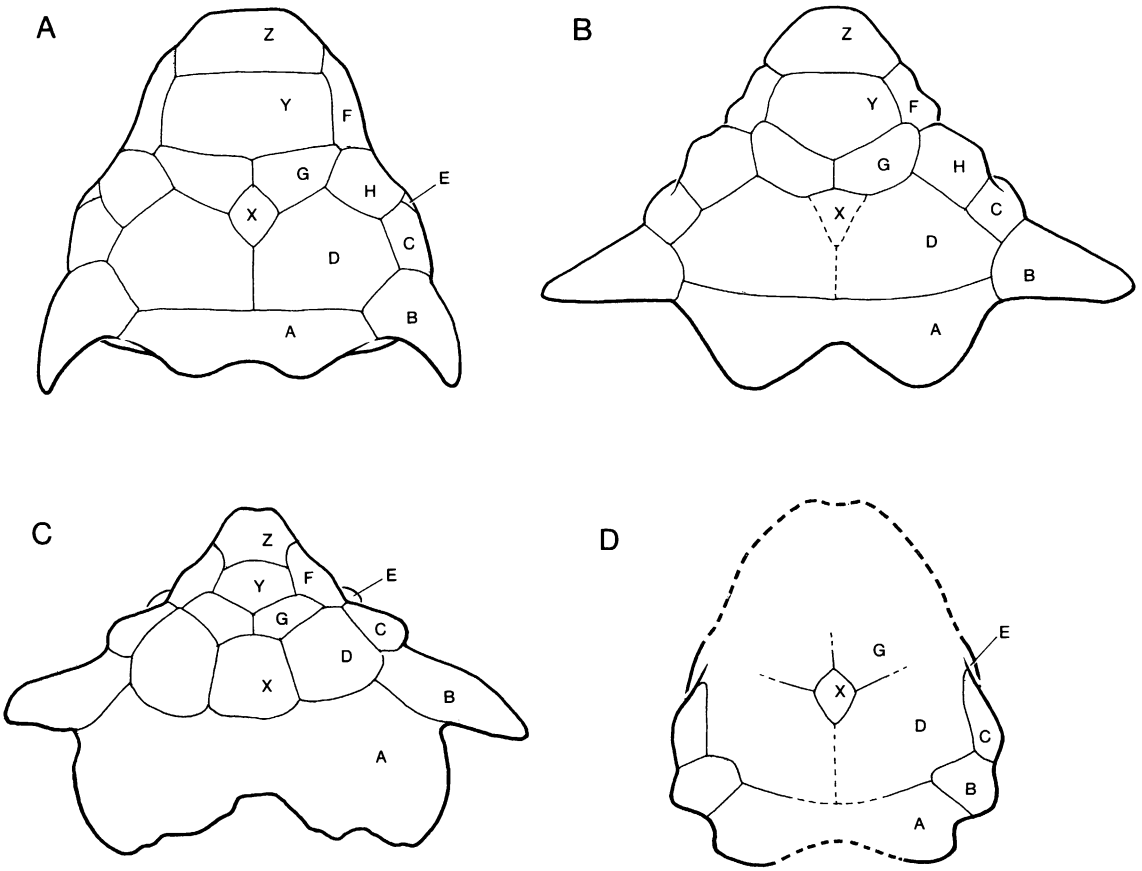


Fig. 90. Meiolaniid skulls in dorsal view. Scale terminology from Gaffney (1983). **A,** *Meiolania platyceps* (after Gaffney, 1983); **B,** *Ninjemys oweni* (after Owen, 1881, and BMNH R391); **C,** *Niolamia argentina* (after Woodward, 1901, and cast); **D,** *Warkalania carinaminor* (after Gaffney, Archer and White, 1992).

tween the Wyandotte species and *Meiolania platyceps,* there is clear evidence of homoplasy in slender versus squat B horn cores in *Meiolania.*

Discussion: The only way these ratios can be used is to compute the median ratios. If this is done for all *Meiolania platyceps* cores, the median is 0.64, but if only skulls are used then 0.72 is the result. For *Meiolania mackayi* the median is 0.50, for *Meiolania brevicollis* it is 0.32, and for the Wyandotte species it is 0.43. If slender is derived, 0.43 and 0.32 form a group, and 0.43, 0.32, and 0.50 form a larger group with the most squat 0.64 of *Meiolania platyceps* outside. Again, this must be considered extremely tentative.

7. A scale small and not forming large shelf: no = 0; yes = 1.

Morphology: The cranial scales of meiolaniids are described in Gaffney (1983) and Gaffney et al. (1992), see also figures presented here (figs. 90, 91).

Primitive condition: Polarizing the A scale morphology is based on accepting *Niolamia* as having the primitive character.

Homoplasy: None known.

Discussion: Reduction of the large shelf at the back of the skull can be examined in terms of the scales covering it. While the shelf itself is interpreted as being present in *Warkalania* as well as *Niolamia* and *Ninjemys* (character 3) the large A scale area of *Niolamia* and

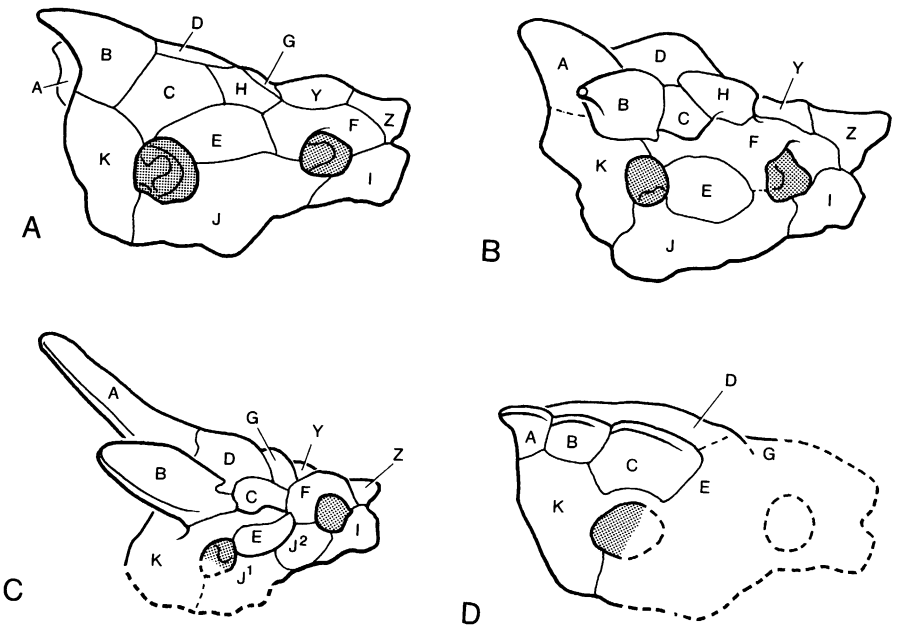


Fig. 91. Meiolaniid skulls in lateral view, as in fig. 90.

Ninjemys is considerably smaller in *Warkalania* and *Meiolania,* thus uniting the latter two.

8. A scale small: A scale very large = 0; A scale comparable in size to B scale = 1.

Morphology: The cranial scales of meiolaniids are described in Gaffney (1983) and Gaffney et al. (1992), see also figures presented here (figs. 90, 91).

Primitive condition: Polarizing the A and B scale morphology is based on accepting *Niolamia* as having the primitive condition.

Homoplasy: None known.

Discussion: Another aspect of the shelf reduction at the back of the skull is the very large A scale area seen only in *Niolamia* and presumed to be the primitive condition.

9. Y and Z scales relatively large: small = 0; large = 1.

Morphology: The cranial scales of meiolaniids are described in Gaffney (1983), see also figures presented here (figs. 90, 91).

Primitive condition: Polarizing the Y and Z scale morphology is based on accepting *Niolamia* as having the primitive condition.

Homoplasy: None known.

Discussion: Reflecting the small snout of *Niolamia,* the Y and Z scales of *Ninjemys* and *Meiolania* are large in comparison to *Niolamia.* The snout of *Warkalania* is not preserved.

10. Snout broad: narrow = 0; broad = 1.

Morphology: Dorsal views of meiolaniid skulls are in this paper (figs. 90, 91), Gaffney (1983), Megirian (1992), Owen (1881), Woodward (1901), and Gaffney, et al. (1992).

Primitive condition: Primitive eucryptodires such as sinemydids and plesiochelyids are all narrow snouted, as are *Kayentachelys,* baenids, and other primitive cryptodires.

Homoplasy: Broad snouts occur in testudinids and carretochelyids (which have the largest snouts in turtledom).

Discussion: A broad snout is best considered as a *Meiolania* synapomorphy at present. The snout of *Warkalania* is not preserved, making the distribution of this character ambiguous. The snout is narrow in *Niolamia* and *Ninjemys.*

11. Nasal bones unusually large: nasals relatively small = 0; nasals larger than in any other turtle = 1.

Morphology: Detailed description and figures of the nasal bones in *Meiolania platyceps* are in Gaffney (1983). The large, overhanging nasals are characteristic of meiolaniids and

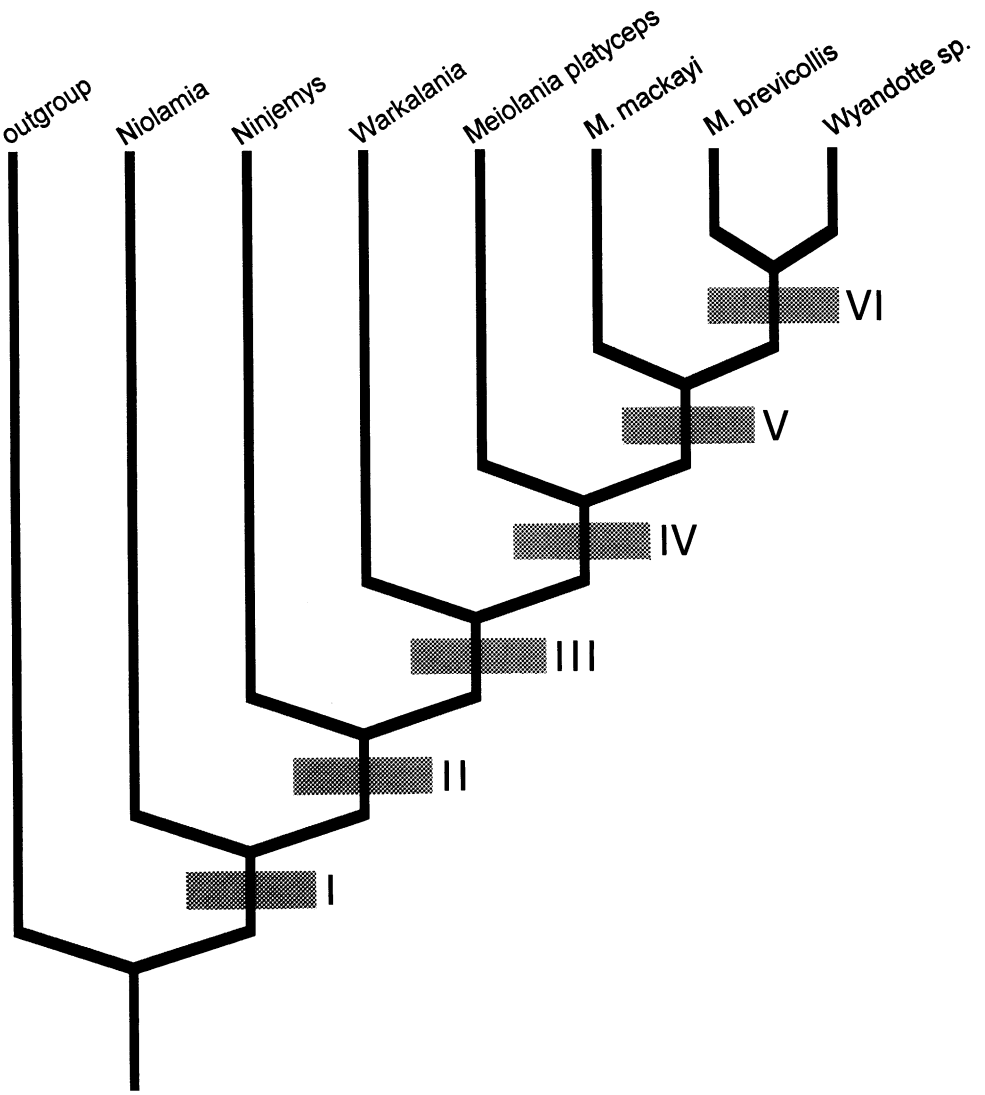


Fig. 92. Shortest cladogram for Meiolaniidae generated by PAUP Version 3.1.1 (Swofford, 1993), tree length 23 steps, CI = 1.00. Data set in table 17 and fig. 93.

differ from large nasals in other taxa like *Proganochelys* by having lateral extensions that curve ventrolaterally. The nasals in *Meiolania* are larger than in any other turtle.

Primitive condition: Proganochelys has the presumed primitive condition for nasal size in turtles (Gaffney, 1990). Although relatively large, the *Proganochelys* nasals are smaller than in *Meiolania.*

Homoplasy: Due to their relatively simple morphology, the size of nasals would be hard to homologize. Meiolaniids, however, have such large nasals, that they are best interpreted as unique to the group.

Discussion: The large nasals of meiolaniids may be related to the nasal sinuses developed in meiolaniids.

12. Nasomaxillary sinus: absent = 0; present = 1.

Morphology: Nasomaxillary sinuses are described and figured for *Meiolania* in Gaffney (1983). They are also present in *Ninjemys*

and *Meiolania brevicollis.* These lateral pockets of the fossa nasalis are formed by the nasals dorsally and the maxillae ventrally.

Primitive condition: The absence of nasal sinuses is found throughout turtles as described in Gaffney (1983).

Homoplasy: The nasomaxillary sinuses are unique to meiolaniids and do not occur outside the group, but their presence/absence can only be determined in *Ninjemys* and *Meiolania.*

Discussion: There is no evidence of the function of these sinuses.

13. Intrapterygoid slit: absent = 0; present = 1.

Morphology: The intrapterygoid slit is described and figured by Gaffney (1983) for *Meiolania* and *Niolamia,* the only two meiolaniid taxa which have the region preserved. The slit, as interpreted by Gaffney (1983), has two conditions, treated here as a separate character (**14**).

Primitive condition: Following the work of Brinkman and Nicholls (1993), Brinkman and Peng (1993a, 1993b) and Gaffney and Ye (1992), it has become apparent that many primitive eucryptodires have the palatine artery entering the pterygoid/basisphenoid via a separate foramen, as in *Sinemys gamera* (Brinkman and Peng, 1993b), or via a steplike opening, as in *Dracochelys.* The *Dracochelys* condition of the foramen caroticum laterale (Gaffney and Ye, 1992: figs. 3, 5) is an appropriate model for the primitive condition of the intrapterygoid slit in *Niolamia* (as reconstructed in Gaffney, 1983: fig. 60). Further separation and posterior extension of the ventral plate of the pterygoid in *Dracochelys* would come very close to the condition in *Niolamia.*

Homoplasy: The intrapterygoid slit is unique to meiolaniids.

Discussion: The principal problem with the use of this character as a meiolaniid synapomorphy is that the area is preserved only in *Niolamia* and *Meiolania* and not in *Warkalania* or *Ninjemys.*

14. Intrapterygoid slit extensive, completely covering foramen caroticum basisphenoidale: no = 0; yes = 1.

Morphology: The primitive condition, as seen in *Niolamia,* and the advanced condition, as seen in *Meiolania,* are described and figured in Gaffney (1983: see fig. 60).

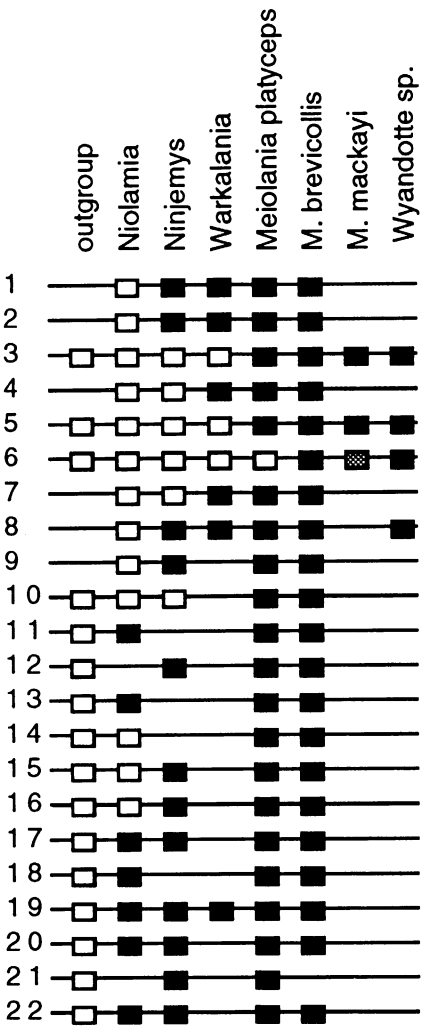


Fig. 93. Character distributions for Meiolaniidae data set.

Primitive condition: Compared with *Meiolania, Niolamia* has a less extensive intrapterygoid slit, leaving the foramen caroticum basisphenoidale uncovered in ventral view. The *Niolamia* condition could be hypothesized as intermediate between *Dracochelys,* which is primitive for eucryptodires, and *Meiolania,* showing the advanced meiolaniid condition.

Homoplasy: The intrapterygoid slit is unique to meiolaniids. The extensive slit condition is unique to *Meiolania.*

Discussion: This character and the presence of the intrapterygoid slit could be com-

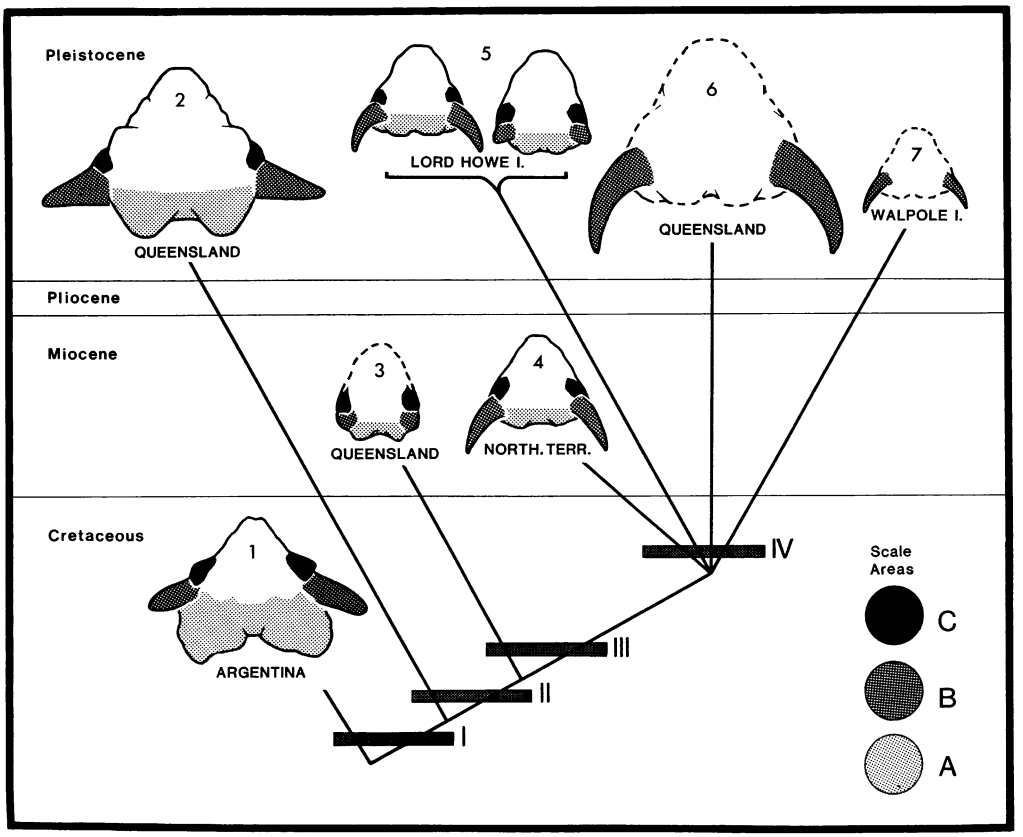


Fig. 94. Cladogram of meiolaniid turtles with skulls showing three scale areas (A, B, C) for comparison. Temporal range incomplete and not to scale. See text for characters and discussion of Groups I–IV. Taxa are: **(1)** *Niolamia argentina,* **(2)** *Ninjemys oweni,* **(3)** *Warkalania carinaminor,* **(4)** *Meiolania brevicollis,* **(5)** *Meiolania platyceps* showing two extremes of horn variation, **(6)** *Meiolania* sp., Wyandotte, **(7)** *Meiolania mackayi.*

bined as one multistate character, however, the shortest cladogram would not change.

15. Apertura narium externa divided: not divided = 0; divided by both nasal and premaxilla = 1.

Morphology: The meiolaniids have a thick, variably overhanging shelf formed by the nasals above the apertura narium externa (further description in Gaffney, 1983). In *Ninjemys, Meiolania platyceps,* and *Meiolania brevicollis* the nasal sends a process ventrally and the premaxilla sends a process dorsally to divide the apertura into two openings.

Primitive condition: Divided nares are primitive for turtles, both *Proganochelys* and *Kallokibotion* have divided nares. However, in *Proganochelys* they are divided by dorsal processes of the premaxillae rather than by the nasals and premaxillae as in meiolaniids. The situation is unclear in *Kallokibotion* but the division seems to be by the nasals. In the *Kallokibotion*-like turtle from Mongolia, the nares are not divided. In meiolaniids the processes are recessed within the apertura rather than formed on the surface as in *Proganochelys* and *Kallokibotion.* The most likely primitive condition for meiolaniids is an apertura without median division. An undivided apertura is present in baenids and primitive eucryptodires such as plesiochelyids and macrobaenids.

