

THE CRANIAL MORPHOLOGY OF  
THE EXTINCT HORNED TURTLE,  
*MEIOLANIA PLATYCEPS*, FROM  
THE PLEISTOCENE OF  
LORD HOWE ISLAND,  
AUSTRALIA

EUGENE S. GAFFNEY

BULLETIN  
OF THE  
AMERICAN MUSEUM OF NATURAL HISTORY  
VOLUME 175 : ARTICLE 4                      NEW YORK : 1983







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Volume 175, article 4, pages 361–480, figures 1–65, tables 1–3

Issued November 30, 1983

Price: \$8.50 a copy



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## ABSTRACT

*Meiolania platyceps* is the best known of the extinct horned turtles of the Southern Hemisphere. Five skulls and hundreds of cranial elements have been collected from Pleistocene rocks on Lord Howe Island, New South Wales, over the past 100 years. The skull of *Meiolania platyceps* has the following features of the family Meiolaniidae: (1) Squamosal and supraoccipital produced into large posteriorly and posterolaterally directed processes that extend clear of the skull roof; (2) Medial plate of pterygoid separated ventrally from

basisphenoid to form intrapterygoid slit. *Meiolania platyceps* can be identified as Cryptodira on the possession of: (1) A processus trochlearis oticum on the anterior edge of the otic chamber; (2) A pterygoid that extends posteriorly between quadrate and braincase; (3) A descending process of the prefrontal that meets the vomer ventromedially. Within the Cryptodira, *Meiolania platyceps* can be identified as Eucryptodira based on the posterior position of the foramen posterius canalis carotici interni.

## INTRODUCTION

The extinct meiolaniid turtles of the Southern Hemisphere are probably the most fascinating and enigmatic of the chelonians. Their appearance (fig. 1) is bizarre, with cranial horns and frills and a tail club, and their relationships have been the subject of controversy for a century. They have been considered to be lizards (Owen, 1881), cryptodires (Huxley, 1887; Baur, 1889a, 1889b), pleurodires (Boulenger, 1887) and survivors of a supposedly ancestral turtle group, the "Amphichelydia" (Anderson, 1925; Simpson, 1938). They have features (for example a tail club, and cervical ribs) found in the earliest turtles and a geographic distribution consistent with a Southern Hemisphere continent, Gondwanaland. Phylogenetic studies of meiolaniids, however, have been hampered by a paucity of morphologic information, known skulls usually lack sutures, and articulated postcranial material is rare. As part of an extensive study of the meiolaniids it is my intention in this paper to describe the cranial morphology of one species, *Meiolania platyceps*. This species is the best known member of the family, with hundreds of specimens, including a number of complete skulls available for this study, which will serve as a basis for further comparative work using the remaining meiolaniid material. *Meiolania platyceps* is found on Lord Howe Island (fig. 2), a small volcanic remnant about 630 km. east of the Australian mainland, that has Pleistocene dune and shoreline deposits containing the extinct turtle. Although there is a brief discussion of the phylogenetic significance of characters in *Meiolania platyceps*,

the main treatment of meiolaniid phylogeny must await publication of the papers on *Meiolania platyceps* postcranial morphology and the studies of the Triassic turtles, all of which are presently under way. I also include a brief summary of Lord Howe Island geology as it pertains to the occurrence of *Meiolania* fossils, a history of the discovery of *Meiolania* on Lord Howe Island, and a review of previous scientific work on meiolaniids. Lists of all specimens of *Meiolania platyceps* known to me are added to the end of the present paper.

My intentions are to deal with the entire group of meiolaniids, including the South American, mainland Australian, and New Caledonian forms, in a future paper. Until then references to those forms can be found in Gaffney (1981). I have already come to some systematic conclusions regarding these taxa, although the arguments will be developed later. I think that *Meiolania* is a good genus, but I would restrict it to the Lord Howe species, *platyceps*, and the Walpole Island species, *mackayi*. The Queensland skull, usually referred to as *Meiolania oweni*, I would refer to its own genus, because few characters support monophyly of a group containing only *oweni*, *platyceps*, and *mackayi*. For the purposes of this paper, I have used quotation marks when referring to "*Meiolania*" *oweni* until such time as a new generic assignment is made.