Homoplasy: As discussed above, a divided apertura narium externa occurs in *Proganochelys* and *Kallokibotion.* The specific meiolaniid morphology, however appears to be unique. Within *Meiolania platyceps* the de-

TABLE 17
Meiolaniid Data Set

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
outgroup	?	?	0	?	0	0	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0
Niolamia	0	0	0	0	0	0	0	0	0	0	1	?	1	0	0	0	1	1	1	1	?	1
Ninjemys	1	1	0	0	0	0	0	1	1	0	?	1	?	?	1	1	1	?	1	1	1	1
Warkalania	1	1	0	1	0	0	1	1	?	?	?	?	?	?	?	?	?	?	1	?	?	?
Meiolania platyceps	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Meiolania brevicollis	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1
Meiolania mackayi	?	?	1	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Wyandotte sp	?	?	1	?	1	2	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?

gree of division varies with some specimens having no actual contact between nasal and premaxilla (Gaffney 1983).

Discussion: The snout is not preserved in *Warkalania* so the nares condition is unknown but based on casts and Woodward's (1901) figures, *Niolamia* seems to have an undivided apertura narium externa. *Ninjemys* and *Meiolania* have the divided condition.

16. Accessory ridge on triturating surface: absent = 0; present = 1.

Morphology: In addition to figures presented here (figs. 56, 57, 63, 66, 68), Gaffney (1983), Woodward (1901), and Owen (1881) describe and figure meiolaniid palates.

Primitive condition: Primitive eucryptodires such as plesiochelyids (Gaffney, 1976), *Dracochelys* (Gaffney and Ye, 1992), *Sinemys* (Brinkman and Peng, 1993b), and *Ordosemys* (Brinkman and Peng, 1993a, and Brinkman personal commun.) do not have accessory ridges on the triturating surface. It is most likely that this is the primitive condition for a meiolaniid outgroup.

Homoplasy: Accessory triturating ridges on the maxilla appear frequently in both cryptodires and pleurodires, e.g., *Podocnemis,* testudinids, batagurids, emydids (Gaffney, 1979b). Triturating surface morphology that is particularly similar to *Meiolania* occurs in testudinids like *Hesperotestudo* (Gaffney, 1979b, 1983).

Discussion: An accessory triturating ridge occurs in *Ninjemys, Meiolania platyceps* and *Meiolania brevicollis,* but not in *Niolamia.* This distribution is significant because despite widespread homoplasy in this character, the complete absence of an accessory ridge in primitive eucryptodires substantiates the position of *Niolamia* as the sister group of all other meiolaniids. *Warkalania* does not have any of the palatal area preserved.

17. Broad squamosal/quadratojugal contact below incisura columellae auris: absent = 0: present = 1.

Morphology: The broad contact of squa-

TABLE 18
Unambiguous Synapomorphies for Meiolaniidae Cladogram (fig. 92)

Group I. Family Meiolaniidae
- 11. Nasal bones very large
- 13. Intrapterygoid slit
- 17. Broad squamosal-quadratojugal contact
- 18. Squamosal-supraoccipital contact
- 19. Squamosal process
- 20. Horizontal plate on supraoccipital

Group II
- 1. D scales meet in midline
- 2. X scale small
- 8. A scale small
- 9. Y and Z scales large
- 15. Apertura narium externa divided
- 16. Accessory ridge on maxillary triturating surface

Group III
- 4. D scale low
- 7. A scale small

Group IV, Genus *Meiolania*
- 3. A, B, C scales do not form shelf
- 5. B scale a recurved horn core

Group V
- 6. B horn width/length less than 0.6

Group VI
- 6. B horn width/length less than 0.48

mosal and quadratojugal ventral to the cavum tympani and incisura columellae auris has been described in Gaffney (1983). The ventral process of the squamosal extends behind and below the cavum tympani to meet a deepened quadratojugal. The incisura columellae auris contains both stapes and eustachian tube.

Primitive condition: In all other cryptodires the squamosal lacks a ventral process behind and below the cavum tympani. This condition is described and figured in Gaffney (1983).

Homoplasy: This character is described only for meiolaniids.

Discussion: Due to the general fusion of sutures in meiolaniids, the quadratojugal/squamosal contact is described only in *Meiolania platyceps* (Gaffney, 1983). However, the bony sheet beneath the cavum tympani is known in *Ninjemys* and *Warkalania.*

18. Squamosal/supraoccipital contact: Completely separated = 0; extensive contact = 1.

Morphology: This condition is described and figured in Gaffney (1983), for *Meiolania* and in Simpson (1938) for *Niolamia* ("*Crossochelys*").

Primitive condition: Primitive eucryptodires such as *Sinemys* (Brinkman and Peng, 1993b) and *Dracochelys* (Gaffney and Ye, 1992) have a well-developed temporal emargination and this seems to be the condition for any plausible meiolaniid outgroup.

Homoplasy: Although some turtles (e.g., *Pseudemydura*) seem to have independently acquired a squamosal/supraoccipital contact, the condition is relatively rare.

Discussion: Although sutures for these bones are known only in *Meiolania platyceps* and *Niolamia,* the condition is presumed to occur in *Ninjemys* and *Warkalania* based on the similar morphology.

19. Squamosal with posterolateral processes: absent = 0; present = 1.

Morphology: In addition to figures presented here (figs. 90, 91), meiolaniid squamosals are described in Simpson (1938), Anderson (1925), and Gaffney (1983).

Primitive condition: The primitive condition of the squamosal can be seen in primitive eucryptodires described by Brinkman and Peng (1993a, 1993b) and Gaffney and Ye (1992). Other eucryptodires such as plesiochelyids and chelydrids are described in Gaffney (1979b).

Homoplasy: The horns and processes of meiolaniid squamosals are unique.

Discussion: The squamosal of meiolaniids is a clear synapomorphy that strongly differentiates the group from all other turtles. Further reliance on the scale areas and horns of the squamosal for systematic analysis within Meiolaniidae is less secure, however.

20. Supraoccipital with horizontal plate: no = 0; yes = 1.

Morphology: This character is described in Gaffney (1983) for *Meiolania* and Simpson (1938) for *Niolamia* ("*Crossochelys*").

Primitive condition: The primitive condition of the supraoccipital for cryptodires is a narrow crista supraoccipitalis without a horizontal plate. This condition is described for cryptodires in Gaffney (1979b).

Homoplasy: Some turtles (e.g., *Pseudemydura*) have independently evolved a plate on the supraoccipital.

Discussion: The completely roofed skull of meiolaniids is formed by the expansion of a number of elements, the large supraoccipital being one of the principal components. This character and the squamosal/supraoccipital could be interpreted as one character because they are so closely interrelated. As with other characters in this analysis within the Meiolaniidae, I have preferred separating out as many characters as seems reasonable.

21. Tail club: absent = 0; present = 1.

Morphology: The dermal tail ossifications of meiolaniids are described in Gaffney (1985a) for *Meiolania,* and in Owen (1882) for *Ninjemys.*

Primitive condition: It is becoming clearer that the tail club of meiolaniids should not be considered homologous with the tail club of *Proganochelys,* rather, it is best interpreted as a synapomorphy unique to the family. Gaffney (1985a) concluded that the tail clubs of *Proganochelys* and meiolaniids were homologous and that the club would have been lost independently in pleurodires, baenids, and primitive eucrypotodires. However, in contrast to the recent discoveries showing a wide distribution of another primitive character, free cervical ribs, there has been no increase in the distribution of caudal ossifi-

cations. Given the cladograms of Gaffney and Meylan (1988), Gaffney et al. (1991), and the cryptodire cladogram presented here, it is more parsimonious to hypothesize the tail club as independently evolved in *Proganochelys* and meiolaniids. The most likely primitive condition for the meiolaniid tail club would be the unarmored tail seen in plesiochelyids and sinemydids.

Homoplasy: As discussed above, it is likely that a tail club arose independently in *Proganochelys* and meiolaniids. There are morphologic distinctions between the clubs in the two taxa in symmetry and the pattern of fusion, as described in Gaffney (1985a). Some extinct testudinids (Hay, 1908) and an undescribed pelomedusid have caudal bucklers, flat plates at the distal end of a short tail for covering the anus. But these are quite distinct from the elongate cylinders of *Proganochelys* and meiolaniids.

Discussion: Tail clubs are known for *Ninjemys* and *Meiolania* but not the other meiolaniids. In *Ninjemys* the tail club has two segments while in *Meiolania platyceps* there are four segments.

22. Tail rings: absent = 0; present = 1.

Morphology: The tail rings of meiolaniids are described in Gaffney (1985a) for *Meiolania,* in Owen (1882) for *Ninjemys,* and in Woodward (1901) for *Niolamia.*

Primitive condition: A tail without dermal ossifications, as seen in *Kayentachelys,* baenids, plesiochelyids, and macrobaenids is the most likely primitive condition for cryptodires.

Homoplasy: No other turtles have ossified rings that completely or nearly surround the tail. *Proganochelys* (Gaffney, 1990) has dermal ossifications in the form of spikes and plates that cover the dorsal surface of the tail. *Chelydra* has loose dermal ossifications on the dorsal surface of the tail (Newman, 1906).

Discussion: The very close similarity of the tail rings and the tail clubs in meiolaniids make the tail clubs appear to be fused sets of tail rings (see Gaffney, 1985, for further discussion). Presumably rings and clubs occur in all the meiolaniids, however, the known distribution of these elements is not identical. A tail ring is known for *Niolamia* (Woodward, 1901) but no club is preserved, while *Ninjemys* and *Meiolania* have both tail ring and tail club preserved. I am using rings and clubs as different characters to reflect this, but they are probably the same synapomorphy. *Ninjemys* and *Niolamia* have a completely enclosed circle as a tail-ring segment, but *Meiolania* has an incomplete ring with the ventral part open (Gaffney, 1985); these are scored the same.

BIOGEOGRAPHY

The Meiolaniidae have a distribution (figs. 95, 96) that seems to fit a combination of Mesozoic vicariance and Tertiary "escalator hopscotch" patterns (McKenna, 1983). The mainland Australian and South American records are consistant with a Cretaceous predrift continental contact through Antarctica (fig. 97). The preferred cladogram (fig. 94) of *Niolamia* as the sister group to a monophyletic Austral–New Caledonian group is consistent with break-up of these continents occurring sometime in the Cretaceous. The island forms, however, require a more complex explanation. New Caledonia and Lord Howe Island have biotic elements in common in addition to *Meiolania* (Holloway, 1979, and literature cited; Paramonov, 1958, 1960; Hindwood, 1940) that appear to be relatively archaic in comparison to other elements of their biota. Although geologically complex, New Caledonia may have been emergent since the Cretaceous (Holloway, 1979). Lord Howe Island is a volcanic seamount that was formed in the late Miocene (McDougall et al., 1981). Lord Howe Island is one of a series of seamounts, some eroded, some emergent, in the Tasman Sea that have formed as the lithosphere rode over hot spots in the mantle (ibid.). Lord Howe Island itself is on the Lord Howe Rise, a section of crust thought to have been adjacent to eastern Australia about 80 million years ago, before the opening of the Tasman Sea (Hayes and Ringis, 1993).

This situation, where a relatively archaic

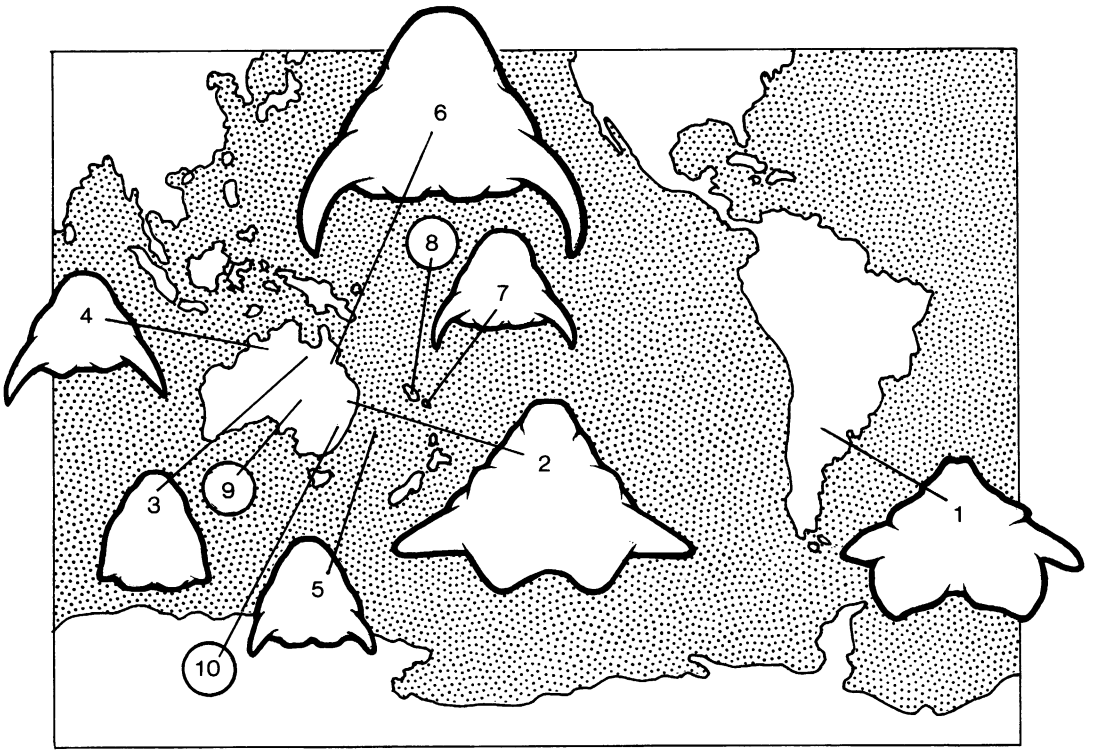


Fig. 95. Global distribution of meiolaniids. The better preserved taxa identifiable to genus are represented by skulls. Three geographically important taxa identifiable only to family are represented by circles.

(1) *Niolamia argentina,* Eocene, Chubut Province, Argentina. **(2)** *Ninjemys oweni,* Late Pleistocene, King's Creek, Queensland. **(3)** *Warkalania carinaminor,* Early Miocene, Riversleigh Station, Queensland. **(4)** *Meiolania brevicollis,* Middle Miocene, Bullock Creek, Northern Territory. **(5)** *Meiolania platyceps,* Late Pleistocene, Lord Howe Island. **(6)** *Meiolania* sp. Wyandotte, Late Pleistocene, Queensland. **(7)** *Meiolania mackayi,* Late Pleistocene, Walpole Island. **(8)** Indeterminate meiolaniid, Late Pleistocene, Pinda, New Caledonia. **(9)** Indeterminate meiolaniid, Late Oligocene, Lake Pitikanta, South Australia. **(10)** Indeterminate meiolaniid, Middle Miocene, Gulgong, New South Wales.

biota is found on relatively young oceanic islands, has been explained by a biogeographic model termed "escalator hopscotch" by McKenna (1983).

> Based on the model provided by the Hawaiian Islands, it is possible to envision a situation in which new islands arise at one end of an island chain while others sink at the other end. Some new islands would coalesce, but others would be separated by short water gaps. This process could go on for a very long time and islands (not necessarily the same islands) would have been continuously present during that time. Rocks on any particular island now above sea level would be very young, but that would not mean that the biota of the islands have necessarily arrived in the islands recently or that all members of the biota would have had to cross whatever oceanic barriers now isolate the islands from other land masses. Dispersals among and to the ongoing sequence of islands could have occurred over a very long time and truly ancient inhabitants might be present that had never had to cross more than minor water barriers in order to be present on at least one island at any particular time (McKenna, 1983: 479).

In addition to the Hawaiian Islands, recent studies (Christie et al., 1992) argue that the Galapagos Islands also show this pattern of archaic faunal elements on young oceanic islands, where the older biota has survived at the end of a chain of submerged seamounts.

RELATIONSHIPS OF MEIOLANIIDAE TO OTHER CRYPTODIRES

BASIC TAXA

The purpose of this analysis is to determine the relationships of the meiolaniids, and in order to do this as many likely taxa are included as possible. Meiolaniids are, in a general sense, primitive eucryptodires, so eucryptodires have been emphasized in the list of taxa. As is often the case with fossils, many potentially important taxa are excluded because they are too incomplete to be resolved usefully in an analysis like this one.

All the terminal taxa in this analysis are monospecific or have been hypothesized as monophyletic, and these hypotheses have been accepted for the reasons given below. The following list also summarizes references for the basic taxa. Six of the basic taxa are not eucryptodires and the inclusion of these more primitive cryptodires is an attempt to clarify the polarity and distribution of some of the characters.

The numbers with the taxon names refer to their position on the preferred cladogram (fig. 98).

Proganochelys (Taxon 1)

This Late Triassic turtle is one of the two oldest known turtles, the other being the pleurodire *Proterochersis. Proganochelys* is known from a series of nearly complete skeletons described in Gaffney (1990). *Proganochelys* has been repeatedly hypothesized as the sister group of all other turtles (Gaffney, 1975a, 1984, 1990; Gaffney and Meylan, 1988; Gaffney et al., 1991) and it is used as the outgroup in this analysis.

An Early Jurassic turtle, *Australochelys,* has been hypothesized (Gaffney and Kitching, 1994, 1995) as the sister group of pleurodires + cryptodires with *Proganochelys* the sister group of *Australochelys* + cryptodires + pleurodires. *Australochelys* is not included because it is known only from the skull, and postcranial characters are crucial in this analysis.

Pleurodira (Taxon 2)

There is little contest to the hypothesis of pleurodire monophyly. The most recent treatment by Gaffney et al. (1991) utilizes Triassic and Jurassic pleurodires as well as the Chelidae and Pelomedusidae. An important recent contribution to the understanding of characters in the primitive Pleurodira, is the redescription of *Notoemys* (Fuente and Fernandez, 1989; Fernandez and Fuente, 1994) from the Late Jurassic of Argentina.

Kayentachelys (Taxon 3)

The Early Jurassic *Kayentachelys* described in Gaffney et al. (1987) is a single species represented by a large suite of specimens. It has been argued to be the sister group of all other cryptodires (Gaffney et al., 1987; Gaffney and Meylan, 1988) which was disputed by Gauthier et al. (1989) and answered by Gaffney et al. (1991).

Kallokibotion (Taxon 4)

The Late Cretaceous *Kallokibotion* is a monotypic genus most recently redescribed by Gaffney and Meylan (1992) who argue that it is the sister group of all Selmacryptodira *sensu* Gaffney and Meylan (1988). The material is represented by a variably preserved suite of specimens that includes most of the skeleton. Information on *Kallokibotion* itself has been supplemented by an undescribed Mongolian Late Cretaceous turtle that is very similar to, and seems to be a close relative of, *Kallokibotion.* Photographs of Russian specimens of this turtle have been identified as a new taxon, "*Mongolochelys*" in publications (Rozhdestvensky, 1973) that unfortunately do not include a type description, type specimen, or other data that would make

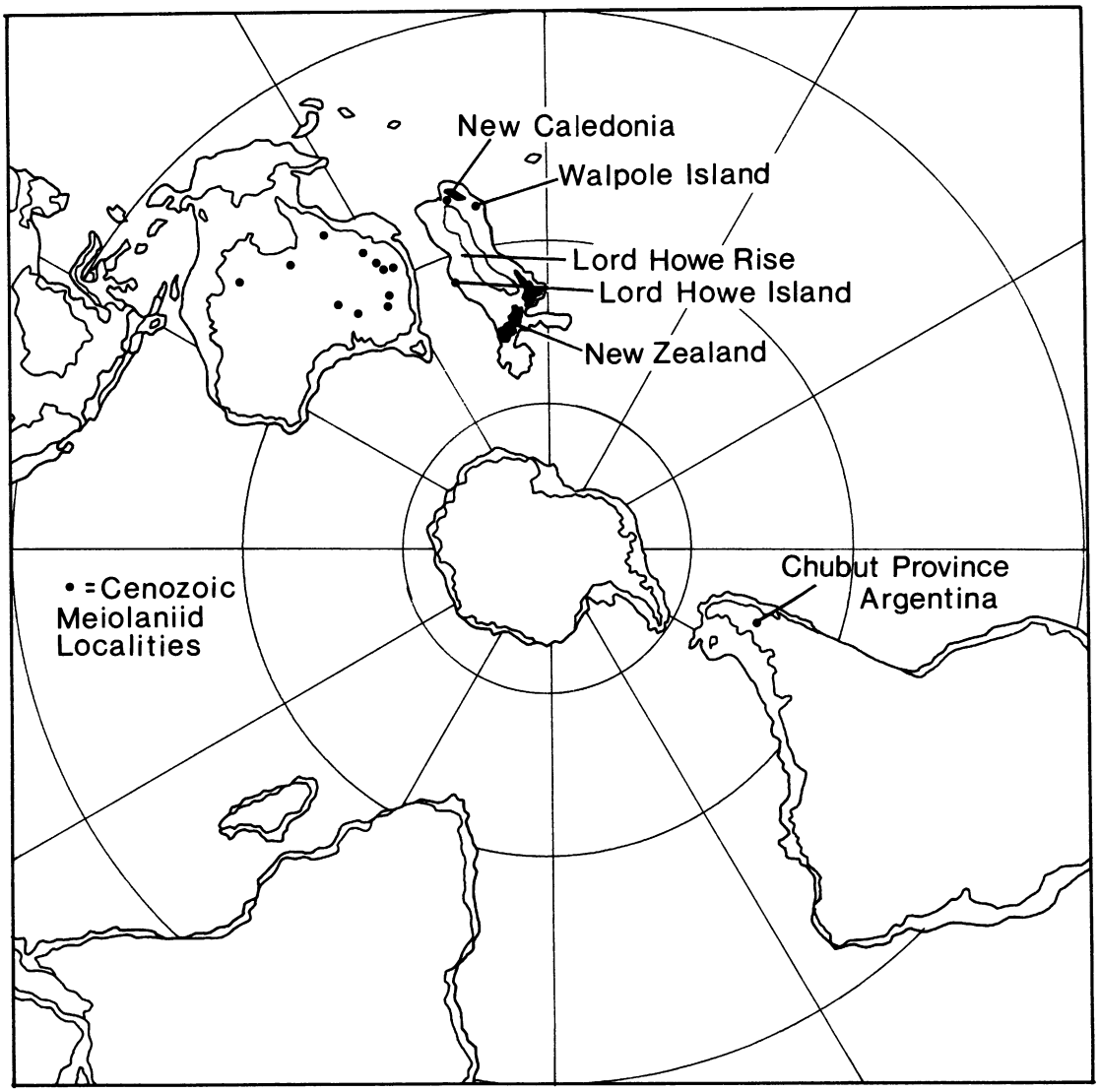


Fig. 96. Present continental and continental shelf arrangement with meiolaniid distribution indicated. Emergent land on Lord Howe Rise shown solid. New Zealand labeled only for position, no meiolaniids known. Base map from Smith and Briden (1977).