During the 1980 field season on Lord Howe Island, a combined Australian Museum-American Museum of Natural History expedition collected new *Meiolania platyceps*



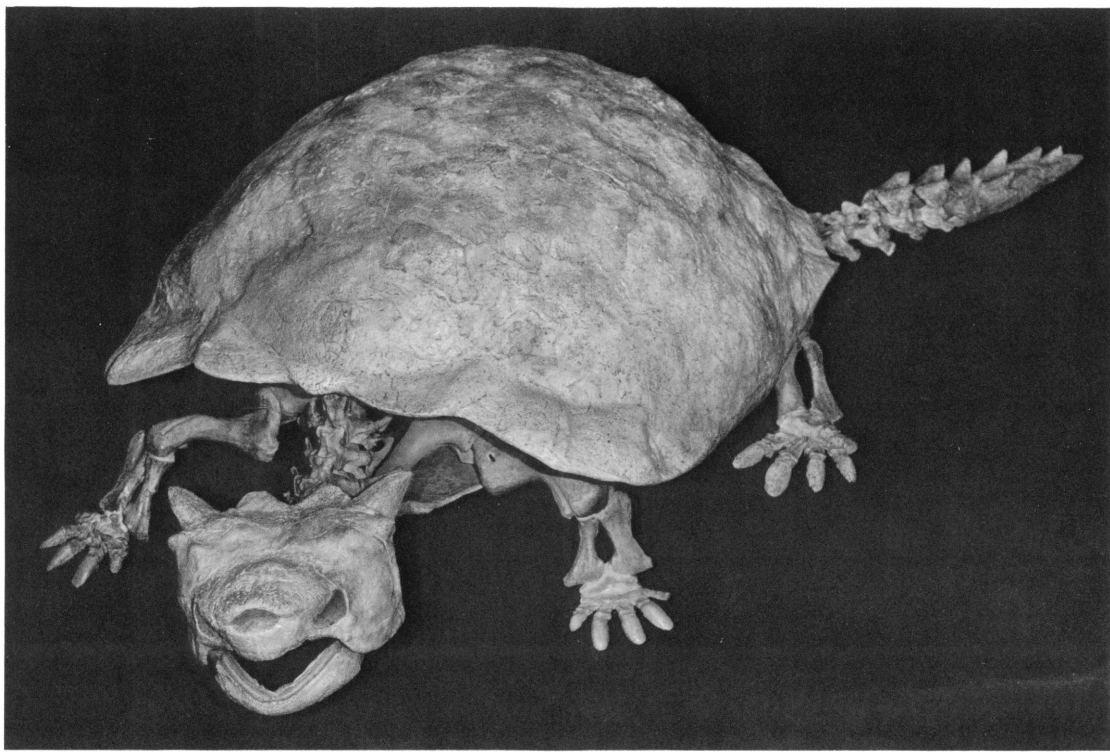


FIG. 1. Reconstructed skeleton of *Meiolania platyceps*, from Pleistocene calcarenites of Lord Howe Island, New South Wales. About 60 percent of the skeleton consists of AM F:57984, found in excavation for Ocean View Guest House swimming pool (fig. 15) with remaining areas restored from other specimens. Skull is illustrated in figures 21 and 22. See Burke, Anderson, Weld, and Gaffney, 1983.

material, including a nearly complete skull and numerous cranial elements. Unfortunately, due to shipping delays and time-consuming preparation, I am unable to include much information from these specimens in the present paper. I plan to write a separate paper on this material and on a sectioned braincase of *Meiolania platyceps*.

I assume that the reader has some familiarity with my earlier (Gaffney, 1979) review of turtle skull morphology and has access to that paper for comparison with the *Meiolania platyceps* figures presented here.

#### ACKNOWLEDGMENTS

I am particularly grateful to the Australian Museum in Sydney, New South Wales, for awarding me a Visiting Curatorship in 1980, which enabled me to spend a considerable amount of time studying their collection of

*Meiolania platyceps*, the largest in the world. The Australian Museum also supported travel to other Australian museums that have meiolaniid material, and, in cooperation with the American Museum of Natural History, the Explorers' Club, and Columbia University, supported fieldwork on Lord Howe Island in 1980. Dr. Alex Ritchie, Mr. Bob Jones, and Miss Dorothy Jones of the Australian Museum considerably aided my work on *Meiolania*. I am indebted to Dr. John Pickett of the Mining and Geological Museum in Sydney for repeatedly helping me with *Meiolania* specimens in his care. Dr. Angela Milner, Mr. Cyril Walker, and Ms. Sandra Chapman deserve thanks for helping me with the British Museum (Natural History) collection.

The American Museum of Natural History contingent of the June 1980 expedition to Lord Howe Island consisted of Dr. Barbara



FIG. 2. Lord Howe Island, New South Wales. View looking south across lagoon. Outcrops in foreground are the Pleistocene Ned's Beach Calcarene showing high angle cross-beds which are interpreted as wind-blown dune deposits. Mt. Lidgbird on left (777 m.) and Mt. Gower on right (875 m.) form southern portion of island. Mountains consist of Mt. Lidgbird Basalt, interpreted by McDougall, Embleton, and Stone (1981) as lava flows infilling a large caldera formed by collapse of a shield volcano in the late Miocene. Photo by Barghoorn, June 1980.

Gaffney, Ms. Karen Gaffney, Dr. Steven Barghoorn, Mr. Paul Sereno, and myself. The Australian Museum personnel were Dr. Alex Ritchie and Mr. Bob Jones. Various other people aided us for shorter periods of time, in particular Drs. Thomas and Patricia Rich of the National Museum of Victoria and Monash University, Dr. Charles Phipps of Sydney University, and Mr. Ed Wilson, then of the Australian Museum.

In July 1982 the American Museum of Natural History returned to Lord Howe Island with the following field crew: Dr. Barbara Gaffney, Ms. Karen Gaffney, Ms. Ann Burke, Dr. Steven Barghoorn, and myself. Although the rewards did not always seem to be consistent with the amount of hard and tedious labor accomplished by these people often under trying circumstances, it is clear to me that they made a significant contri-

bution to an understanding of *Meiolania platyceps*.

During both field seasons we were aided, often to a great extent, by the residents of Lord Howe Island, particularly Messrs. Ian Hutton, Les King, Ron Peyton, Hans Rueckert, Mrs. Ilma Sainsbury, the late Robert Spencer, and Mrs. Carole Williamson. Mrs. Sainsbury followed a family tradition, her father, Reginald Hines and her grandfather, William Nichols, were both notable *Meiolania* hunters. Special thanks to Mr. James Dorman, Curator of the Lord Howe Island Museum, who gave us access to the museum facilities and encouragement over a glass of beer.

The quality of the figures is due to the talent and attentiveness of Ms. Lorraine Meeker and Mr. Chester Tarka, both of whom spent many hours over the past six years working on these



figures. The shaded drawings (figs. 32 to 37) of Mr. Tarka and the stipple drawings (figs. 45 to 47) of Ms. Meeker represent the acme of scientific illustration.

I commend Drs. S. B. McDowell, Rutgers University, and George Zug, National Museum of Natural History, Smithsonian Institution, for their careful reading of the manuscript. I appreciate the time they spent on it.

The paper was supported in part by NSF grant DEB8002885.

### ABBREVIATIONS

#### INSTITUTIONAL:

AM, Australian Museum, Sydney  
AMNH, American Museum of Natural History, New York  
BMNH, British Museum (Natural History), London  
MM, Mining and Geological Museum, Sydney

#### ANATOMICAL:

am, area articularis mandibularis  
ane, apertura narium externa  
ang, angular  
ani, apertura narium interna  
ap, antrum postoticum  
art, articular  
ast, aditus canalis stapedio-temporalis  
bc, basis columellae  
bo, basioccipital  
bs, basisphenoid  
btb, basis tuberculi basalis  
ca, columella auris  
cai, canalis alveolaris inferior  
caj, cavum acustico jugulare  
cas, canalis alveolaris superior  
cc, canalis cavernosus  
cci, canalis caroticus internus  
ccl, canalis caroticus lateralis  
ccm, canalis cartilaginis meckelii  
ccp, canalis carotico-pharyngealis  
ccr, cavum cranii  
cdb, crista dorsalis basioccipitalis  
cio, canalis infraorbitalis  
cip, canalis intrapalatinus  
cl, cavum labyrinthicum  
cm, condylus mandibularis  
cna, canalis nervi abducentis  
cnf, canalis nervi facialis  
cnv, canalis nervi vidiani  
co, condylus occipitalis  
cor, coronoid  
cp, crista pterygoidea  
cs, crista supraoccipitalis