"*Mongolochelys*" a legitimate name. Recently collected specimens of this taxon made available to me show that the skull is close to *Kallokibotion* and that it has cervical ribs.

Pleurosternidae (Taxon 5)

This family is used *sensu* Gaffney (1979a) and Gaffney and Meylan (1988) to consist only of *Glyptops* and *Pleurosternon* (including *Mesochelys* Evans and Kemp, 1975, as a synonym). The family has only one synapomorphy and possible problems with it are discussed in the papers just mentioned and Gaffney et al. (1991).

Baenidae (Taxon 6)

Recent work by Brinkman and Nicholls (1993) suggests that contrary to Gaffney (1972) and Gaffney and Meylan (1988), *Neurankylus* is a close relative of the Baenidae,

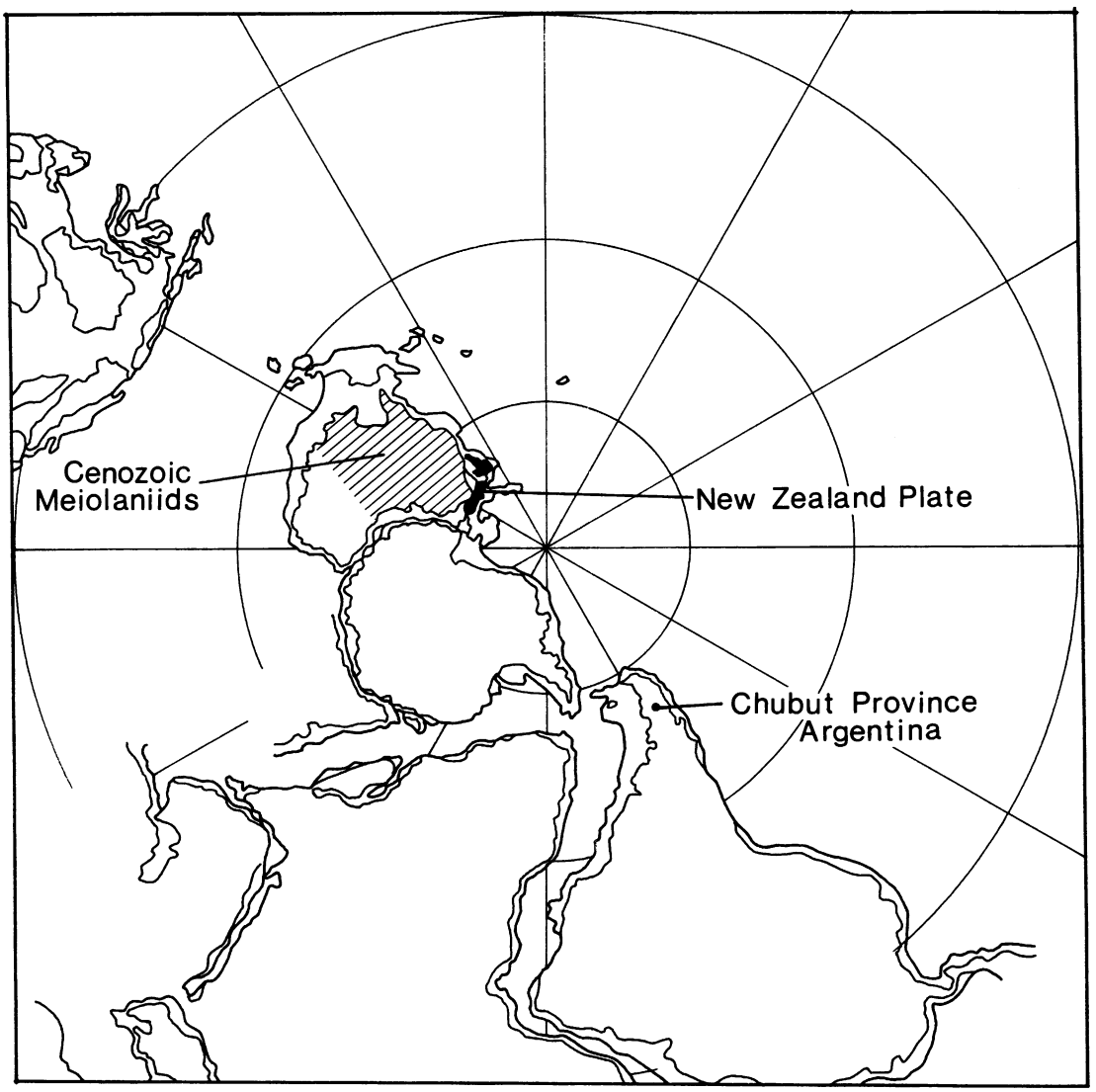


Fig. 97. Cretaceous continental positions with meiolaniid distribution indicated. New Zealand shown in solid only for position, no meiolaniids known. Base map from Smith and Briden (1977).

probably the sister group of the Baenodd of Gaffney (1972). In Brinkman and Nicholls' (1993) new analysis, the absence of some areas in the only known skeleton of *Trinitichelys* leaves the position of this taxon in doubt. I consider it to be a member of the Baenidae but *incertae sedis,* in this analysis.

Brinkman and Nicholls (1991) is important for character distributions in this family because they identify the presence of cervical ribs in it for the first time.

Plesiochelyidae (Taxon 7)

These Jurassic marine turtles are most recently discussed in Gaffney and Meylan (1988) who include three genera: *Plesiochelys, Thalassemys,* and *Portlandemys.* Peng and Brinkman (1993) show that most Asian records of *Plesiochelys* are *Xinjiangchelys* or other taxa, not *Plesiochelys.*

See Bram (1965), Gaffney (1976), and Rieppel (1980) for morphology.

Xinjiangchelys (Taxon 8)

Based on material originally described as species of *Plesiochelys,* our current understanding of *Xinjiangchelys* is based primarily on Peng and Brinkman's (1993 and included references) review and Kaznyshkin et al. (1990) descriptions including a partial skull. This Late Jurassic turtle is still incompletely known and has more missing data than any other basic taxon used here. However, the presence of unformed vertebrae and a generalized plastron along with a eucryptodiran carotid pattern suggest that this taxon could be phylogenetically close to plesiochelyids and meiolaniids as "basal" or particularly primitive eucryptodires.

Meiolaniidae (Taxon 9)

The monophyly and previous work on this family is discussed elsewhere in this paper.

Sinemys (Taxon 10)

Recent descriptions by Brinkman and Peng (1993b) of this Early Cretaceous eucryptodire from Asia, have greatly improved knowledge of this form. The best-preserved material is from *Sinemys gamera,* a *winged* species known from nearly complete skeletons (ibid.). Gaffney et al. (1991) complained about the lack of information on the "sinemydid/macrobaenid" group of early eucryptodires. The work of Brinkman and Peng (1993a, 1993b) and Peng and Brinkman (1993) greatly improves this situation and has allowed inclusion in this analysis of *Xinjiangchelys, Sinemys,* and *Ordosemys.*

Draco/Hanga (Taxon 11)

Dracochelys is a skull described by Gaffney and Ye (1992) from the Early Cretaceous of Xinjiang province, China. It is similar to *Hangaiemys* Sukhanov and Narmandakh, 1974, from the Early Cretaceous of Mongolia, known from skulls and shells. It is likely that these two taxa are closely related to each other, and I have made the assumption that they would have the same states of the characters used here. Some support for this supposition comes from Brinkman's current work in the Xinjiang region where he has found postcranial material that probably belongs to *Dracochelys* (personal commun.).

Ordosemys (Taxon 12)

Ordosemys was described by Brinkman and Peng (1993a) on the basis of a partial skull and skeleton from the Early Cretaceous of Inner Mongolia. Since that time, an undescribed complete skull and other additional specimens have been found that allow most of the characters used here to be determined (Brinkman, personal commun.). Brinkman and Peng (1993a) hypothesized that *Ordosemys* was the sister group of Polycryptodira with Meiolaniidae their sister group.

TMP 87.2.1 (Taxon 13)

This taxon is based on a nearly complete, undescribed skeleton from the Late Cretaceous of Dinosaur Provincial Park. This specimen and others closely related to it are being studied by Dr. H. Hutchison. He feels that although it may not be the same species, it is closely related to a species originally described as *"Clemmys" bachmanni* by Russell (1934).

Chelydridae (Taxon 14)

Gaffney (1975b) and Gaffney and Meylan (1988) argue for including *Platysternon* in the Chelydridae as the sister group of *Macroclemys.* Others (e.g., Bickham and Carr, 1983) do not follow this assessment and there are character contradictions. *Platysternon* has double articulations between the seventh and eighth cervicals, and apparently derived character found in chelonioids, trionychoids, and testudinoids but not other chelydrids. *Platysternon* also lacks the derived plastral morphology seen in other chelydrids. The relationships of *Platysternon* should be re-examined in light of the new discoveries of Asiatic eucryptodires named above. However, in this analysis, *Platysternon* is deleted from consideration and the characters of the Chelydridae are based on *Chelydra, Macroclemys,* and *Protochelydra.*

Chelonioidea (Taxon 15)

Gaffney and Meylan (1988) argue that *Toxochelys* is the sister taxon to all other chelonioids, and this hypothesis is accepted here.

Trionychoidea (Taxon 16)

The monophyly of this large group has most recently been discussed in Meylan and Gaffney (1989). Relying on their analysis produces the character states used here for Trionychoidea. The Cretaceous trionychoids *Adocus* (Meylan and Gaffney, 1989) and *Emarginachelys* (Whetstone, 1978, *Emarginachelys* is a trionychoid not a chelydrid *contra* Whetstone) are particularly relevant to the primitive conditions of characters for Trionychoidea.

Testudinoidea (Taxon 17)

Unfortunately the systematics of this, the largest group of living cryptodires, is still in some flux. While Gaffney and Meylan (1988) provides the most recent cladistic analysis, the unpublished studies of Seidel et al. (1992 abstract only) suggest alternate cladograms. For the purposes of this analysis, I have used the character states of *Mongolemys* as suggested by the Seidel et al. (1992) work as the basis for the characters of the group.

Testudines (Taxon 18)

Monophyly of turtles is discussed in Gaffney and Meylan (1988). Monophyly of Testudines is not tested here and characters relevant to this question have not been included in the analysis and data matrix.

Casichelydia (Taxon 19)

Monophyly of this group is discussed in Gaffney and Meylan (1988). The discovery of *Australochelys* has caused modifications to this earlier analysis and these are discussed in Gaffney and Kitching (1994, 1995). A new diagnosis of Casichelydia is in Gaffney and Kitching (1995). Most characters relevant to defining Casichelydia have not been included in this analysis and data matrix.

Cryptodira (Taxon 20)

Cryptodira has four synapomorphies: the processus trochlearis oticum (character **7**), the vertical flange on the processus pterygoideus externus (character **4**), the absence of supramarginal scales (character **36**) and the prefrontal-vomer contact (character **3**). Further discussion of these characters are in Gaffney and Meylan (1988) and Gaffney et al. (1991). The Cryptodira is judged to be a relatively well-tested monophyletic group.

Selmacryptodira (Taxon 21)

This group is all cryptodires except *Kayentachelys* and is tested with three synapomorphies: closed interpterygoid vacuity (character **6**), middle ear with pterygoid floor (character **8**), and entoplastron broadly in contact on midline (character **38**). In this analysis there are no homoplasies within the Cryptodira and this group is judged to be relatively well tested.

Daiocryptodira (Taxon 22)

The hypothesis that *Kallokibotion* is the sister group of all other cryptodires except *Kayentachelys* was advanced by Gaffney and Meylan (1992). It is tested by three synapomorphies: the internal carotid artery is at least partially enclosed by the pterygoid (character **9**), there is at least some degree of posterior temporal emargination (character **17**) and the dorsal process of the epiplastron is absent (character **37**). Meiolaniids, some pelomedusids, and some emydids show a completely roofed skull with no temporal emargination but none of these exhibits the presumed primitive condition seen in *Kallokibotion* and *Kayentachelys*. The epiplastral process is highly homoplastic and was apparently lost independently in a number of cryptodires. Although this group is not as strong as others in this analysis, it is relatively well tested.

Paracryptodira (Taxon 23)

The union of Pleurosternidae + Baenidae to form the Paracryptodira is based on three characters: a small fenestra perilymphatica (Brinkman and Nicholls, 1993) (character **15**), a foramen posterius canalis carotici interni formed by the basisphenoid and pterygoid (character **14**) and the complete enclosure of the canalis caroticus internus and the canalis caroticus lateralis in bone (character **11**). This idea originally proposed by Gaffney (1972) was countered by Evans and Kemp (1976) and accepted by Gaffney (1979a). However, Brinkman and Nicholls (1993) have re-affirmed Gaffney's original arguments (hoo-

ray!) and reinterpreted the Paracryptodira as a valid taxon.

Eucryptodira (Taxon 24)

This group is tested by two unambiguous synapomorphies: enclosure of carotid artery by pterygoid (character **10**) and loss of mesoplastra (character **34**). No homoplasies are shown in this analysis, but chelids loose mesoplastra within pleurodires and the enclosure of the carotid by the pterygoid has been argued by Rieppel (1980) to be variably developed within Plesiochelyidae. Gaffney and Meylan (1988) and Gaffney (1976) argue that Rieppel's supposed cline is due to variable erosion in the available specimens.

Unnamed taxon (Taxon 25)

Two unambiguous characters form this group. The posteriorly placed transverse processes (character **21**) and the ligamentous carapace/plastron attachment (character **35**). Both characters are homoplastic in this analysis. Another problem at this node is *Xingiangchelys* which is missing the most data of the basic taxa used in this analysis. See further discussion in Centrocryptodira (Taxon 26).

Centrocryptodira (Taxon 26)

This group is the Centrocryptodira of Meylan and Gaffney (1988), here consisting of meiolaniids + sinemydids + Polycryptodira. Three unambiguous synapomorphies are: formed cervical central articulations (character **20**), fourth cervical biconvex (character **24**), eighth cervical procoelous (character **25**). The last two characters are multistate and reflect specific patterns of cervical articulations. These characters also have the effect of weighting the presence of formed centra.

A fourth synapomorphy at this level is the thick floor of the canalis caroticus internus (character **12**). This character occurs in meiolaniids and the Polycryptodira (taxon 30) and is interpreted as being reversed in the Sinemydids. However, the carotid floor is unusually thick in *Meiolania* and may not be homologous to the polycryptodiran condition. It is just as likely that this character evolved separately in meiolaniids and polycryptodirans.

Xinjiangchelys is very tenuously resolved as the sister group to meiolaniids plus remaining eucryptodires. With more information on the missing characters in *Xinjiangchelys* its position could be changed. This particular resolution, however, clearly separates the amphicoelous taxa like *Xinjiangchelys* and plesiochelyids from the eucryptodires with formed centra. In its present resolution, *Xinjiangchelys* requires homoplasy in having a reduced first thoracic rib (character **32**), otherwise known only in taxon 30 and in the anterior position of the transverse process on cervicals (character **21**). An alternative consistent with these two characters would place *Xinjianghchelys* in taxon 27, an unnamed taxon consisting of sinemydids and Polycryptodira.

Meiolaniids are included in the Centrocryptodira here as well as in previous analyses: Gaffney and Meylan (1988), Gaffney et al. (1991). There are two homoplasies required for this. Character **17**, posterior temporal emargination, is absent in the skull of meiolaniids, although there is good morphologic reason to think that this is secondary (Gaffney, 1983). Character **21**, the anterior position of the transverse process on cervicals, is lacking in meiolaniids which have the more primitive middle or posterior position. This character involves the position of *Xinjiangchelys* relative to meiolaniids as the sister group to remaining Centrocryptodira. *Xinjiangchelys* has a homoplasy in character **32**, the reduced first thoracic rib, which is consistent with *Xinjianghchelys* being placed higher on the cladogram. The skull in *Xinjiangchelys* is poorly known and further work could alter its position relative to meiolaniids. Otherwise, the position of meiolaniids as the sister group to sinemydids + Polycryptodira seems well founded.

Unnamed taxon (Taxon 27)

This taxon unites sinemydids and Polycryptodira with meiolaniids as their sister group. The resolution of sinemydids is poor with collapse of this part of the cladogram only one step away, but the monophyly of

the entire group is relatively good with six unambiguous synapomorphies.

The unambiguous characters at Taxon 27 are: paired pits on basisphenoid (character **16**), parietal separated from squamosal (character **18**), biconcave caudal (character **29**), at least some caudals procoelous (character **30**), a narrow epiplastron (character **39**), and only one set of anterior plastral scales (character **40**).

Sinemydidae (Taxon 28)

The history of the terms Sinemydidae and Macrobaenidae is complex and reviewed in both Gaffney and Ye (1992) and Brinkman and Peng (1993a, 1993b) which should be used as introductions to the literature. In this analysis only a relatively few well known taxa, ascribable to what have been included in Sinemydidae or Macrobaenidae, have been included. Nonetheless, the characters diagnosing this taxon in this analysis are sufficient to exclude *Macrobaena* itself. *Macrobaena* (Tatarinov, 1959) has a procoelous eighth cervical rather than the biconvex eighth cervical diagnostic of the group. For this reason I am using Sinemydidae, as *Sinemys* is a member of the group. This does not mean that I think this designation is conclusive. The primitive eucryptodires are currently in a state of taxonomic flux, relatively speaking, as new taxa are described and older taxa become better known and susceptible to character analysis.

The unambiguous characters at this node are: a thin floor of the canalis caroticus internus (character **12**) and cervical 8 biconvex (character **25**). The first character can also be interpreted as retained primitive and reversed in meiolaniids which have a thick floor. This would remove it as a sinemydid synapomorphy. At present it is a sinemydid synapomorphy only because meiolaniids have a thick floor and are the sister group to sinemydids + polycryptodires. The biconvex cervical 8, however, is almost unique to sinemydids. The only other cryptodire group in which it occurs is testudinoids and there the centra have double articulations and are much wider with a very different shape. Within pleurodires, chelids have a biconvex cervical 8 but the primitive condition for pleurodires is very likely amphicoelous cervicals.

Unnamed taxon (Taxon 29)

In this analysis, three unambiguous characters define this taxon and unite *Sinemys* and *Dracochelys/Hangaiemys*. The foramen palatinum posterius is very large (character **5**) and cervical 4 is opisthocoelous (character **24**). Both of these characters are unique to this group as interpreted in this analysis. However, the size of the foramen palatinum posterius varies widely in cryptodires and is difficult to homologize, and opisthocoelous cervicals also appear within the Trionychoidea, although there is good evidence that they are not primitive for that group (Meylan and Gaffney, 1989). The third character is the absence of a postorbital/squamosal contact (character **19**) but this condition is known only for *Sinemys* and not in *Dracochelys* or *Hangaiemys*.

Polycryptodira (Taxon 30)

TMP 87.2.1, attributed to a species close to *"Clemmys" bachmani* (H. Hutchison, personal commun.), is united with the Polycryptodira by six characters, all but one of which are homoplastic in this analysis. Nonetheless, three are characters that are found in Polycryptodira and not in other eucryptodires, clearly separating TMP 87.2.1 from the sinemydids.

The unambiguous characters are: prefrontals meet on midline (character **2**, also occurs in *Dracochelys*), palatine artery and internal carotid artery fully embedded in bone (character **11**), posterior cervicals with strong ventral process (character **22**), cervical ribs absent (character **23**), single transverse process on cervicals (character **27**, also occurs in *Sinemys* but not *Dracochelys*), first thoracic rib fails to reach peripherals (character **32**, also in *Xinjiangchelys*).

Unnamed taxon (Taxon 31)

Four unambiguous characters at this taxon separate TMP 87.2.1 from all other Polycryptodira: absence of nasals (character **1**),

absence of basisphenoid pits (character **16**, reversed), neural spine on cervical 8 low (character **28**), and first thoracic centrum faces strongly anteroventrally (character **33**). Characters **28** and **33** are unique to this group, which consists of the living cryptodires.

Procoelocryptodira (Taxon 32)

This group consists of the Chelonioidea + Trionychoidea, + Testudinoidea and has been recognized earlier by Gaffney and Meylan (1988) and Gaffney et al. (1991) among others. The characters at this node are: the absence of the biconcave caudal with all caudals procoelous (character **29**), double articulation between the seventh and eighth cervicals (character **26**), chevrons small or absent with a short tail (character **31**). Only the biconcave caudal is homoplastic and this character is absent in all cryptodires except sinemydids, TMP 87.2.1, and chelydrids. This analysis interprets the biconcave caudal as primitive for all eucryptodires at Taxon 27 and its loss at Taxon 32 is synapomorphic for the Procoelocryptodira.

Chelomacryptodira (Taxon 33)

The only synapomorphy testing this group in Gaffney and Meylan (1988) was the homoplasy-prone extreme temporal emargination, separating postorbital and squamosal. In the present analysis there are two additional characters that also test this group. Both characters are reversals that reflect the fact that these turtles have shells that have closer similarities to more primitive cryptodires such as plesiochelyids and baenids than to the more closely related sinemydids and chelydrids. Primitively, trionychoids and testudinoids have broad epiplastra and tightly sutured plastron/carapace contacts as in primitive cryptodires, but it is very likely that the primitive condition within eucryptodires at taxon 27 is a shell with narrow epiplastra and a ligamentous plastron/carapace contact. Therefore, the unambiguous characters for Chelomacryptodira in this analysis are: postorbital/squamosal contact absent (character **19**), carapace/plastron contact sutured, not ligamentous (character **35** reversed), and broad epiplastron (character **39** reversed).

CHARACTERS USED IN THE ANALYSIS

From Owen's (1881) first identification of meiolaniids as horned lizards, the relationships of these turtles have been marked by controversy. The combination of poorly preserved specimens and highly derived features have obscured the relationships of meiolaniids for over a hundred years. As better material has been discovered, newer assessments have at least narrowed the limits for the phylogenetic position of meiolaniids.