csa, canalis semicircularis anterior  
csh, canalis semicircularis horizontalis  
csp, canalis semicircularis posterior  
cst, canalis stapedio-temporalis  
ct, cavum tympani  
ctm, canalis chorda tympani mandibularis  
ctq, canalis chorda tympani quadrati  
ctr, cartilago transiliens  
den, dentary  
ds, dorsum sellae  
epi, epipterygoid  
ex, exoccipital  
faa, foramen arteriae anteriovidianae  
faci, foramen anterius canalis carotici interni  
fact, foramen anterius chorda tympani  
fae, foramen arteriaevidianae  
faf, fossa acustico-facialis  
fai, foramen alveolare inferius  
fas, foramen alveolare superius  
fav, foramen aqueducti vestibuli  
fc, foramen cavernosum  
fcb, foramen caroticum basisphenoidale  
fce, fossa cartilaginis epipterygoidei  
fcl, foramen caroticum laterale  
fcp, foramen carotico-pharyngeale  
fcti, foramen chorda tympani inferius  
fcts, foramen chorda tympani superius  
fd, foramen dentofaciale majus  
fe, fissura ethmoidalis  
fi, foramen intermaxillaris  
fib, foramen intermandibularis oralis  
fic, foramen intermandibularis caudalis  
fim, foramen intermandibularis medius  
fio, foramen interorbitale  
fja, foramen jugulare anterius  
fjp, foramen jugulare posterius  
fm, foramen magnum  
fmk, fossa meckelii  
fn, fossa nasalis  
fna, foramen nervi auriculotemporalis  
fnv, foramen nervi vidiani  
fo, fenestra ovalis  
fon, foramen orbito-nasale  
for, fossa orbitalis  
fp, foramen praepalatinum  
fpa, foramen palatinum accessorium  
fpci, foramen posterius canalis carotici interni  
fpct, foramen posterius chorda tympani  
fpe, fenestra perilymphatica  
fpn, foramen pro ramo nervi vidiani  
fpo, fenestra postotica  
fpp, foramen palatinum posterius  
fr, frontal  
fs, fenestra subtemporalis  
fsm, foramen supramaxillare  
fso, foramen supraorbitale  
fst, foramen stapedio-temporale  
fti, fossa temporalis inferior

fts, fossa temporalis superior  
 ha, hiatus acusticus  
 hp, hiatus postlagenum  
 ica, incisura columellae auri  
 is, intrapterygoid slit  
 IXe, foramen externum nervi glossopharyngei  
 IXi, foramen internum nervi glossopharyngei  
 IXm, foramen medialis nervi glossopharyngei  
 ju, jugal  
 la, lacrimal  
 mc, meatus choanae  
 mx, maxilla  
 ns, nasomaxillary sinus  
 op, opisthotic  
 pa, parietal  
 pal, palatine  
 pas, processus articularis  
 pc, processus coronoideus  
 pf, prefrontal  
 pfr, postfrontal  
 pe, processus epipterygoideus  
 pi, processus interfenestralis  
 pip, processus inferior parietalis  
 pl, processus clinoides  
 pm, premaxilla  
 po, postorbital  
 pp, processus paroccipitalis  
 ppe, processus pterygoideus externus  
 pr, prootic

pra, prearticular  
 pt, pterygoid  
 pto, processus trochlearis oticum  
 ptp, processus trochlearis pterygoidei  
 qj, quadratojugal  
 qu, quadrate  
 rb, rostrum basisphenoidale  
 rlo, recessus labyrinthicus opisthoticus  
 rlp, recessus labyrinthicus prooticus  
 rls, recessus labyrinthicus supraoccipitalis  
 rst, recessus scalae tympani  
 sc, sulcus cavernosus  
 scm, sulcus cartilaginis meckelii  
 sf, sulcus olfactorius  
 sl, sella turcica  
 sm, septomaxilla  
 so, supraoccipital  
 sp, splenial  
 sq, squamosal  
 st, supratemporal  
 sur, surangular  
 sv, sulcus vomeri  
 tb, tuberculum basioccipitale  
 V, foramen nervi trigemini  
 VI, foramen nervi abducentis  
 VII, foramen nervi facialis  
 VIII, foramen nervi acustici  
 vo, vomer  
 XII, foramen nervi hypoglossi

## A BRIEF REVIEW OF LORD HOWE ISLAND GEOLOGY WITH EMPHASIS ON *MEIOLANIA*-BEARING ROCKS

R. D. Fitzgerald (in Hill, 1870) was apparently the first trained geologist to examine Lord Howe Island but he wrote only three short paragraphs summarizing his observations. He accurately noticed the two primary divisions "coral and trap" and the red clay horizons. Regarding the age of the "coral" he had the "feeling . . . that it is comparatively of very recent origin" (Hill, 1870).

Wilkinson (in Wilson, 1882) gave a brief description of rock units but produced the first geological map of Lord Howe Island, a map (repeated in Etheridge, 1889b) that was not superseded until Standard's work of 1963. Etheridge (1889b) was the first relatively comprehensive description of Lord Howe Island geology. He described the volcanic rocks (including a petrologic addendum by Edgeworth David), recognized the "red clay bed" and described the "coral-sand rock Series." Etheridge astutely concluded that most of the

"coral-sand rock Series" was of eolian origin, but he was puzzled by the high-angle cross beds, not realizing that they were the normal angle for dune laminations.

Although various workers, such as Anderson (1925) made reference to geologic features of Lord Howe Island over the succeeding decades, there were no substantive studies of the island's geology until 1963. In that year Standard published a new geologic map and description of the island, but his study was relatively brief and in some ways not improved over that of Etheridge (1889b). Etheridge (and David in Etheridge) suggested that the Mt. Lidgbird-Mt. Gower basalts were younger than the more northern volcanic rocks which they thought had been tilted (more recent studies identify the tilted rocks as intrusive dike swarms). Standard (1963, p. 110), however, described calcarenite lying on the northern volcanics as "tilted and bro-

ken" thereby giving evidence of relatively recent volcanic activity. We are not aware of any signs of vulcanism in the calcarenites and later workers (Game, 1970; McDougall, Embleton, and Stone, 1981) have concluded that the northern volcanics are older than the Lidgbird–Gower basalts. Standard named the Ned's Beach Calcarenite and gave some descriptions of its distribution but a comprehensive study of the sedimentology and stratigraphy of the calcarenite is still lacking. A program under way by C. V. G. Phipps of Sydney University should correct this deficiency (see Phipps, 1981). Also, in 1963, a short paper by Squires was published which is of some importance in providing the only absolute dates for the Ned's Beach Calcarenite and the first observation that *Meiolania* bones occur in sands of shallow marine origin (see below). Game (1970) studied the petrology of the Lidgbird–Gower volcanics and mapped the dike swarms on the island, but it is the recent work by McDougall, Embleton, and Stone (1981) that has finally provided absolute dating for the volcanics and a basis for discussions of the island's history.

Lord Howe Island is the emergent portion of a volcanic seamount that lies on the western edge of the Lord Howe Rise, a northwest–southeast trending, submarine plateau, about 2000 km. long and 300 km. wide. The rise is formed from crustal continental rocks that were apparently separated from the eastern margin of the Australian plate during the Maestrichtian, when the Tasman Sea formed (Hayes and Ringis, 1973). The particular region of the Lord Howe Rise near Lord Howe Island is complicated by the presence of the Lord Howe Basin and the Dampier Ridge which lies to the west of Lord Howe Island itself (Willcox et al., 1980). Lord Howe Island and Balls Pyramid lie on a large, nearly truncated seamount that is the southernmost of a line of seamounts and guyots that extend north for more than 1000 km. It is hypothesized (McDougall, Embleton, and Stone, 1981) that this seamount chain was caused by the intermittent activity of a single subcrustal magma source or "hot spot" as the Australian plate moved north during the Tertiary. A similar seamount chain lies in the Tasman Sea between the Lord Howe Rise and the eastern margin of Australia. The sea-

mounts in these chains are characterized (to the extent that they are known) by a wave-truncated volcanic platform capped by biogenic calcareous deposits (Slater and Goodwin, 1973).