Owen's (1881) identification of the large Queensland meiolaniid (now known as *Ninjemys oweni*) as a varanid lizard was based on the mixing of the turtle skull elements with the vertebrae of a giant varanid (*Megalania prisca*). Owen later (1886b) added a skull from Lord Howe Island to the material he was identifying as a horned lizard. This skull, as well as some Lord Howe Island caudals, were quickly identified by Huxley (1887) as a turtle that he compared with *Chelydra*. Boulenger (1887) substantiated the idea of *Meiolania* as a turtle but argued that it was a pleurodire. In 1888, Owen's last word on the horned turtle subject was the creation of the "Ceratosauria" as a group intermediate between turtles and other reptiles (and we say that Owen wasn't an evolutionist!).

The next controversy concerned the position of *Meiolania* within the turtles. Boulenger's claim (1887, 1889) that *Meiolania* was a pleurodire was opposed by Baur (1889a, 1889b) who thought it was a cryptodire and used such currently recognized cryptodire synapomorphies as a processus trochlearis oticum (in Gaffney, 1979b, terminology) as evidence. But the British Museum viewpoint prevailed because Lydekker (1889), with Boulenger's contributions, wrote the summary classifications used by most herpetologists and paleontologists at the time. Meiolaniids were pleurodires for decades in most literature that referred to the group.

In 1925 Charles Anderson of the Australian Museum described new material of the Lord Howe Island *Meiolania platyceps,* and concluded that meiolaniids were members of the Amphichelydia. The Amphichelydia is a taxon characterized by primitive features and supposed to contain the ancestors of Recent

turtles. In practice the Amphichelydia, erected in 1889 by Lydekker, became a waste basket of fossils that did not clearly belong to living groups (see Gaffney, 1975a, and, 1984, for discussion).

In 1938 Simpson described a new meiolaniid that he collected on his Patagonian expeditions. Simpson listed characters, reviewed the work of Boulenger, Baur, and Anderson, and agreed with Anderson that meiolaniids were the relict descendants of ancestral turtles, and Simpson's (1938: 251–252) view of the Amphichelydia could be seen as a preview of the later debate between his school of "evolutionary taxonomy" and phylogenetic systematics:

> The Suborder Amphichelydia . . . is an essentially horizontal diversion for a divergent group of early phyla, mostly Mesozoic, which are distinguished from later forms and united with each other by primitive characters. A strictly phyletic classification, were such possible, would reject this suborder as generally defined, but, as so often happens in practical taxonomy, it is now most convenient if not necessary to recognize it.

In 1972, Gaffney presented a cladistic analysis of the baenids, an extinct group considered central to the Amphichelydia and compared with meiolaniids by both Anderson and Simpson. Gaffney argued that the baenids were cryptodires and in 1975 (1975a) that the Amphichelydia should be discarded in favor of monophyletic Cryptodira and Pleurodira. In the 1975 paper he argued that meiolaniids were cryptodires and, rather than being closely related to baenids, that they were eucryptodires, more closely related to the living cryptodire groups. Gaffney (1984) supported the idea of meiolaniids as eucryptodires and compared alternative phylogenetic hypotheses. Gaffney and Meylan (1988) had more taxa than Gaffney (1984) and hypothesized meiolaniids as the sister group of chelydrids, trionychoids, chelonioids, and testudinoids with plesiochelyids the sister group of meiolaniids plus those living groups. Gaffney et al. (1991) relied on many of the same characters and produced the same conclusions concerning meiolaniids.

The present study attempts a more extensive examination of relationships of the Meiolaniidae within the Cryptodira. A data set of 40 characters is used to analyze 17 basic taxa using the parsimony program PAUP (Swofford 1993), assisted by MacClade (Maddison and Maddison 1992). Further references to these programs, explanations of terminology, and relevant literature, can be found in the manuals acompanying the above programs, in Wiley et al. (1991) and issues of the journal *Cladistics.*

The PAUP analysis results in a single cladogram with 73 steps, a consistency index of 0.58, and a retention index of 0.80. Although there is only one shortest cladogram, it isn't that far from a complete lack of resolution. At 74 steps, one step longer than the shortest cladogram, there are 7 equally parsimonious cladograms that combine to produce a consensus tree (fig. 100). The difference from the shortest cladogram is the multichotomy of the sinemydids and taxon 30 and a multichotomy of plesiochelyids, *Xingiangchelys,* and Taxon 26. The next shortest cladogram at 75 steps, produces 40 equally parsimonious cladograms and a consensus tree seen in figure 101. This tree shows a lack of resolution within the Polycryptodira, and within nearly all the more primitive cryptodires. The groups still maintained are the Cryptodira, and the Polycryptodira. The Chelomacryptodira (Testudinoidea plus Trionychoidea) also hold together.

The character discussion emphasizes characters relevant to the position of *Meiolania.* Characters at more basal levels are discussed in other papers which are noted.

Because there is one shortest cladogram and because there are many alternatives one or more steps longer, I have chosen to look more closely at the distribution of characters in the shortest cladogram rather than examine possible alternatives.

List of Characters

1. Nasal bones: Present = 0; Absent = 1.

Morphology: Skull figures showing distribution of nasal bones are in Gaffney (1979b).

Primitive condition: Paired nasals are present throughout amniotes and in *Proganochelys.*

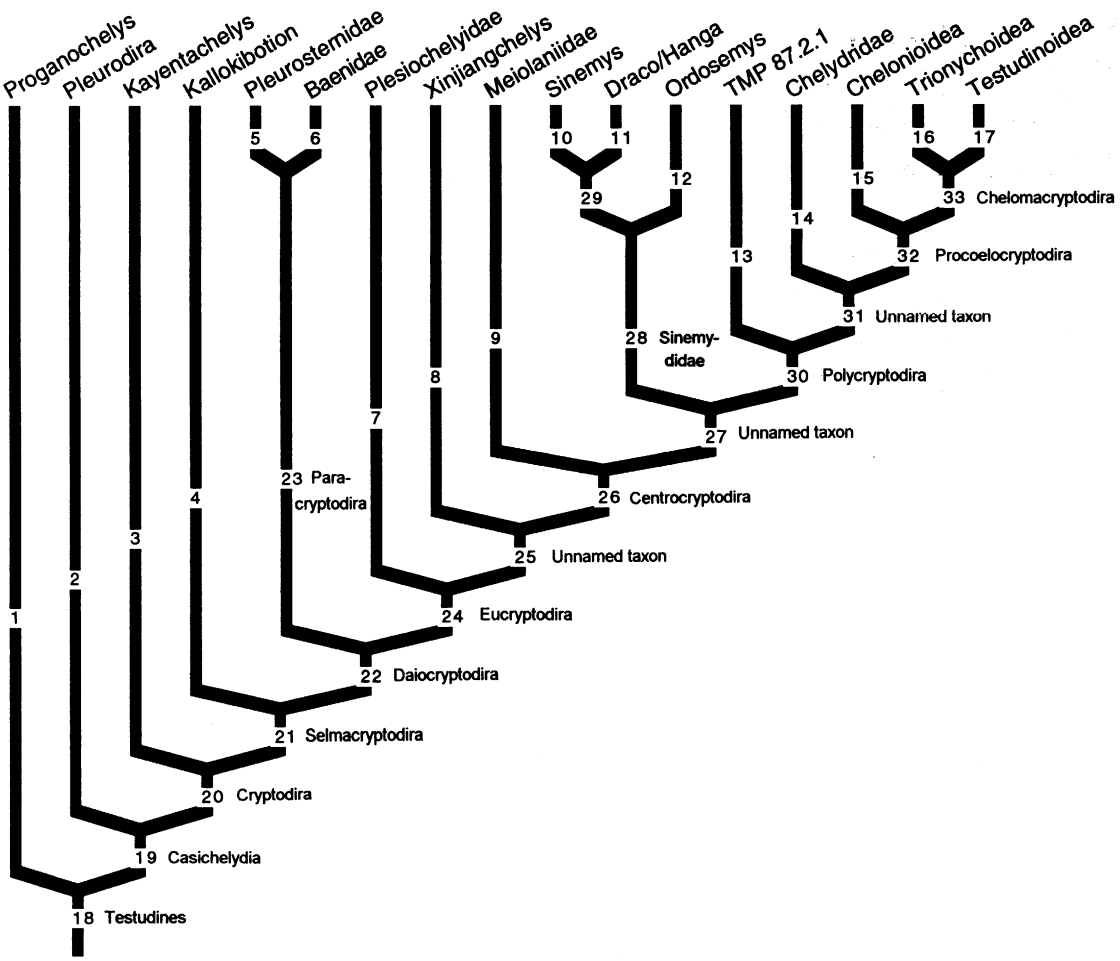


Fig. 98. Shortest cladogram for Cryptodira produced by PAUP version 3.1.1 (Swofford, 1993), tree length 73, CI = 0.58, RI = 0.80. Data set in table 19 and fig. 99.

Homoplasy: There is strong evidence of independant loss of nasals within turtles, once within pleurodires (pelomedusids) and probably more than once within cryptodires (baenids, chelonioids, Polycryptodira). The preferred cladogram shows a consistency index for this character of 0.5, but this does not reflect the very likely multiple loss of nasals among cryptodires.

Discussion: Meiolania platyceps (Gaffney, 1983) and *Meiolania brevicollis* (Megirian, 1989, 1992) have nasal bones. Other meiolaniids are not well-enough preserved to determine presence or absence of nasals.

2. Prefrontals: Do not meet in midline = 0; Meet in midline = 1.

Morphology: Skull figures of various prefrontal conditions are in Gaffney (1979b).

Primitive condition: Captorhinids as well as other generalized amniotes such as procolophonids and pareiasaurs have the dorsal lappets of the prefrontals separated by contact of nasals and frontals. *Proganochelys* (Gaffney, 1990) also has this condition.

Homoplasy: Medial meeting of the prefrontals appears twice in the preferred cladogram of Gaffney et al. (1991) and Gaffney and Meylan (1988), and three times (C.I. of 0.33) in the preferred cladogram presented here. Pelomedusids and most eucryptodires have medially meeting prefrontals.

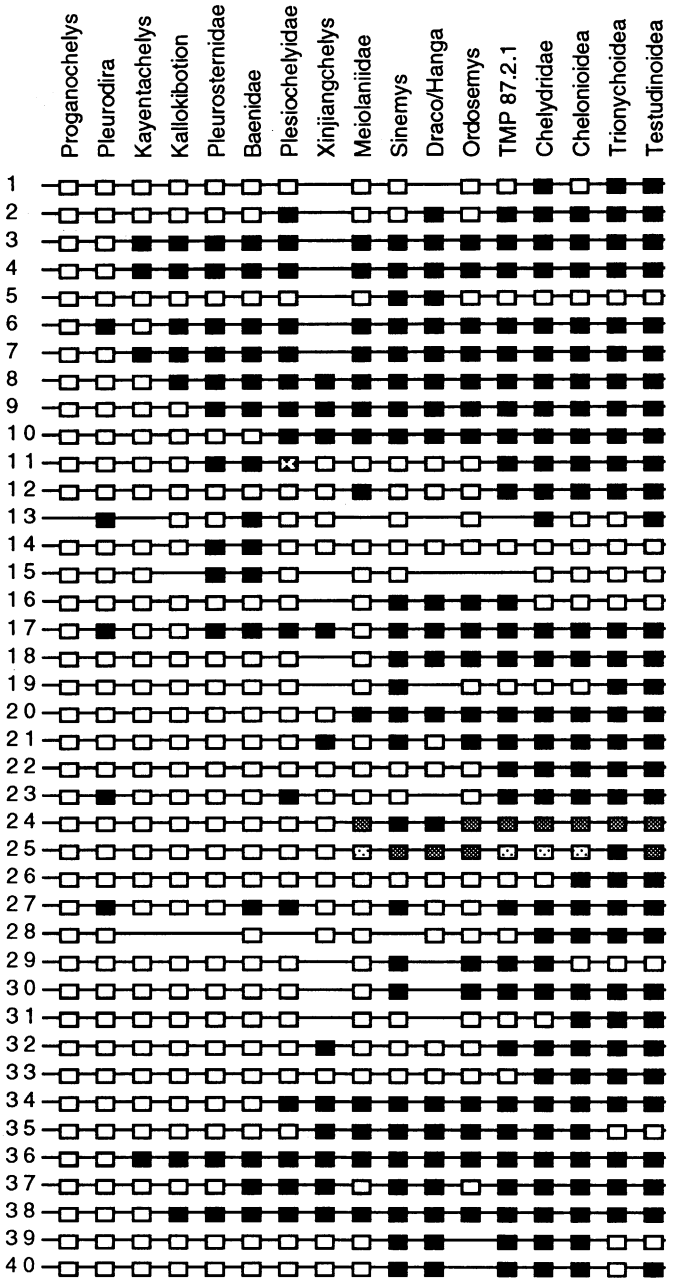


Fig. 99. Character distributions for Cryptodira data set.

Discussion: Plesiochelyids and the living cryptodires have medially meeting prefrontals as does TMP 97.2.1 and probably *Hangaiemys. Meiolania, Ordosemys,* and *Sinemys* however, have the prefrontals separated by nasal/frontal contact.

3. Prefrontal/vomer contact: Contact absent = 0; Contact present = 1.

Morphology: Gaffney (1979b) has figures of cryptodires showing the presence of this feature. Discussion and description is also in Gaffney (1990).

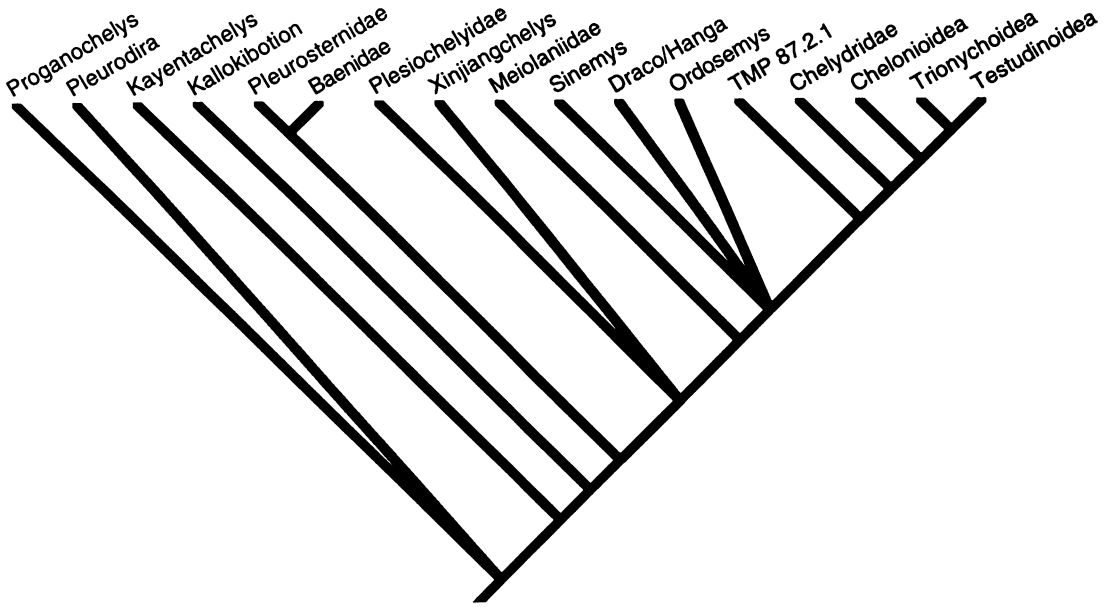


Fig. 100. Strict consensus cladogram of 7 trees at 74 steps and shorter (one step longer than shortest cladogram).

Primitive condition: The absence of a prefrontal/vomer contact is general among amniotes considered likely turtle outgroups (Gaffney, 1990).

Homoplasy: None apparent within turtles, consistency index is 1.0 for the preferred cladogram.

Discussion: Gaffney and Meylan (1988) and Gaffney et al. (1991) argued for this character as a cryptodire synapomorphy. It is clearly present in *Meiolania* (Gaffney, 1983).

4. Vertical flange on processus pterygoideus externus: Absent = 0; Present = 1.

Morphology: The flange is described in Gaffney (1979b).

Primitive condition: The character is absent in all other amniotes.

Homoplasy: None known, consistency index for preferred cladogram is 1.0.

Discussion: See Gaffney et al. (1991: 320). This character is a cryptodire synapomorphy present in *Meiolania.*

5. Foramen palatinum posterius: Relatively small = 0; Relatively large = 1.

Morphology: The foramen palatinum posterius is described in Gaffney (1979b). *Sinemys, Dracochelys,* and *Hangaiemys* have unusually large palatine foramina and this character is restricted to the condition shown in these taxa (Brinkman and Peng; 1993a; Gaffney and Ye, 1992; Sukhanov and Narmandakh, 1974).

Primitive condition: The relative size of the foramen palatinum posterius varies a great deal in turtles and this character is limited to the extreme condition. Based on *Proganochelys* and *Kayentachelys,* a smaller foramen size is primitive.

Homoplasy: The simple nature of the character and the fact that size of the foramen is highly variable in turtles makes homoplasy likely. As defined here, however, the character has a consistency index of 1.0.

Discussion: This character is suggested by Brinkman and Peng (1993a) as a possible common feature of "macrobaenids" (here equal to sinemydids) and Gaffney and Ye (1992) use it to help link *Dracochelys* and *Hangaiemys.* Nonetheless, the character is variable.

In plesiochelyids the foramen palatinum posterius is open laterally in *Portlandemys* (Gaffney, 1976). This has been coded as small because it is unlikely to be homologous with the condition in *Dracochelys* and *Hangaiemys.*

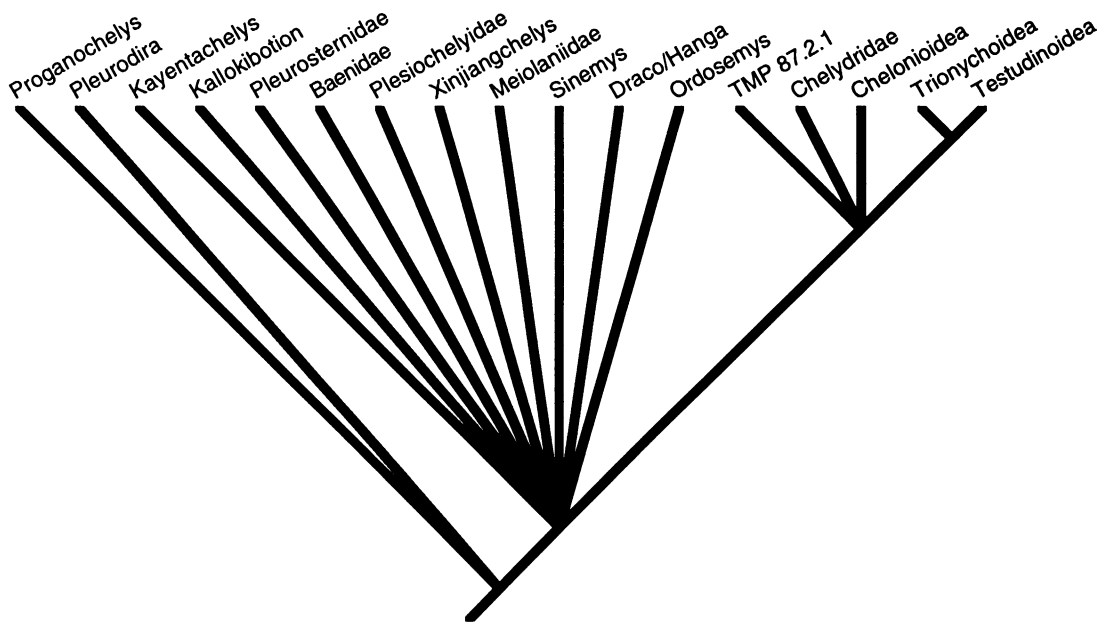


Fig. 101. Strict consensus cladogram of 40 trees at 75 steps and shorter (two steps longer than shortest cladogram).

6. Interpterygoid vacuity: Open = 0; Closed = 1.

Morphology: The vacuity is described for *Proganochelys* in Gaffney (1990), *Australochelys* in Gaffney and Kitching (1994, 1995), and *Kayentachelys* in Gaffney, et al. (1987). The closed condition is described in Gaffney (1979b).

Primitive condition: The open interpterygoid vacuity is the primitive amniote condition and is seen in all proposed turtle outgroups.

Homoplasy: Gaffney and Meylan (1988) and Gaffney, et al. (1991) required independent evolution of this character in pleurodires and in selmacryptodires. In the preferred cladogram of the present study, the consistency index is 0.5.

Discussion: See Gaffney et al. (1991) for discussion.

7. Processus trochlearis oticum: Absent = 0; Present = 1.

Morphology: Schumacher (1973) and Gaffney (1975a, 1979b) describe this character.

Primitive condition: This character is absent in all other amniotes.

Homoplasy: None known, consistency index is 1.0.

Discussion: See Gaffney et al. (1991) for discussion. This character is an important cryptodire synapomorphy present in meiolaniids.

8. Middle ear with ossified floor formed by posteromedial process of pterygoid: Pterygoid process absent = 0; Pterygoid process present = 1.

Morphology: Gaffney (1979b) describes and figures the process.

Primitive condition: The process is absent in all pleurodires, *Proganochelys, Australochelys,* and the early cryptodire *Kayentachelys.* It is absent in all other amniotes and this is interpreted as the primitive condition.

Homoplasy: None known, consistency index 1.0.

Discussion: See Gaffney et al. (1991) and Gaffney et al. (1987). The process is a synapomorphy of the Selmacryptodira, and it is present in meiolaniids.

9. Canalis caroticus internus at least partially formed by pterygoid: Not formed by pterygoid to any extent = 0; Partially or entirely formed by pterygoid = 1.