The recent work of McDougall, Embleton, and Stone (1981) has greatly clarified the pre-Pleistocene geologic history of Lord Howe Island and the following summary is based on their paleomagnetic and K-Ar analyses of the volcanic rocks. Lord Howe Island began about 6.9 million years ago with the eruption and buildup of a large oceanic shield volcano that grew from about 1800 m. below present sea level to 1000 m. or more above present sea level. In its later phases the summit collapsed and formed a caldera which was filled with basalt flows so prominently exposed on Mount Gower and Mount Lidgbird (fig. 2). The original volcano, now largely truncated into a seamount (see McDougall, Embleton, and Stone, 1981, fig. 2) was about 25 km. in diameter. Locally prominent breccias, tuffs, and dike swarms also show features typical of oceanic volcanoes. Paleomagnetic studies confirm the notion that Lord Howe Island has had no postvolcanic tectonism or tilting; however, subsidence or emergence cannot be ruled out.

Calcarenite (see a general text such as Friedman and Sanders, 1978, and references in it) is a rock type defined as consisting of more than 50 percent calcium carbonate grains of sand size (1 mm. to 0.062 mm. in diameter). Generally, the grains are broken down from organic skeletons; algae, foraminifera, coral, and molluscan skeletons being common sources. Calcarenite deposits formed by wind were termed eolianites by Sayles (1931) for deposits of this sort in Bermuda, but, strictly speaking, eolianites need not be composed of calcareous sediment, they need only to be deposited by wind. The Pleistocene was apparently unusual because during that period of earth history calcareous eolianites were formed along thousands of miles of coastline in the tropical and subtropical regions of the world to an unprecedented extent. Although these deposits are thought to have formed as a result of rapidly fluctuating changes in sea level and climate, there have been no studies comparing the various deposits worldwide to seek common causes.



Detailed chronologic studies of these units are rare and even the best studied Pleistocene calcarenites, the Bermudan sequence, lacks absolute dating for some prominent depositional units (Harmon, Schwarcz, and Ford, 1978). A considerable problem in the development of stratigraphic hypotheses in these rocks is that in contrast to most other sediment types the coastal calcarenites consist of depositional units (dunes, beaches, etc.) that are laterally discontinuous and often accretionary so that the most dependable tool of stratigraphy, the lateral tracing of lithologies, can only be applied for very short distances.

Although sedimentary rock on Lord Howe Island had been mentioned earlier, Wilkinson (in Wilson, 1882) was the first to present scientific analyses and a geologic map (reprinted in Etheridge, 1889b, pl. 10) of the formation. The unit was referred to by him and nearly all writers up to 1963 as the "coral-sand rock." The best described area was a large block of eolianite on Johnson's Beach that was figured in Wilson (1882, reproduced here as fig. 5), and Etheridge (1889b, pl. 7). Standard (1963) gave the unit a formal geologic name, the Ned's Beach Calcarenite, but did not specifically denote a type section, nor present a measured profile of it. It is quite obvious, however, that he picked the Ned's