Morphology: Gaffney (1979b) and Gaffney (1990) described the primitive and advanced

TABLE 19
Cryptodira Data Set

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Proganochelys	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
Kayentachelys	0	0	1	1	0	0	1	0	0	0	0	0	?	0	0	0	0	0	0	0
Kallokibotion	0	0	1	1	0	1	1	1	0	0	0	0	0	0	?	0	0	0	0	0
Pleurosternidae	0	0	1	1	0	1	1	1	1	0	1	0	0	1	1	0	1	0	0	0
Baenidae	0	0	1	1	0	1	1	1	1	0	1	0	1	1	1	0	1	0	0	0
Plesiochelyidae	0	1	1	1	0	1	1	1	1	1	0&1	0	0	0	0	0	1	0	0	0
Xingjiangchelys	?	?	?	?	?	?	?	1	1	1	0	0	0	0	?	?	1	?	?	0
Meiolaniidae	0	0	1	1	0	1	1	1	1	1	0	1	?	0	0	0	0	0	0	1
Sinemys	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1
Draco/Hanga	?	1	1	1	1	1	1	1	1	1	0	0	?	0	?	1	1	1	?	1
Ordosemys	0	0	1	1	0	1	1	1	1	1	0	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
Chelydridae	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	1	1	0	1
Chelonioidea	0	1	1	1	0	1	1	1	1	1	1	1	0	0	0	0	1	1	0	1
Trionychoidea	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1
Testudinoidea	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1

morphologies of the internal carotid artery and its associated structures.

Primitive condition: In generalized amniotes, *Proganochelys, Kayentachelys,* and *Notoemys* the canalis caroticus internus is entirely enclosed by the basisphenoid and this is interpreted as the primitive condition for turtles.

Homoplasy: None known, consistency index 1.0.

Discussion: This character has been considered a synapomorphy of the Selmacryptodira by Gaffney et al. (1991). Meiolaniids have the advanced condition of the canalis caroticus internus.

10. Canalis caroticus internus formed entirely by pterygoid posteriorly (distally): Formed partially or not by pterygoid = 0; Formed entirely by pterygoid = 1.

Morphology: This character is described in Gaffney (1979b), see also Gaffney and Meylan (1988, figs. 5.5 and 5.6).

Primitive condition: The primitive condition for this character is seen in *Kallokibotion* (Gaffney and Meylan, 1992), pleurosternids (Gaffney, 1979a), and baenids (Brinkman and Nicholls, 1993).

Homoplasy: None known, consistency index 1.0.

Discussion: The completely enclosed internal carotid artery is a synapomorphy for the Eucryptodira of Gaffney (1975a) and Gaffney and Meylan (1988). Meiolaniids clearly have the eucryptodiran condition of this character.

11. Canalis caroticus internus and canalis caroticus lateralis completely embedded in bone: Both canals open ventrally = 0; Both canals embedded in bone = 1.

Morphology: In the living cryptodire groups, the Polycryptodira, the palatine artery and the position where it originates from the internal carotid artery is enclosed in bone (Gaffney, 1979b). In many fossil groups it is apparent that the area around and anterior to the origin of the palatine artery is not ossified (Brinkman and Nicholls, 1993). In primitive cryptodires such as *Kallokibotion,* (Gaffney and Meylan, 1992) most of the length of the canalis caroticus internus and the posterior portion of the canalis caroticus lateralis are also unenclosed. In pleurosternids, baenids, and plesiochelyids the posterior part of the canalis caroticus internus is exposed and the canalis caroticus laterale and anterior part of the canalis caroticus internus are enclosed. Sinemydids and *Xinjiangchelys,* have the canalis caroticus lateralis exposed, although the posterior part of the canalis caroticus internus is enclosed (Brinkman and Nicholls, 1993, fig. 3; Gaffney and Ye, 1992).

Primitive condition: The exposed (pre-

TABLE 19—(*Continued*)

	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
Pleurodira	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Kayentachelys	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	1	0	0	0	0
Kallokibotion	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	1	0	1	0	0
Pleurosternidae	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	1	0	1	0	0
Baenidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0
Plesiochelyidae	0	0	1	0	0	0	1	?	0	0	0	0	0	1	0	1	1	1	0	0
Xingjiangchelys	1	0	0	0	0	0	0	0	?	?	?	1	0	1	1	1	1	1	0	0
Meiolaniidae	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0
Sinemys	1	0	0	2	2	0	1	?	1	1	0	0	0	1	1	1	1	1	1	1
Draco/Hanga	0	0	?	2	2	0	0	0	?	?	?	0	0	1	1	1	1	1	1	1
Ordosemys	1	0	0	1	2	0	0	0	1	1	0	0	0	1	1	1	0	1	?	?
TMP 87.2.1	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	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1
Chelonioidea	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	1	1	1	1	0	1	1	1	1	1	0	1	1	1	0	0
Testudinoidea	1	1	1	1	2	1	1	1	0	1	1	1	1	1	0	1	1	1	0	1

sumed) palatine and cerebral carotid arteries of *Proganochelys* (Gaffney, 1990), *Kayentachelys* (Gaffney et al., 1987) and *Kallokibotion* (Gaffney and Meylan, 1992), are interpreted as the primitive cryptodiran condition.

Homoplasy: The consistency index for this character is 0.66. The shortest cladogram requires two or three independent acquisitions of this character, depending on whether multiple loss or multiple acquisition is chosen at nodes 22 and 24 (fig. 98). Brinkman and Nicholls (1993) have argued for the multiple acquisition of this character from a *Kallokibotion*-like condition. The retained primitive condition seen in such eucryptodires as *Sinemys* and *Orodosemys,* does differ from *Kallokibotion* in being more restricted by bony margins encroaching on the arterial areas. Some eucryptodires like *Dracochelys,* however, appear to be widely open and approach the *Kallokibotion* condition.

Discussion: The basicranial morphology of *Meiolania platyceps* is described in Gaffney (1983). In *Meiolania* the presumed path of the palatine artery is contained in and covered ventrally by bone, but the intrapterygoid slit, a structure unique to meiolaniids, is developed along the basisphenoid/pterygoid contact and involves the path of the palatine artery. There is no canalis caroticus lateralis completely formed in bone, the medial wall of this canal is missing and the canal is confluent with the intrapterygoid slit. As interpreted in Gaffney (1983: 429–435, 462), meiolaniids have the primitive condition of the canalis caroticus lateralis and not the advanced condition seen in Polycryptodira.

12. Thickness of pterygoid floor of canalis caroticus internus: Thin or absent = 0; Thick = 1.

Morphology: The advanced condition is described in Gaffney (1979b) and the thin-floored condition in plesiochelyids is described in Gaffney (1976).

Primitive condition: The thin floor of the canalis caroticus internus is interpreted as primitive because it is similar to the early stages of development as seen in emydids (Kunkel, 1912). In some *Plesiochelys* specimens the enclosed canalis has a seam or suture still present (Gaffney, 1976), possibly indicating an early morphologic stage in the development of the canalis caroticus internus.

Homoplasy: Although such forms as plesiochelyids and *Dracochelys* have very thin pterygoid floors in contrast to living cryptodires, some of the fossil groups may be more intermediate in thickness and not clearly one extreme or the other. Such distinctions are not included in this analysis, but the potential

TABLE 20
Unambiguous Synapomorphies for the Cryptodire Cladogram (fig. 98)

Taxon 20. *Cryptodira*
3. Prefrontal vomer contact present
4. Vertical flange on processus pterygoideus externus
7. Processus trochlearis oticum present
36. Supramarginal scales absent

Taxon 21. *Selmacryptodira*
6. Interpterygoid vacuity closed
8. Middle ear with ossified floor formed by posteromedial process of pterygoid
38. Entoplastron separating epiplastra

Taxon 22. *Daiocryptodira*
9. Canalis caroticus internus at least partially formed by pterygoid
17. Posterior temporal emargination at least partially developed
37. Dorsal process on epiplastron absent

Taxon 23. *Paracryptodira*
11. Canalis caroticus internus and canalis caroticus lateralis embedded in bone
14. Foramen posterius canalis carotici interni formed by basisphenoid and pterygoid, midway along basisphenoid-pterygoid suture
15. Fenestra perilymphatica relatively small

Taxon 24. *Eucryptodira*
10. Canalis caroticus internus formed entirely by pterygoid posteriorly (distally)
34. Mesoplastra absent

Taxon 25. Unnamed taxon
21. Transverse process of cervical vertebrae on anterior of centrum
35. Ligamentous attachment of carapace and plastron

Taxon 26. *Centrocryptodira*
12. Floor of canalis caroticus internus thick
20. Formed central articulations of cervical vertebrae
24. Fourth cervical biconvex
25. Eighth cervical procoelous

Taxon 27. Unnamed taxon
16. Paired pits on basisphenoid present
18. Parietal-squamosal contact absent
29. Biconcave caudal present
30. At least first two caudal centra procoelous
39. Epiplastra narrow
40. Plastral scale set 2 (gulars/extragulars) absent

Taxon 28. *Sinemydidae*
12. Floor of canalis caroticus internus thin
25. Eighth cervical biconvex

Taxon 29. Unnamed taxon
5. Foramen palatinum posterius large
19. Postorbital-squamosal contact present
24. Fourth cervical opisthocoelous

TABLE 20—(*Continued*)

Taxon 30. *Polycryptodira*
2. Prefrontals meet in midline
11. Canalis caroticus internus and canalis caroticus lateralis completely embedded in bone
22. Posterior cervicals with strong ventral process
23. Cervical ribs absent
27. Cervicals with double transverse process
32. First thoracic rib extends less than halfway across first costal

Taxon 31. Unnamed taxon
1. Nasals absent
16. Basisphenoidal pits absent
28. Eighth cervical neural spine low
33. First thoracic vertebral centrum faces anteroventrally

Taxon 32. *Procoelocryptodira*
26. Double central articulation between seventh and eighth cervicals
29. Biconcave caudal near base of tail
31. Chevrons small or absent

Taxon 33. *Chelomacryptodira*
19. Postorbital-squamosal contact absent
35. Sutured carapace-plastron articulation
39. Broad epiplastra

for a problem exists. The consistency index of 0.5 does not reflect the variation in thickness between the extremes.

Discussion: Meiolaniids have an unusually thick floor to the canalis caroticus internus and differ strongly from other primitive eucryptodires such as plesiochelyids and sinemydids. This character was used by Gaffney and Meylan (1988) and Gaffney et al. (1991) to separate plesiochelyids as the sister group to all other eucryptodires.

13. Canalis caroticus lateralis versus canalis caroticus internus: Canalis caroticus lateralis equal to or larger than canalis caroticus internus = 0; Canalis caroticus lateralis smaller than canalis caroticus internus = 1.

Morphology: The canals of the internal carotid arterial system are summarized in Gaffney (1979b). The canal size is presumed to reflect the size of the artery.

Primitive condition: The original assessment of the primitive condition of this character (Gaffney, 1975a) was based on comparison with living sauropsids outside turtles. In Squamata, the palatine artery is usually

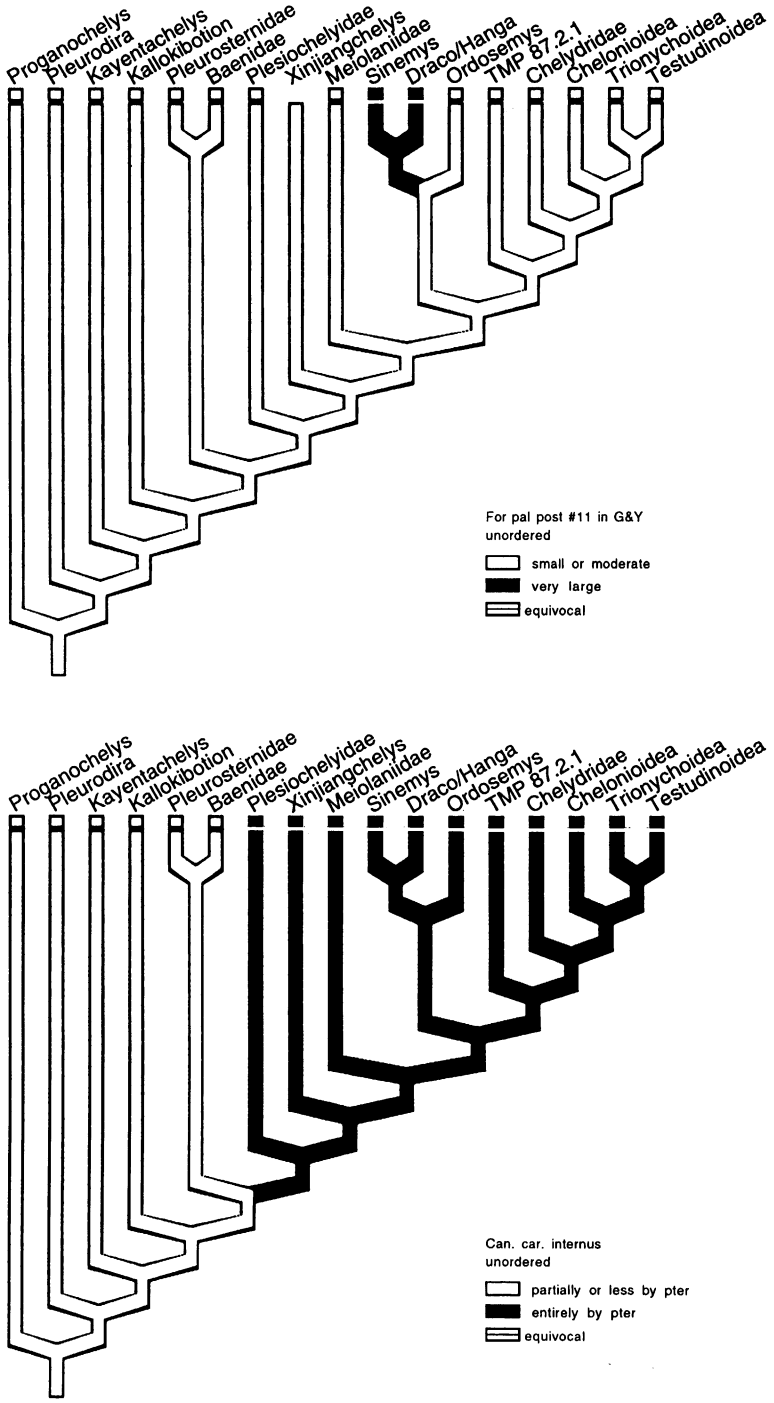


Fig. 102. Distribution of characters **5** and **10** on the preferred cladogram.

smaller than the internal carotid and this is the case in many Recent turtles. In *Proganochelys* and *Kayentachelys* the interpterygoid vacuity is open and there is no canalis caroticus lateralis. As more fossils have become available since 1975, the distribution of an

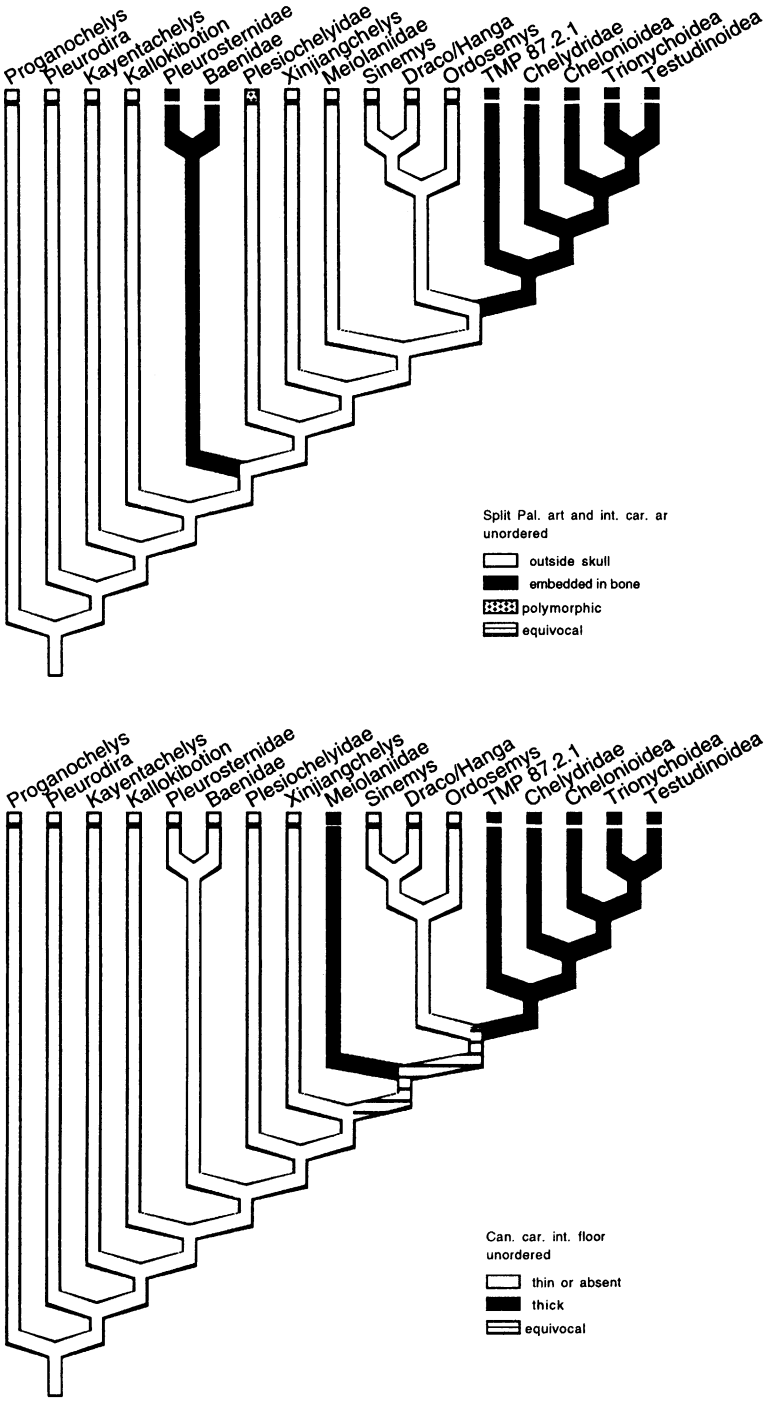


Fig. 103. Distribution of characters **11** and **12** on the preferred cladogram.

equally sized canalis caroticus lateralis has increased. *Kallokibotion* (Gaffney and Meylan, 1992), the most primitive selmacryptodiran, has equally sized arterial canals and is probably representative of the primitive condition for cryptodires.

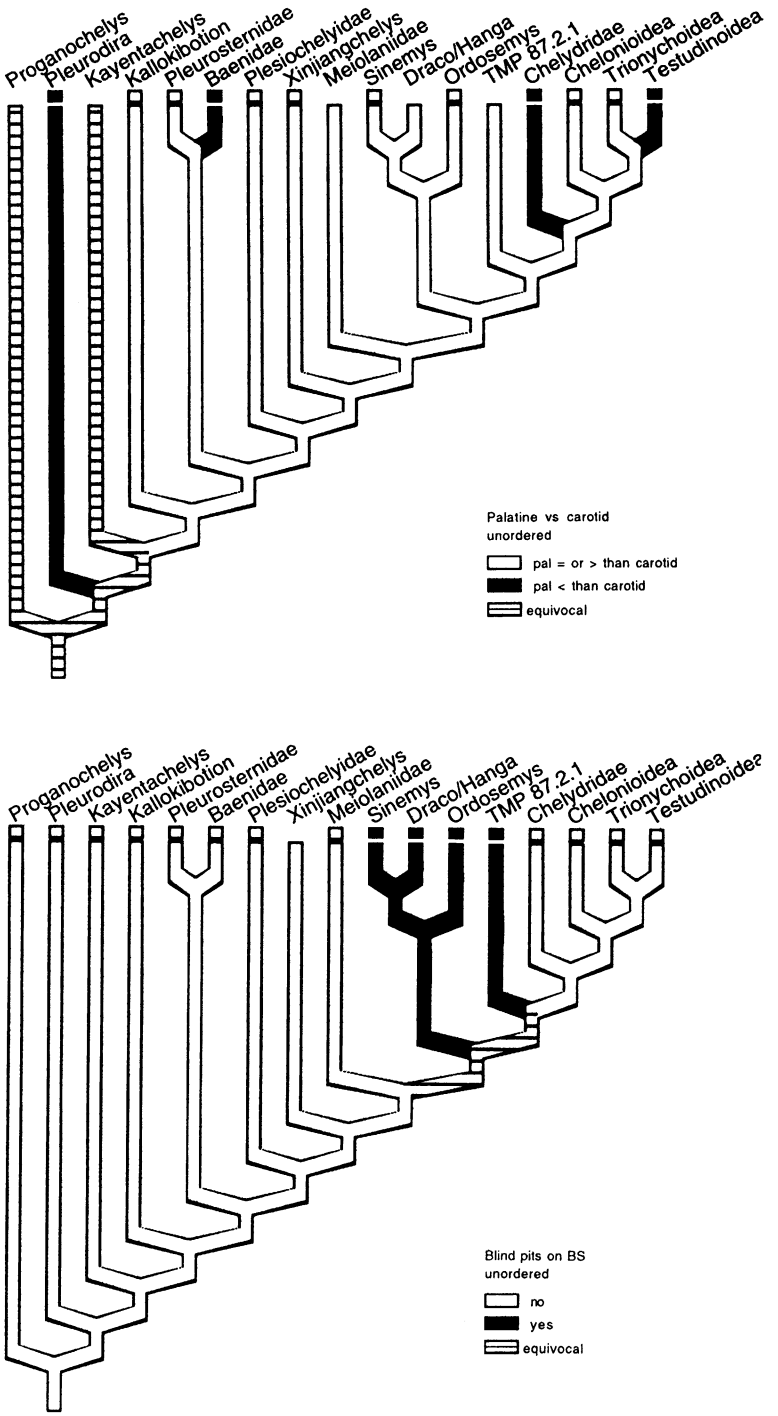


Fig. 104. Distribution of characters **13** and **16** on the preferred cladogram.

Homoplasy: With a CI of .250 this character is one of the most homoplastic used in this analysis. The shortest tree requires each instance of this character to be independently derived and no groups are formed by this character.

Discussion: This character was originally interpreted with palatine smaller than carotid being the primitive condition. The palatine equal or larger than carotid was used (Gaffney, 1975a, 1976) as an advanced character linking plesiochelyids and chelonioids. The tree showing the distribution (fig. 104) of what is here interpreted as the advanced condition (i.e., the palatine smaller than the carotid) shows the sporadic occurence of the character. Dropping this character results in the same shortest tree.

14. Foramen posterius canalis carotici interni: Not formed by basisphenoid and pterygoid = 0; Formed by basisphenoid and pterygoid, midway along basisphenoid/pterygoid suture = 1.