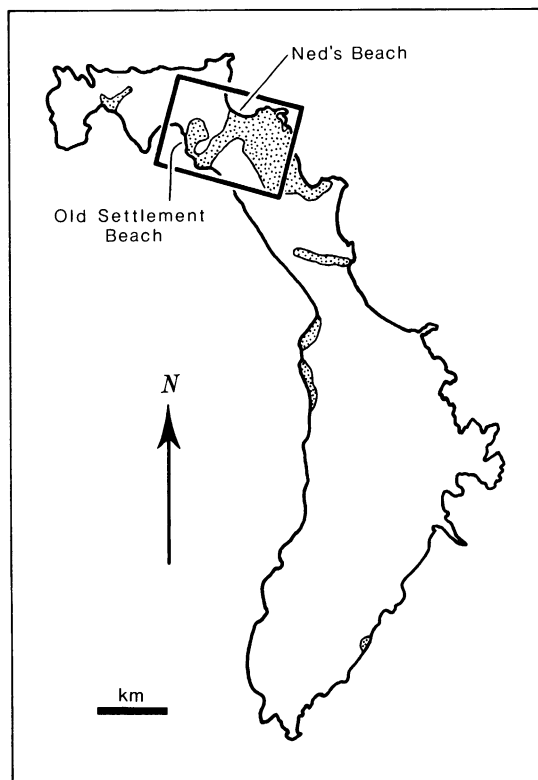


FIG. 3. Outline map of Lord Howe Island, showing the exposures of Ned's Beach Calcarenite in stipple. Rectangle delimits area shown in airphoto, figure 4.

FIG. 4. Airphoto of northern section of Lord Howe Island, New South Wales, showing more important *Meiolania* localities. See figure 3 for orientation. 1. Old Settlement Beach: a number of specimens have come from supratidal exposures along the shore, the most important one being AM F:61110, a skull (figs. 34, 35, 40, 41), carapace and partial skeleton collected by Alex Ritchie in 1977. See also figure 19. 2. "Trader Nick's": this property was owned by William Nichols (fig. 8) in the nineteenth century when he collected *Meiolania* bones for Robert Etheridge (fig. 20) of the Australian Museum. The land was subdivided among his descendants and one portion, now bearing "Trader Nick's" department store and flats, was the source of the partial skull, AM F:18668 (fig. 44), as well as hundreds of cranial and postcranial elements collected by Max Nicholls (fig. 12) and Reginald Hines (fig. 13) in the 1920s. See also figures 10, 11, and 14. 3. Ocean View Guest House swimming pool: the best *Meiolania platyceps* skeleton known to-date is AM F:57984 (fig. 1), which was found in 1971 during the swimming pool excavation. See also figure 15. No other specimens were found and once the pool was completed there were no more exposures in the immediate vicinity. 4. Ned's Beach tidal exposures: beneath the sand on Ned's Beach is a Pleistocene beach deposit containing scattered *Meiolania* and bird bones. Sand usually covers most of this deposit but in 1980 the sand was temporarily washed away and the AMNH-AM field party collected a skull (AM F:64471) and numerous other specimens here (fig. 18). 5. Ned's Beach cliff: the type exposure of Standard's (1963) Ned's Beach Calcarenite and one of the most spectacular calcarenite exposures on the island. A nearly complete skull, AM F:43183 (figs. 13, 15, 18, 19) was found here by Phyllis M. Ross in 1947 (or earlier). A nearly complete shell and skeleton (AM F:49141, lacking a skull, however) was discovered in the cliff by Elizabeth Pope in 1959 and numerous other specimens of *Meiolania* bones, eggs, and bird bones have been found here. See also figure 17. Airphoto by New South Wales Department of Lands, June 11, 1975 (NSW 2318, Misc. 923, Run 4, Frame 39).





FIG. 5. Mt. Gower (right) and Mt. Lidgbird (left) in the background with the eolianite facies of Ned's Beach Calcarenite outcropping on Johnson's Beach in the foreground. Photograph by John Sharkey, photographer of the J. B. Wilson *Thetis* expedition, from Wilson (1882).

Beach cliff exposure, the thickest exposure of calcarenite on Lord Howe Island.

The extent of calcarenite exposure on Lord Howe (fig. 3) is as follows (from north to south):

(1) A relatively small exposure on the east side of the head of North Bay extends up the slope of North Ridge to a height of at least 100 m. (McDougall, Embleton, and Stone, 1981), the highest points of calcarenite exposure on Lord Howe. A series of caves (Gooseberry, Banyon, Big Cave) are developed in the calcarenite near the contact between it and the underlying volcanics. No fossils are known from the calcarenite here but the caves have yielded bird and bat bones (McKean, 1975).