Morphology: This character is figured in Gaffney (1972, 1979a, 1979b, 1982) and Brinkman and Nicholls (1993).

Primitive condition: The primitive condition is the carotid entering the skull at the foramen caroticum basisphenoidale as in *Proganochelys.* The absence of this condition is also characteristic of the eucryptodiran carotid system, in which the foramen posterius canalis carotici interni is formed at the posterior end of the pterygoid canal.

Homoplasy: None known, CI is 1.0.

Discussion: Gaffney (1975a) used the position of the foramen posterius canalis carotici interni as a synapomorphy of Pleurosternidae + Baenidae to form the Paracryptodira. Evans and Kemp (1976) questioned this assessment and Gaffney (1979a) accepted their interpretation that the position of the carotid in baenids and pleurosternids was primitive for eucryptodires. However, as more taxa and better specimens of primitive cryptodires have been discovered, Gaffney's original 1975 (1975a) interpretation appears more likely. Brinkman and Nicholls (1993), in their description of the skull of *Neurankylus,* revive the Paracryptodira and argue that the baenid carotid morphology is not primitive for other cryptodires. In the primitive cryptodires, *Kallokibotion* and *Kayentachelys,* the carotid enters the skull at the foramen caroticum basisphenoidale, formed entirely by the basisphenoid just as in *Proganochelys.* This appears to be the condition from which all other cryptodire patterns are derived. In the primitive eucryptodires *Dracochelys* (Gaffney and Ye, 1992), *Xinjiangchelys* (Kaznyshkin et al., 1990), *Sinemys* (Brinkman and Peng, 1993b), and *Hangaiemys* (Sukhanov and Narmandakh, 1974) the posterior part of the canalis caroticus internus is covered by the pterygoid but the entry of the palatine artery and cerebral carotid artery are variably exposed. The result is a persistently visible foramen caroticum basisphenoidale in the basisphenoid. A baenidlike foramen posterior canalis carotici interni is not formed in any of these taxa. Instead the eucryptodiran carotid condition is more parsimoniously derived from something like *Kallokibotion* only by the posterior formation of the canalis caroticus internus in the pterygoid. Following Brinkman and Nicholls (1993), the anterior flooring of the palatine artery in pleurosternids and baenids is best interpreted as a synapomorphy uniting these taxa, even though a similar condition also occurs in all Polycryptodira and in plesiochelyids. However, the formation of a distinct carotid entry foramen midway along the pterygoid/basisphenoid suture along with the complete enclosure of the palatine and cerebral carotid arteries is unique to the Paracryptodira.

15. Fenestra perilymphatica: Relatively large = 0; Relatively small = 1.

Morphology: The primitive condition of this character is described and figured in Gaffney (1979b, particularly figures 48–51) for Polycryptodira and in Gaffney (1983, fig. 52) for *Meiolania.* The derived condition is figured for the baenid, *Chisternon,* in Gaffney (1979b: fig. 94).

Primitive condition: As described in Gaffney (1979b, 1990; figured in Gaffney [1990, fig. 43], but unfortunately mislabeled as "fenestra jugulare anterius," labeled correctly in fig. 45C). The interpretation of Brinkman and Nicholls (1993) is followed here, in that the large fenestra, as seen in *Proganochelys* is primitive.

Homoplasy: None known, but age may be a factor as noted by Brinkman and Nicholls (1993), CI is 1.0.

Discussion: See Brinkman and Nicholls (1993).

16. Paired pits on ventral surface of basisphenoid: Pits absent = 0; Pits present = 1.

Morphology: The pits are described and figured for *Ordosemys* in Brinkman and Peng

(1993a: fig. 6C) and for *Sinemys* in Brinkman and Peng (1993b: fig. 10B).

Primitive condition: The absence of pits is found throughout the more primitive turtles *Proganochelys, Kayentachelys,* etc.

Homoplasy: Although these pits are simple morphologically they are very restricted in their distribution, occurring only in *Sinemys, Hangaiemys, Ordosemys,* and TMP 87.2.1. *Dracochelys* lacks the pits, but because of its close similarity to *Hangaiemys* I have scored the combined taxon as having the pits. The cladogram topology is unchanged when run with the pits missing in the combined taxon. Nonetheless an additional instance of homoplasy is present. In the shortest tree, TMP 87.2.1 is the sister taxon to Polycryptodira and not to sinemydids so this character must have been twice evolved or once lost, resulting in a consistency index of 0.5.

Discussion: The paired basisphenoid pits are apparently related to neck muscle attachments but there is no obvious relationship to cervical features. This is another character present at the "sinemydid level" of primitive eucryptodires and further work on this group should provide better information on its distribution. The hypothesis of a larger Sinemydidae, including TMP 87.2.1 is supported by other characters, but is two steps longer than the shortest tree produced by this analysis.

17. Posterior temporal emargination: Not developed = 0; At least partially developed = 1.

Morphology: The primitive condition can be seen in *Kayentachelys* (Gaffney et al., 1987) and *Kallokibotion* (Gaffney and Meylan, 1992). The advanced condition is in *Glyptops* and *Pleurosternon* (Gaffney, 1979a; Evans and Kemp, 1976).

Primitive condition: The complete absence of posterior temporal emargination seen in *Proganochelys* persists in *Kayentachelys* and *Kallokibotion* and is best interpreted as primitive for cryptodires.

Homoplasy: The consistency index is 0.33 for this character but within cryptodires only the meiolaniids provide an example of homoplasy in this character, although there is an undescribed, extinct emydid with a fully roofed skull (Hutchison, personal commun.). Meiolaniids have no temporal emargination but the proportions of the elements making up the skull roof differ significantly from the primitive condition. In *Kayentachelys* and *Kallokibotion* the parietal and postorbital are elongate and there is little if any exposure of the supraoccipital on the skull roof. In *Meiolania* the parietal and postorbital are relatively small (as in other eucryptodires with emargination) and the supraoccipital is very large. The entire posterior portion of the skull roof in *Meiolania* is formed by the expanded supraoccipital plus the uniquely enlarged squamosal. It is very likely that the lack of emargination in meiolaniids is a secondary condition.

Discussion: See above.

18. Parietal/squamosal contact: Present = 0; Absent = 1.

Morphology: The skull roof of turtles is described in Gaffney (1979b) with recent additions in Gaffney (1990) and Gaffney and Meylan (1992).

Primitive condition: The presence of a parietal/squamosal contact is widespread in primitive tetrapods and amniotes, and is present in *Proganochelys,* which is interpreted here as the primitive condition for turtles.

Homoplasy: This character reflects the degree of posterior temporal emargination of the skull roof. Turtles show a general trend toward temporal emargination, but this is a variable character with a simple morphology and is often hard to homologize using only presence or absence of a bone contact. Gaffney et al. (1991: 323) stated: "there is ... good evidence that homoplasy of this character has occurred in baenids, meiolanids, pleurodires, and chelonioids." See Gaffney et al. (1991) for further discussion. For the preferred cladogram, however, the consistency index is 1.0.

Discussion: Meiolaniids have an extensively roofed skull, as thoroughly roofed as any other turtle, and more roofed than the primitive condition of turtles as seen in *Proganochelys.* Both Gaffney (1983) and Gaffney et al. (1991) argued that the unusually small parietal, the unusually large squamosal and supraoccipital strongly suggest that meiolaniids are derived from a more emarginate ancestor. Whether that ancestral condition would be with or without a parietal/squamosal contact cannot really be determined.

The loss of a parietal/squamosal contact was used by Gaffney (1984) and Gaffney and

Meylan (1988) as a synapomorphy for the Daiocryptodira, a group including eucryptodires and baenids but excluding pleurosternids and *Kallokibotion.* It is very likely that meiolaniids are a member of this group and that their parietal/squamosal contact is secondary.

19. Postorbital/squamosal contact: Present = 0; Absent = 1.

Morphology: Described in Gaffney (1979b) and Gaffney (1990).

Primitive condition: The large postorbital contacting the squamosal is the primitive condition within turtles based on *Proganochelys, Kayentachelys,* and *Kallokibotion.*

Homoplasy: This character's drawbacks are similar to the previous character involving temporal emargination. Emarginate and well-roofed conditions have repeatedly evolved in turtles and the simple morphology of the region makes it difficult to test homology arguments. In the preferred cladogram, the CI of 0.5 reflects the parallel evolution of this character in *Sinemys.*

Discussion: This character was used by Gaffney (1984) and Gaffney and Meylan (1988) to unite the Trionychoidea and Testudinoidea. Although these authors emphasized the weak nature of this character, no preferred alternatives have been proposed. Further discussion is in Gaffney and Meylan (1988: 192) and Gaffney et al. (1991: 326).

Meiolaniids have a well-developed postorbital/squamosal contact but the postorbital itself is not as large as the primitive condition seen in such taxa as baenids, *Chelydra,* and *Toxochelys.* Nonetheless, it would be very difficult to argue that meiolaniids have the derived condition of this character.

20. Central articulations of cervical vertebrae: Unformed (Platycoelous or amphicoelous) = 0; Formed (Concavo-convex) = 1.

Morphology: Gaffney (1990) described the primitive and advanced conditions for turtle cervicals. Meiolaniid cervicals are described in Gaffney (1985a).

Primitive condition: The primitive condition for amniote cervicals appears to be the widespread amphicoelous pattern. *Proganochelys* is amphicoelous and this condition is interpreted as primitive for turtles (see Gaffney, 1990, for further discussion).

Homoplasy: There is considerable evidence that formed centra have evolved at least three times in turtles: within pleurodires, within baenids (see Gaffney et al., 1991: 328), and within eucryptodires. Since basal pleurodires (*Notoemys,* Fuente and Fernandez, 1989; Fernandez and Fuente, 1994) and basal baenids (*Trinitichelys,* Gaffney, 1972) are amphicoelous, these groups are scored with the primitive condition. Therefore, in the preferred cladogram the CI is 1.0.

Discussion: Gaffney (1984) and Gaffney and Meylan (1988) used the presence of formed central articulations (among other characters) to diagnose the Centrocryptodira, which consists of all eucryptodires except the amphicoelous Plesiochelyidae. Meiolaniids have well-developed cervical central articulations and a biconvex fourth cervical, the commonest pattern within the Centrocryptodira.

21. Transverse processes of cervical vertebrae: On middle of centrum = 0; On anterior of centrum = 1.

Morphology: The primitive condition can be seen in *Proganochelys* (Gaffney, 1990, figs. 109, 111, 112) and *Meiolania* (Gaffney, 1985a). The derived condition is seen in Polycryptodira (Williams, 1950; Hoffstetter and Gasc, 1969).

Primitive condition: The transverse process is on the middle of the centrum in *Proganochelys,* pleurodires, *Kayentachelys,* and other primitive cryptodires, and this is interpreted as the primitive condition.

Homoplasy: The preferred cladogram has a consistency index of 0.33 for this character.

Discussion: Brinkman and Peng (1993a, 1993b) use the anterior position of the transverse process in cervicals to unite *Sinemys* and *Ordosemys* with the Polycryptodira. However, likely *Dracochelys* cervicals (Brinkman, personal commun.) have transverse processes in the middle of the centrum. *Xinjiangchelys* also is inconsistent with the preferred cladogram because it has the advanced condition with anteriorly placed processes.

Although requiring multiple reversals, this is still one of the characters uniting sinemydids with Polycryptodira, separating them from meiolaniids. *Meiolania* clearly has the primitive condition.

22. Posterior cervicals with strong ventral process: absent = 0; present = 1.

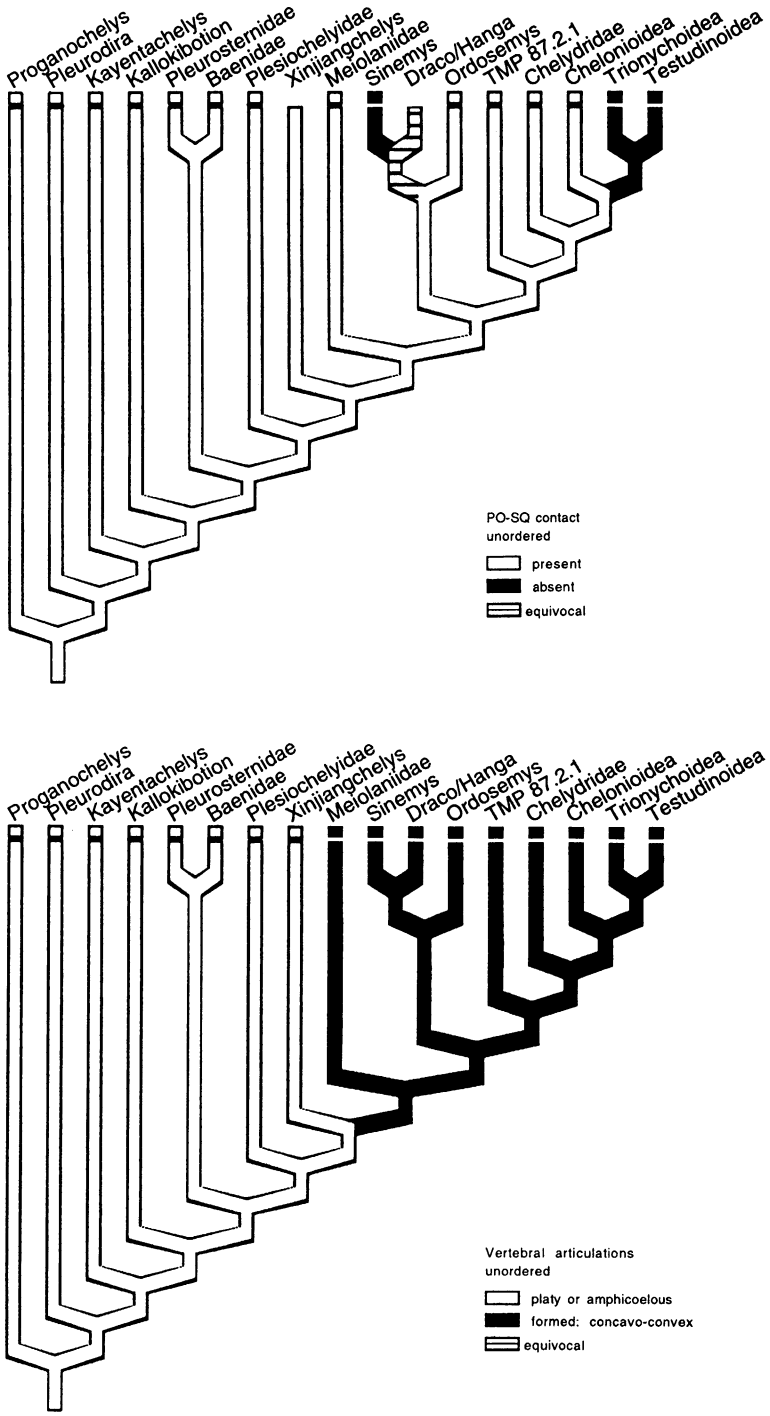


Fig. 105. Distribution of characters **19** and **20** on the preferred cladogram.

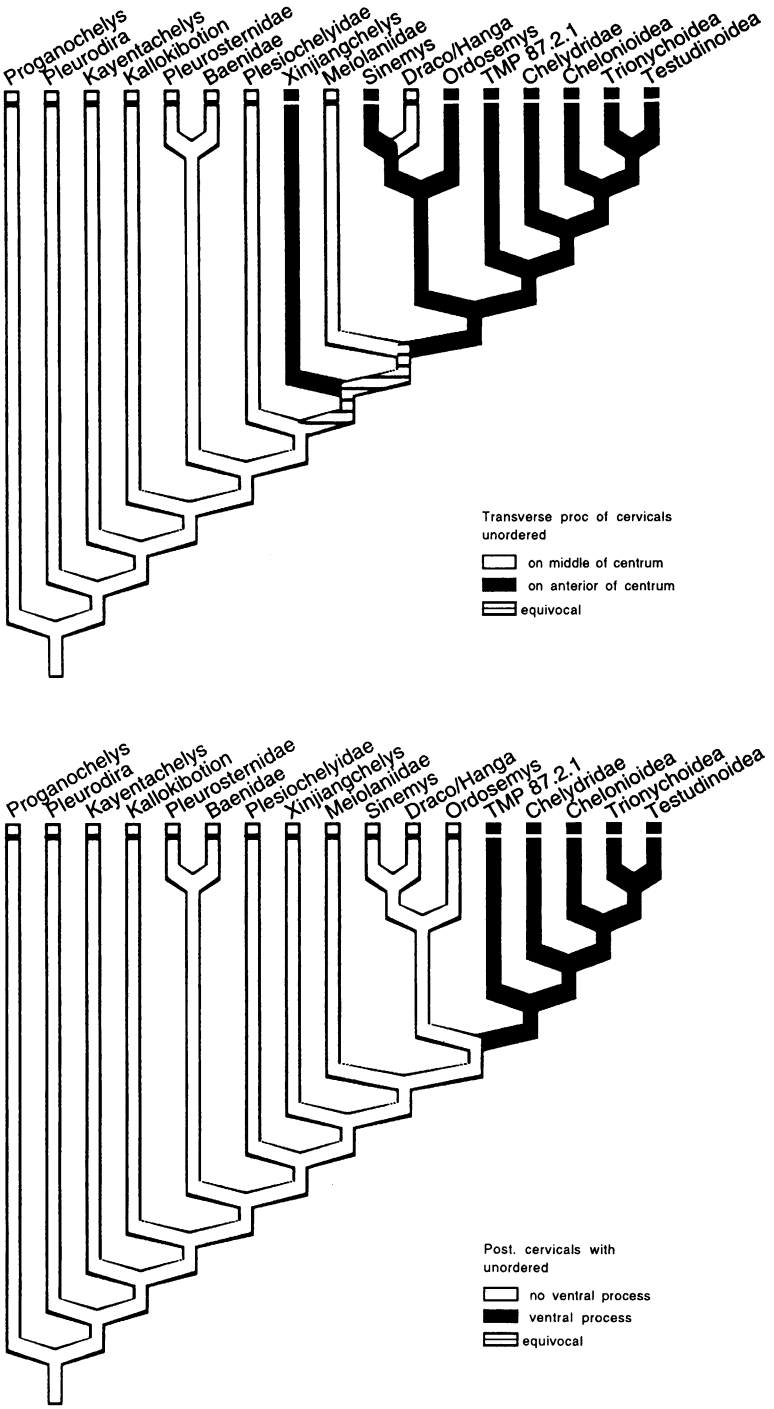


Fig. 106. Distribution of characters **21** and **22** on the preferred cladogram.

Morphology: Posterior cervicals with the ventral ridge or process are described by Williams (1950), Hoffstetter and Gasc (1969), and Vaillant (1881).

Primitive condition: The primitive condition can be seen in *Proganochelys* and *Kayentachelys.*

Homoplasy: The CI for this character is 1.00 as it appears only at taxon 30.

Discussion: Meiolania platyceps and *Meiolania brevicollis* have cervicals that lack a strong ventral process. However, a low ventral keel is present in *Meiolania brevicollis* and absent in *Meiolania platyceps.*

23. Cervical ribs: Present = 0; Absent = 1.

Morphology: Gaffney (1990) described ribs in *Proganochelys* and Gaffney (1985a) described them in *Meiolania* and argued for their presence in *Kayentachelys* and pleurosternids. Brinkman and Peng (1993a) describe ribs in *Ordosemys,* Brinkman and Nicholls (1993) describe cervical ribs in the baenid *Eubaena.*

Primitive condition: Cervical ribs are a primitive amniote feature and occur in *Proganochelys* (Gaffney, 1990) and suggested turtle outgroups.

Homoplasy: The recent discovery of cervical ribs in more eucryptodires (Brinkman and Peng, 1993a, 1993b) makes their presence in meiolaniids less surprising and reduces the likely range of homoplasy. It is very likely that the ribs were lost independently in pleurodires and cryptodires. Within cryptodires at least some baenids seem to have lost them independently of other cryptodires. This also seems to be the case in pleurosternids. However, the preservation of the small, loosely attached cervical ribs is probably a rare occurrence and their absence in a specimen does not necessarily preclude their presence in life. It is hard to say whether the CI of 0.33 reflects true cases of multiple loss or just poor preservation.

Discussion: Meiolania is unusual in having very large and well developed cervical ribs, larger, in fact, than in any other turtle including *Proganochelys.* It's likely that the size of the ribs is autapomorphic, but even their occurrence in other eucryptodires has been unknown until recently. The discovery of cervical ribs in sinemydids (Brinkman and Peng, 1993a, 1993b) strongly suggests that the ribs persisted into the basal Eucryptodira and that their presence in meiolaniids does not indicate relationships outside the Eucryptodira.

24. Fourth cervical central articulation (unordered): amphicoelous = 0; biconvex = 1; opisthocoelous = 2.

Morphology: The central cervical articulations of living turtles have been reviewed and figured by Williams (1950), Hofstetter and Gasc (1969), and Vaillant (1881). The morphology itself is usually clear, even in fossils, but the patterns within groups can be confusing. Here only the primitive members of groups are used to determine the pattern.

Primitive condition: As in all of the central articulation characters, the amphicoelous condition of *Proganochelys, Kayentachelys,* and *Kallokibotion* is considered primitive. The amphicoelous vertebrae reported for *Notoemys* is considered basal for that group.

Homoplasy: This two-state character has a consistency index of 1.0 in this analysis, but within the Trionychoidea and Testudinoidea the fourth cervical often has procoelous or opisthocoelous central articulations. It seems likely, however, that the primitive condition for both groups is a biconvex fourth cervical based on its occurrence in basal members of Testudinoidea and Trionychoidea (Meylan and Gaffney, 1989; Gaffney and Meylan, 1988). In baenids with formed centra, the fourth cervical is biconvex and this must be interpreted as a secondary acquisition. *Neurankylus* has an opisthocoelous fourth cervical, but the primitive condition for the group must be the amphicoelous state in pleurosternids and *Trinitichelys.*

Discussion: Although I much prefer developing the analysis with single-state characters, this character and the other cervical central character (**26**) seem best interpreted as multistate characters. Despite variation within groups, the biconvex fourth cervical is best interpreted as a synapomorphy for taxon 26, Centrocryptodira.

The second state of this character is an opisthoceolous fourth cervical in *Sinemys* and *Dracochelys. Sinemys* cervicals have been described (Brinkman and Peng, 1993b) but they are still undescribed for *Dracochelys* or *Hangaiemys.* However, Brinkman (personal

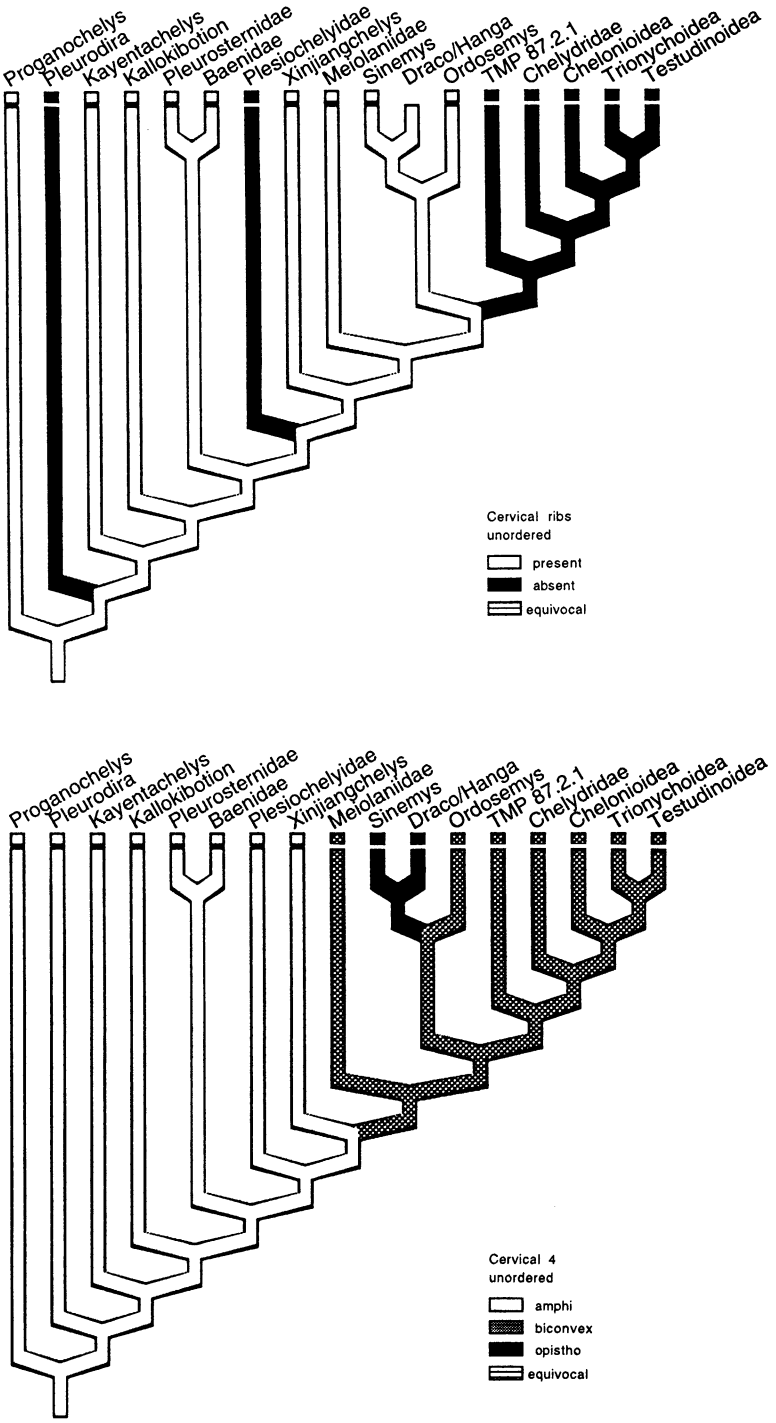


Fig. 107. Distribution of characters **23** and **24** on the preferred cladogram.

commun.) has found cervicals in the Tugulu Series that he feels are probably *Dracochelys* and these are opisthoceolous, thus uniting *Dracochelys* and *Sinemys*.

25. Eighth cervical central articulation (unordered): amphicoelous = 0; procoelous = 1; biconvex = 2.

Morphology: (see character **24**).

Primitive condition: The primitive condition is amphicoelous, see character **24** for discussion.

Homoplasy: The consistency index for this character is 0.66. The independent acquisition of a biconvex eighth cervical in sinemydids and testudinoids required by this cladogram is supported by other morphology of the vertebra. The sinemydid cervicals are all high and thin while in Testudinoids the centrum of the eighth is relatively short and squat, also with a double articulation absent in sinemydids. The Trionychoidae have the autapomorphous condition of opisthocoely (Meylan and Gaffney, 1989). In this analysis, the procoelous eighth cervical is clearly the primitive condition within the Centrocryptodira with the biconvex of sinemydids derived from it.

Discussion: Meiolania has a procoelus eighth cervical that is short and squat, more similar to the eighth cervical in Polycryptodira (taxon 30) than to the high, thin eighth cervical in sinemydids.

26. Double (i.e., transversely paired) central articulations between the seventh and eighth cervicals: absent = 0; present = 1.

Morphology: This character is figured and described in the same references given for character **24.** Williams (1950) particularly notes the distribution of this character among the Recent turtles. Both the procoelous and opisthocoelous conditions are considered the same character if double.

Primitive condition: The primitive condition would be any articulation that was not double. Procoelous, opisthocoelous, and amphicoelous could all be primitive if they were not transversely doubled or paired.

Homoplasy: The consistency index in this analysis is 1.0, but Williams (1950) shows individual variation of this character, including occasional absence within chelonioids and testudinoids. Although most chelydrids (excluding *Platysternon*) lack double articulations, the character does appear as an individual variant in *Chelydra* and *Macrochelys*. This analysis is not the place to explore the relationships of *Platysternon* and it has not been included in the Chelydridae, despite Gaffney (1975b).

Discussion: Meiolaniids clearly lack this character which has been included to help resolve the higher Cryptodira.

27. Cervical vertebra having a distinct double transverse process, i.e., diapophysis and parapophysis: Present in at least some cervicals = 0; Absent in all cervicals = 1.

Morphology: The single, advanced condition, seen in all living cryptodires is described in Hoffstetter and Gasc (1969), Williams (1950), and Vaillant (1881). The double or subdivided transverse processes are described in Gaffney (1990) for *Proganochelys,* Gaffney (1985a) for *Meiolania,* Evans and Kemp (1975) for *Pleurosternon,* Brinkman and Peng (1993a) for *Ordosemys,* and Peng and Brinkman (1993) for *Xinjiangchelys.* The derived condition is present when the transverse process is single, with no distinct ventral articulation for a cervical rib. The primitive condition may be a subdivided process where the parapophysis and diapophysis come close together as in *Ordosemys* or the presumably more primitive condition see in *Proganochelys* where the processes are widely separated.

Primitive condition: Based on outgroup comparison the condition seen in *Proganochelys* is interpreted as primitive.

Homoplasy: With a CI of 0.20 this is the worst character used in this study. The shortest cladogram requires five independent acquisitions of this character in turtles (four within cryptodires). This character and character **23**, the absence of cervical ribs, are closely related. The presence of paired transverse processes with dorsal and ventral articulations of a bifurcate cervical rib is the primitive condition of turtles (Gaffney, 1990) and amniotes in general. Within turtles the ribs are lost and the central articulations are reduced to one transverse process. At the present time, it is most likely that cervical ribs have been lost independently a number of times, three in this analysis. Interestingly

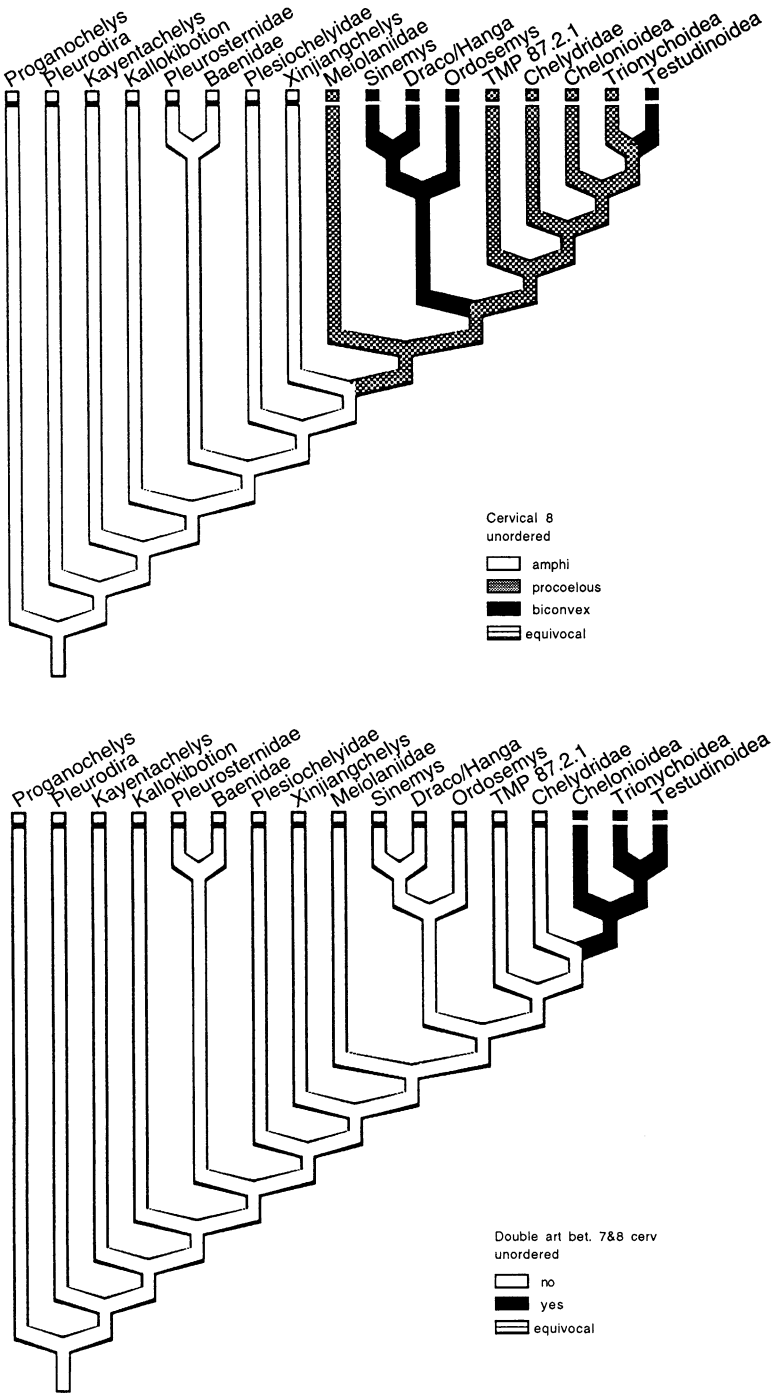


Fig. 108. Distribution of characters **25** and **26** on the preferred cladogram.

enough, it is also likely that the reduction from paired transverse processes to one has not been exactly correlated with the loss of cervical ribs. Baenids (Brinkman and Nicholls, 1991) and *Sinemys* (Brinkman and Peng, 1993b) have been described as having only

a single transverse process and cervical ribs. The ribs in these and other cryptodires are often small and no longer bifucated. So, it is probable that the homoplasy seen in the loss of cervical ribs and the single transverse process are related to each other but not one-to-one, and can thus be used as separate characters.

Discussion: Meiolania is clearly primitive in this character, being particularly similar to *Proganochelys* in retaining widely separated parapophyses and diapophyses. It might be possible to improve the consistency of this character by differentiating the widely spaced condition from the presumably more advanced subdivided condition. However, there is considerable variation in this feature among the cervicals and complete series are necessary which are not presently available for many primitive cryptodires. In any case, the analysis was run without this character and the single, shortest tree was the same.

28. Neural spine on eighth cervical: high = 0; low = 1.

Morphology: The low-spine condition is figured and described in Vaillant (1881), Williams (1950), and Hoffstetter and Gasc (1969). Even though in chelonioids the spine articulates with the carapace, it is still low in comparison to *Meiolania,* baenids, and sinemydids.

Primitive condition: The high spine is present in *Proganochelys* and baenids.

Homoplasy: The consistency index is 1.0 for this character in this analysis. For some taxa, whether the spine is high or low may become subjective, but so far I have not noticed a problem.

Discussion: The principal problem with this character at present is the relatively large number of extinct taxa for which the eighth cervical spine is not complete enough to determine.

29. A biconcave caudal near base of tail: Absent = 0; Present = 1.

Morphology: Hoffstetter and Gasc (1969) mentioned this feature, which is described in more detail in Mlynarski (1980) and Gaffney (1985a). Brinkman and Peng (1993a, 1993b) and Gaffney and Meylan (1988) also discussed the condition.

Primitive condition: Primitive chelonian caudal centra are amphicoelous as seen in the most primitive eucryptodires, the plesiochelyids. Gaffney (1984, 1985a) and Gaffney and Meylan (1988) argued that opisthocoelous centra are primitive within the Centrocryptodira, that is, for cryptodires with formed caudal centra.

Homoplasy: This analysis requires a CI of 0.5, because the character is interpreted as primitive within eucryptodires and then is lost.

Discussion: In the analyses of Gaffney (1984, 1985a), Gaffney and Meylan (1988), and Gaffney et al. (1991) the biconcave anterior caudal appears only once and requires no homoplasy. This character was used to support the monophyly of *Chelydra, Macroclemys, Platysternon,* and *Chelydropsis.* However, Brinkman and Peng (1993a, 1993b) showed that the biconvex anterior caudal has a wider distribution. The present analysis substantiates Brinkman and Peng's (1993a, 1993b) interpretation that the biconcave anterior caudal, preceded by some procoelous caudals and followed by many opisthocoelous caudals, is the primitive condition for the all-procoelous caudal condition (see character **30**).

Meiolaniids clearly lack a biconcave caudal. Even though a complete, articulated tail is unknown for the group, the large number of caudals available for *Meiolania platyceps* show only the opisthocoelous condition.

30. Caudal central articulations: All centra amphicoelous or opisthocolous = 0; At least first two caudals procoelous = 1.

Morphology: Turtle caudal types are figured in Gaffney (1990), *Meiolania* is figured and described in Gaffney (1985a).

Primitive condition: Proganochelys and most amniote outgroups are amphicoelous. Within cryptodires Gaffney (1984, 1985a, and 1990) has argued that opisthocoelous caudals are primitive with respect to procoelous and biconvex caudals.

Homoplasy: For this analysis, the CI of this character is 1.0, but procoelous caudals have arisen at least twice, within pleurodires and within eucryptodires, according to the phylogeny of Gaffney and Meylan (1988).

Discussion: The presence in meiolaniids of the primitive, entirely opisthocoelous caudal condition is one of the principal characters differentiating them from the group having at least some procoelous centra. The chelydrids and sinemydids (Brinkman and Peng,

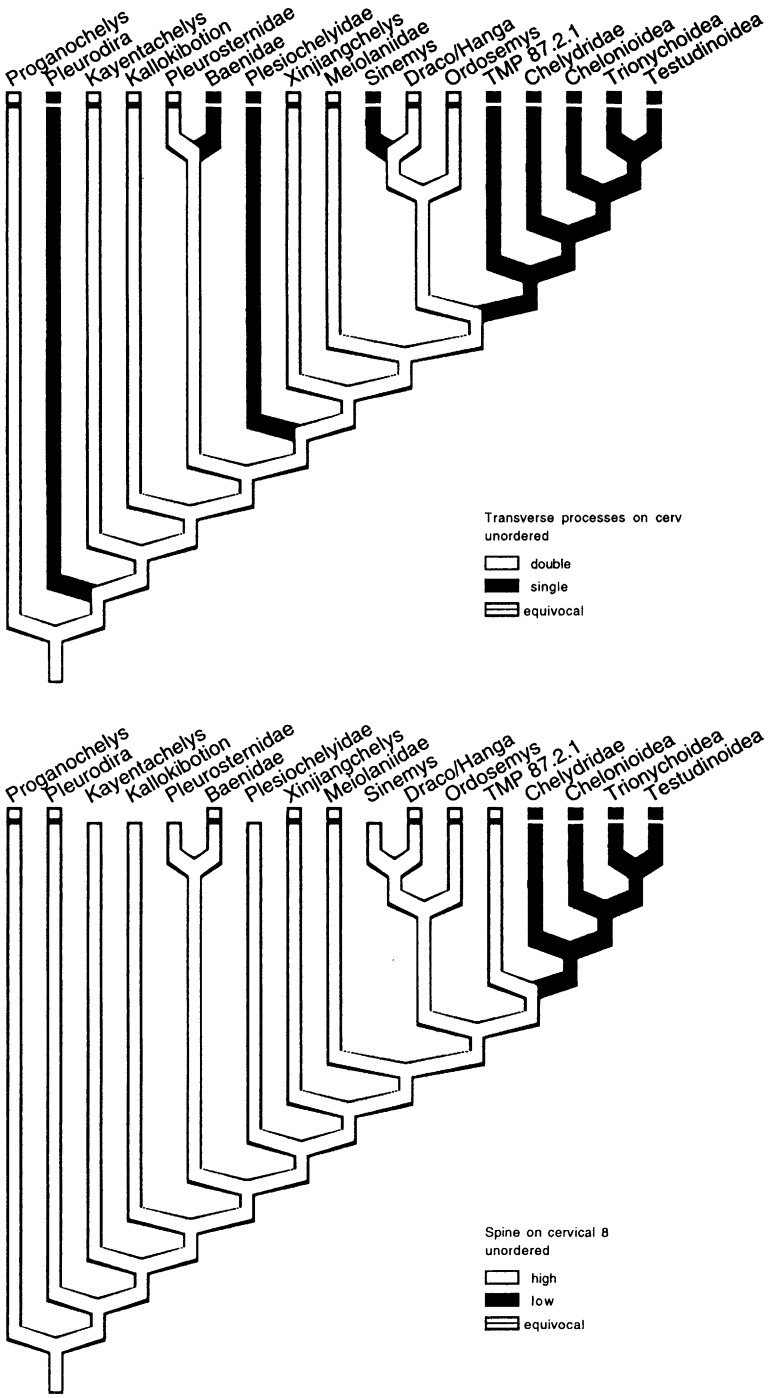


Fig. 109. Distribution of characters **27** and **28** on the preferred cladogram.

1993a, 1993b) have the first two or three caudals procoelous, one biconvex, and the rest opisthocoelous. All other cryptodires have all-procoelous caudals. If Brinkman and Peng's (1993a, 1993b) interpretation is followed, all eucryptodires with any procoelous caudals

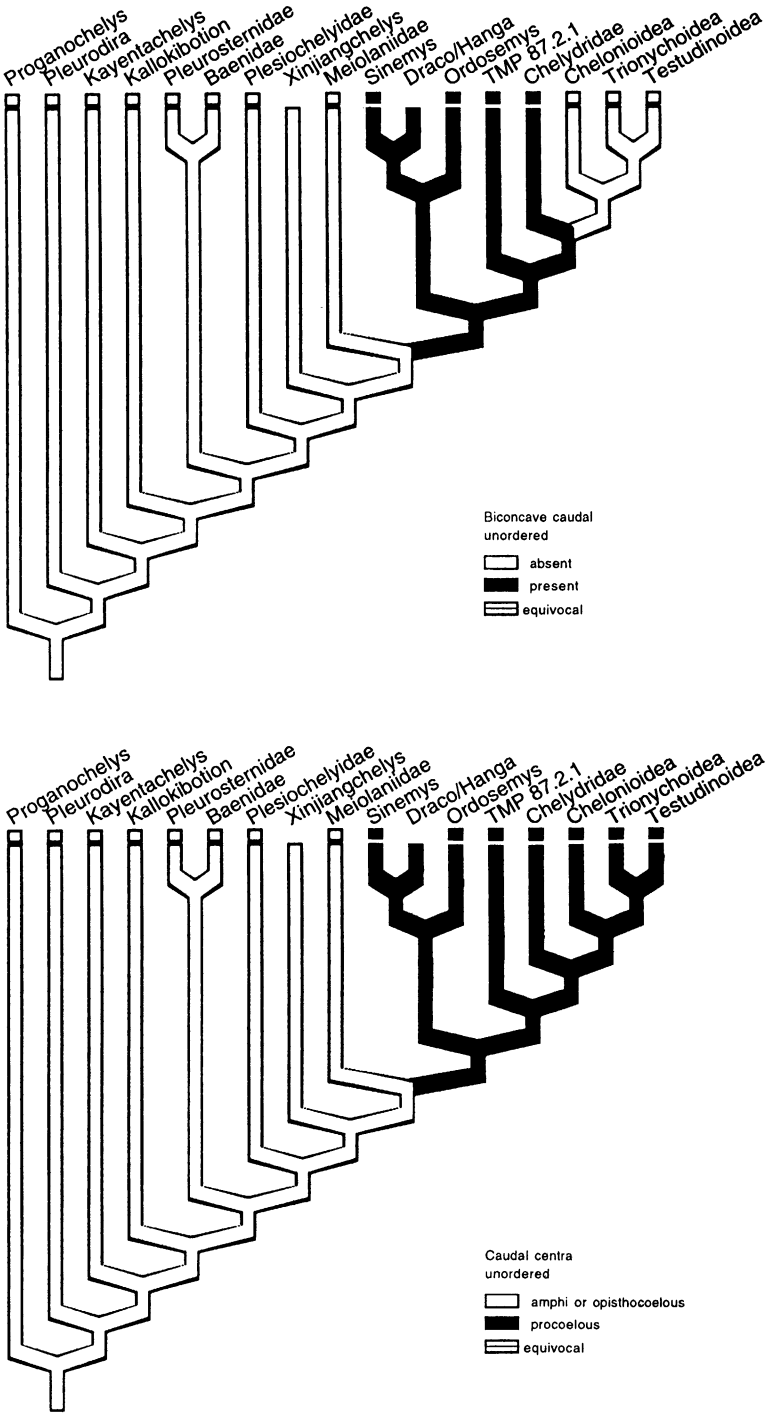


Fig. 110. Distribution of characters **29** and **30** on the preferred cladogram.

form a natural group with meiolaniids the sister group of it.

31. Chevrons: Well developed and present on nearly all caudals = 0; Small to absent (if present, only on a few posterior caudals) = 1.

Morphology: Figures of primitive and advanced conditions are in Gaffney (1990).

Primitive condition: The presence of chevrons is a widespread amniote feature, found in presumed turtle outgroups and *Proganochelys.*

Homoplasy: The CI for this character is 1.0, however, Gaffney and Meylan (1988) required independent loss of chevrons within pleurodires and within eucryptodires. The simple morphology of chevron loss makes rigorous homology assessments difficult.

Discussion: Meiolaniids have well-developed chevrons and a long tail, as in chelydrids and sinemydids.

32. First thoracic rib: Extends to peripherals or nearly so and lies behind the tip of the axillary buttress of the pelvis = 0; Extends less than halfway across first costal = 1.

Morphology: The advanced condition is figured in Meylan and Gaffney (1989), the primitive condition in Gaffney (1990).

Primitive condition: Accepting *Proganochelys* as the sister group of all other turtles is the basis for this polarity assessment. It is supported by the presence of the primitive condition in *Kayentachelys,* the sister group of all other cryptodires, and in *Proterochersis,* and *Platychelys,* primitive sister groups of other pleurodires (Gaffney et al., 1991).

Homoplasy: The advanced condition was acquired independently within pleurodires and within eucryptodires according to the phylogeny of Gaffney and Meylan (1988). In the present analysis, the CI of 0.5 is due to *Xingiangchelys* having this character, independent of the Polycryptodira.

Discussion: Meiolania clearly has the primitive condition of this character, as do *Sinemys* and *Ordosemys* (Brinkman and Peng, 1993a, 1993b). The Tyrrell specimen, however, appears to have the derived condition, thus splitting up the sinemydid group.

33. Anterior articulation of first thoracic centrum: Faces anteriorly or slightly anteroventrally = 0; Faces strongly anteroventrally = 1.

Morphology: The advanced condition is figured in Bojanus (1819) and Meylan and Gaffney (1989). In this analysis the "slightly inclined" condition described by Brinkman and Peng (1993a) in *Ordosemys* is included in the primitive condition. Although there is a degree of inclination in both sinemydids and *Meiolania,* in contrast to *Proganochelys,* it is too arbitrary to discriminate among these at present. Measuring this feature is too dependent on the perceived "normal" position of the carapace, which varies with the degree of doming of the shell. Therefore, it seems best to restrict this character to the extreme condition seen in the Polycryptodira.

Primitive condition: The primitive condition is based on *Proganochelys,* pleurodires, *Kayentachelys,* and *Kallokibotion.*

Homoplasy: None known, CI is 1.0.

Discussion: Meiolania clearly has the primitive condition of this character. In the Recent groups, this character is part of the neck retraction mechanism characteristic of advanced cryptodires. Meiolaniids were probably incapable of neck retraction in any case, due to the large cranial processes, and short cervicals with limited degrees of movement.

34. Mesoplastra: Present = 0; Absent = 1.

Morphology: Primitive conditions are figured in Gaffney (1972, 1990), Gaffney et al. (1987), and Hay (1908). Advanced conditions are figured in Boulenger (1889) and also Hay (1908).

Primitive condition: The presence of mesoplastra as the primitive condition is based on *Proganochelys* as the sister group of all turtles and is supported by *Kayentachelys* as the cryptodire sister taxon and by *Proterochersis* and *Platychelys* as pleurodire sister taxa.

Homoplasy: The CI of this character is 1.0, however, the phylogenies of Gaffney and Meylan (1988) and Gaffney et al. (1991) require loss of mesoplastra independently in chelids and in cryptodires.

Discussion: It is likely that *Meiolania* has no mesoplastra. This corroborates its position as a eucryptodire, as the lack of mesoplastra and the enclosed posterior part of the canalis caroticus internus are found together in the same taxa so far.

35. Ligamentous attachment of carapace and plastron: sutured = 0; ligamentous = 1.

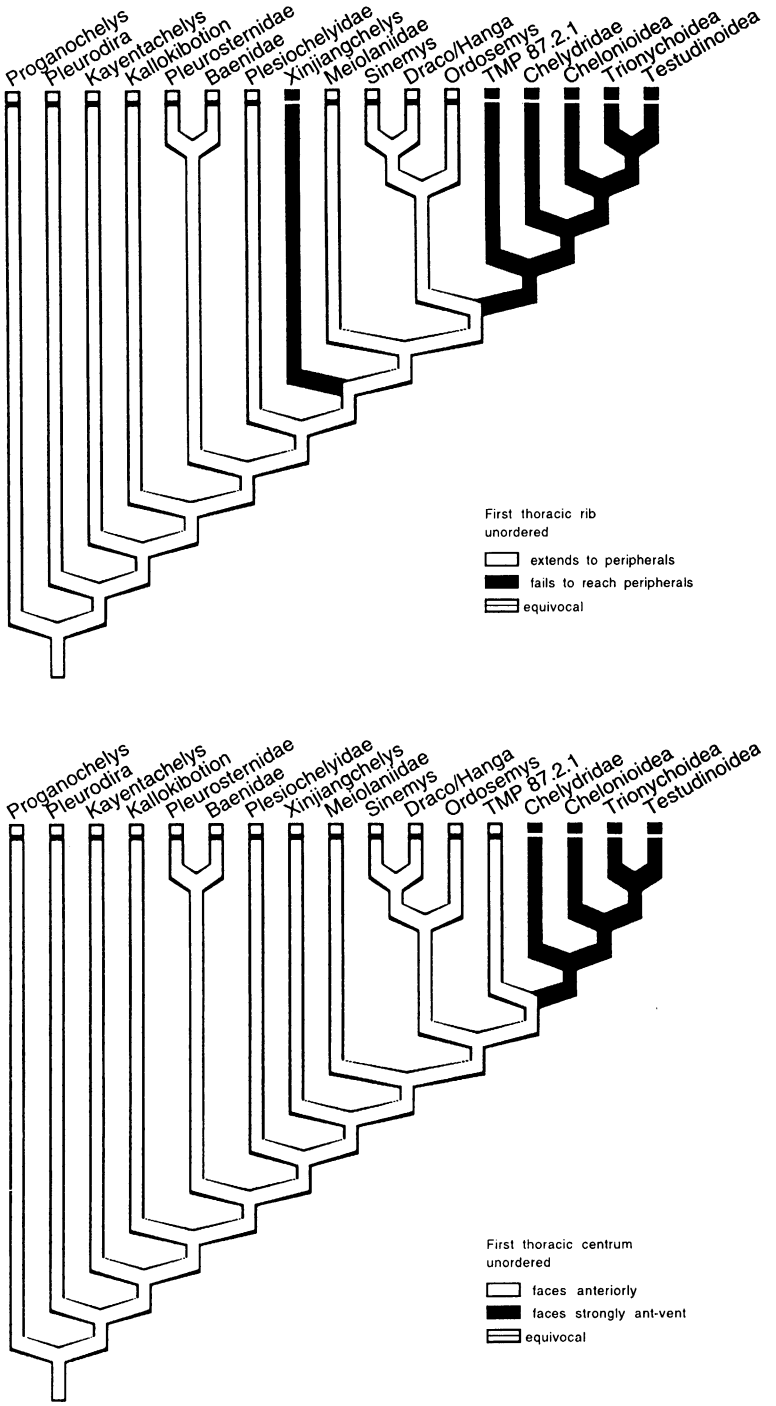


Fig. 111. Distribution of characters **32** and **33** on the preferred cladogram.

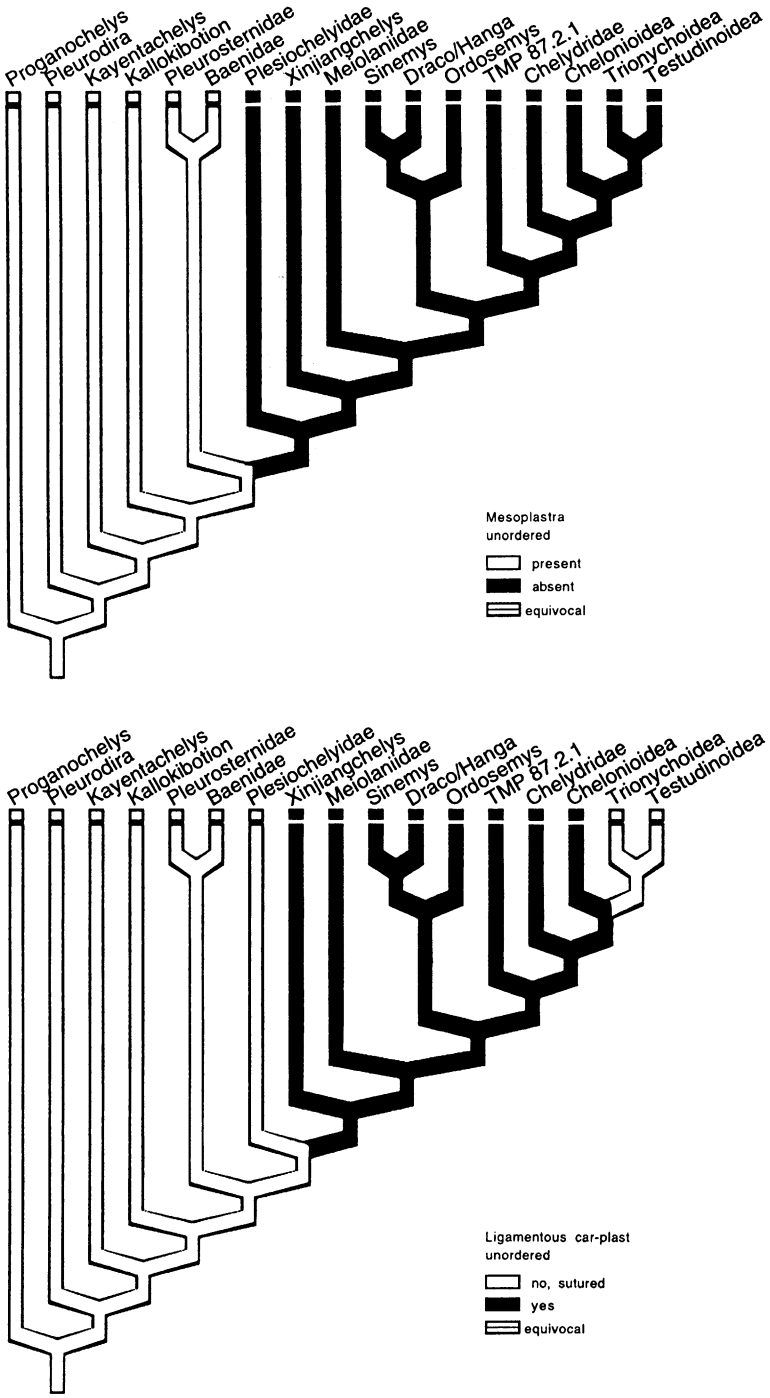


Fig. 112. Distribution of characters **34** and **35** on the preferred cladogram.

Morphology: Typically, the ligamentous carapace/plastron attachment is expressed as strongly digitating processes from the hypoplastron and hyoplastron loosely articulating with pits in peripherals. The sutured condition usually lacks the fingerlike processes and

has a tight contact with many small denticles interfingering from both carapace and plastron. However, many turtles show intermediate degrees of development, and the two conditions are not always clearly defined.

Boulenger (1889) has figures of Recent turtles that show both ligamentous (chelydrids) and sutured (testudinoids) conditions. Bojanus (1819) showed a basically sutured condition but modified by a hinge mechanism. The ligamentous condition is figured in Brinkman and Peng (1993a) for *Ordosemys,* and in Sukhanov and Narmandakh (1974) for *Hangaiemys.*

Primitive condition: The determination of the primitive condition for this character is not clear. At the level of eucryptodires, the presence of tightly sutured shells in plesiochelyids, and cryptodires just outside eucryptodires such as baenids, pleurosternids, *Kallokibotion,* and pleurodires, provides strong evidence that the sutured condition is primitive for eucryptodires. However, *Kayentachelys* seems to have an intermediate condition with sutured and large digitate contacts. *Proganochelys,* at least the completely ossified (i.e., presumed adult) SMNS 17204, has a sutured contact, but there are some digitate processes. The most serious conflict with choosing the sutured condition as primitive, however, is the fact that during development nearly all turtle plastra pass through a stage where the hypoplastra and hyoplastra have strong digitate processes and the carapace/plastron contact is by connective tissue. However, in most cases in development, the carapace and plastron are widely separated and differ from the condition in sinemydids, *Xinjiangchelys,* and *Meiolania.* At present, then, it seems best to choose the ligamentous condition as derived.

Homoplasy: In this analysis, this character has a consistency index of 0.5 with the reversal to a sutured shell a synapomorphy for Chelomacryptodira (taxon 33). However, there is evidence that within some groups this character is homoplastic. Within Trionychoidea the ligamentous condition would need to be evolved at least once, and within plesiochelyids both the sutured and ligamentous conditions exist.

Discussion: Although the carapace of *Meiolania platyceps* appears to be higher domed than in sinemydids and other primitive cryptodires, it has a relatively loose articulation with the plastron. AM F:1208 (fig. 31) and AM F:49141 both show very thin bone and fontanelles along the contact with the axillary and inguinal buttresses forming digitate processes. The *Meiolania* condition is not identical to *Xinjiangchelys* or sinemydids but they are all similar and lack a strongly sutured contact.

Other discussion of this character is in Brinkman and Peng (1993a).

36. Supramarginal scales: present = 0; absent = 1.

Morphology: The derived condition of Polycryptodira can be seen in Boulenger (1889) and the primitive condition in *Proganochelys* and *Proterochersis* is figured in Gaffney (1990).

Primitive condition: Proganochelys has the presumed primitive condition for turtles.

Homoplasy: Although the present analysis shows a consistency index for this character of 1.0, supramarginal scales are also lost within the Pleurodira, according to Gaffney et al. (1991) and Gaffney and Meylan (1988).

Discussion: The scale markings of the carapace in *Meiolania* are hard to see but there is no evidence that supramarginal scales were present. The precise positions of pleural/marginal contacts are unclear, but distal ends of costals show no markings interpretable as supramarginals.

37. Dorsal process on epiplastron: present = 0; absent = 1.

Morphology: The dorsal process of the epiplastron in *Proganochelys* (Gaffney, 1990) is a large extension, similar to the one found in *Proterochersis.* In a number of other cryptodires there is also a distinct process, but it is much smaller although it does rise above the level of the plastron. *Pleurosternon* has a small, low bump that is probably homologous to the process in the other forms but it does not rise above the level of the plastron to the extent seen in *Kayentachelys. Kallokibotion* and *Ordosemys* also have a similar process.

Primitive condition: The presence of the epiplastral process is primitive for turtles based on comparison to other tetrapods (Gaffney, 1990).

Homoplasy: With a CI of 0.25, this process has been lost many times, if we are looking at real homologies.

Discussion: Meiolania platyceps has a midline dorsal process formed by the epiplastra. The process bifurcates dorsally in some specimens but it bears little resemblance to the paired processes seen in *Kayentachelys* or even *Pleurosternon.* Nonetheless, I have considered it to be present in all of these taxa as well as *Meiolania.* If the analysis is run with the character dropped, the same shortest tree is the result.

38. Entoplastron separating epiplastra: yes = 0; no = 1.

Morphology: The primitive condition can be seen in *Proganochelys* and *Proterochersis* (Gaffney, 1990) and *Kayentachelys* (Gaffney et al., 1987). The advanced condition is found in all living turtles (Boulenger, 1889).

Primitive condition: The primitive condition is based on *Proganochelys* (Gaffney, 1990, see for discussion).

Homoplasy: None known, the CI is 1.0.

Discussion: Meiolania platyceps has an entoplastron that comes close to separating the epiplastra in ventral view (at least in the few specimens with sutures). On the dorsal surface, however, the epiplastra contact broadly.

39. Epiplastron: broad = 0; narrow = 1.

Morphology: The narrow epiplastron seen in Recent chelydrids and chelonioids and the broad epiplastron of testudinoids are figured in Boulenger (1889). *Adocus* (Meylan and Gaffney, 1989) has the primitive trionychoid broad epiplastron. Sinemydids (see Brinkman and Peng, 1993a, 1993b, for references) have the narrow condition.

Primitive condition: The broad epiplastron seen in *Proganochelys, Kayentachelys,* and through the early cryptodires to *Xinjiangchelys,* is clearly the primitive condition.

Homoplasy: The consistency index for this character is 0.5, reflecting the reversal required for the broad epiplastron condition in primitive chelomacryptodires like *Adocus,* appears very similar to the broad epiplastron of primitive cryptodires like *Xinjiangchelys* and pleurosternids, giving no support to the secondary evolution of this character required by the preferred cladogram.

Discussion: The epiplastron in *Meiolania* is clearly broad on its anterior margin, in contrast to the narrow anterior margin of sinemydids, chelydrids, and chelonioids. However, the broad condition usually is associated with a short, transverse suture between the epiplastron and the hyoplastron as in plesiochelyids and baenids. *Meiolania* has a long, posterolaterally trending process of the epiplastron similar to that in macrobaenids and chelydrids. However, *Proganochelys* also has a broad epiplastron with a posterolateral process as in *Meiolania,* so the significance of this feature is unclear.

40. Loss of plastral scale set 2 (gulars or extragulars): full set of scales 1 and 2 (gular, extragular fide Hutchison and Bramble, 1981; equal to intergular, gular of older terminology) = 0; one set of scales absent (scale set 2 of Hutchison and Bramble, 1981) = 1.

Morphology: Figures of plastral scales and extensive discussion of homology can be found in Hutchison and Bramble (1981). For sinemydids see literature referred to in Brinkman and Peng (1993a, 1993b).

Primitive condition: Following Hutchison and Bramble (1981) the primitive condition of two pairs of scales on the anterior edge of the plastron is primitive for cryptodires. This is substantiated by the condition in *Kayentachelys* and *Kallokibotion.*

Homoplasy: The relatively simple morphology of scale loss makes rigorous homology assessments difficult. In the preferred cladogram the derived condition would have to have evolved twice because primitive trionychoids, such as *Adocus* (Meylan and Gaffney, 1989), have the full set of anterior plastral scales, but more advanced trionychoids lack at least one set. The CI is 0.5.

Discussion: This character has a similar distribution to the preceding character, the narrow epiplastron, and may be related to it morphologically. Nonetheless, they are treated here as two characters because their distributions are not identical.

Meiolania platyceps clearly has the primitive condition of a full set of two pairs of anterior plastral scales. The pattern is similar to other primitive eucryptodires like *Xinjiangchelys.*

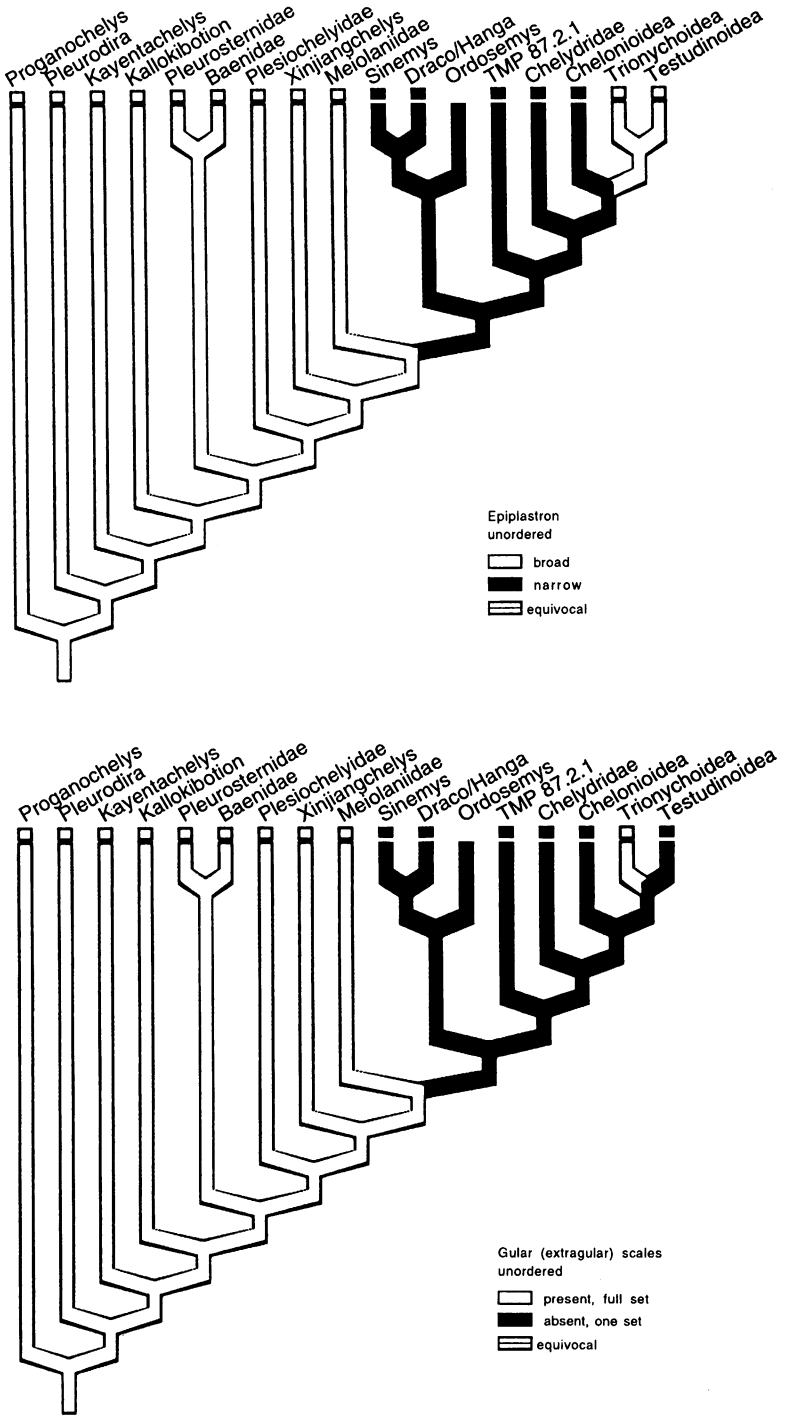


Fig. 113. Distribution of characters **39** and **40** on the preferred cladogram.

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