(2) The most extensive subaerial calcarenite deposit (fig. 4) begins at the base of

Malabar Hill in the north and extends to the base of Transit Hill in the south. On the east this deposit is exposed almost continuously in a line of cliffs from Ned's Beach to Middle Beach, while on the western, or lagoon side of the island, there are exposures just south of Old Settlement Beach to Signal Point, south of which the calcarenite is covered by Recent beach sands. The most settled and cultivated portion of the island lies on this calcarenite deposit. All the *Meiolania* localities are also in this part of the island.

(3) On the south side of Transit Hill and in the low area between Blinky Beach and Prince William Henry Bay are calcarenite exposures but most of the low lying ones are now covered by Recent sand dunes (and by the airstrip). Drilling for the airstrip indicates that the calcarenite extends for some depth.



FIG. 6. Same calcarenite outcrop as that in figure 5 photographed in 1980. The nearly horizontal topset beds (upper) and the high angle foreset beds (lower) of the eolianite facies are shown. The foreset beds represent the downwind slipface of a sand dune that was being deposited in the left-hand (landward) direction. Fossil bird tracks, upright tree trunk cavities, and palm leaf imprints occur in the dune deposits but fossil bone has not yet been found. Although the eolianite facies of the Ned's Beach Calcarenite is more prominent, it is the less obvious beach and near-beach deposits that yield *Meiolania* and bird bones. Photo taken by Gaffney, July 1980.

A fossil egg was found in Mr. Stan Fenton's garden near the airstrip but no *Meiolania* bones are known as yet.

(4) The southern margin of Prince William Henry Bay begins a limited series of calcarenite exposures that extend south along the flanks of the steeply rising volcanic cliffs to Kings Beach. These exposures are cut in half by the volcanics at Lovers Bay. The Johnson's Beach exposure (figs. 5, 6) are in this series. A fossil egg was found on Salmon Beach but no *Meiolania* bones have been recovered.

(5) The slopes of Mt. Lidgbird and Mt. Gower are very high angle and nearly sheer, not good places to expect sand accumulations. However, there are two large talus slopes, and one of them, Big Slope, on the southeast coast of Mt. Gower, has a calcarenite deposit overlying a volcanic talus (brought to our attention by Phipps; see also McDougall, Embleton, and Stone, 1981, fig. 3, p. 163). This exposure was reached (with

some difficulty) by Burke and Barghoorn of the 1982 AMNH expedition but no fossils were seen.

The greatest part of the Ned's Beach Calcarenite consists of calcareous eolianite, cross bedded units showing steep foresets, nearly horizontal topsets, drape-over structures, and other features of wind-deposited dunes. However, none of these eolianites have yielded *Meiolania* fossils. Instead, the *Meiolania* specimens have come from the marine and soil horizons interbedded with the eolianites. Beach deposits have been identified by Squires (1963) and Phipps (1981) at Ned's Beach underlying the thick eolianite deposit (figs. 16, 17) and red clay horizons have been known since Fitzgerald's time (see above). In places the beach deposits contain volcanic cobbles, corals, marine invertebrates, bird bones, and *Meiolania* bones, with the density of these objects varying considerably from locality to locality. The deposits with cobble-sized volcanics and invertebrate fossils seem



to be lacking in bedding but associated with them are other shoreline units showing small-scale aqueous cross bedding and large scale truncated bedding. *Meiolania* bones also occur in clay deposits that may represent washed-in soils. These deposits, apparently similar to ones described on Bermuda by Ruhe, Cady, and Gomez (1961), vary from red clay to very immature "soils of accretion" or regosols with only incipient soil horizon development and a variable eolian component. Land snails are common in some of these units and *Meiolania* bones have been found in a few of them.

Semeniuk and Johnson (1982) have described coastal beach/dune sequences in Recent and Pleistocene sediments in Western Australia that are similar to the Lord Howe calcarenite sequences. In particular their shoreface, foreshore, and backshore environments are lithologically similar to the shoreline deposits on Lord Howe Island. The sedimentology and stratigraphy of these units is not yet well enough known on Lord Howe to make more precise comparisons but the sections of Pleistocene beach to dune sequences illustrated by Semeniuk and Johnson (1982, fig. 7) appear to be similar in bedding and sequential arrangement to the section seen in Ned's Beach Cliff (fig. 17). The only mineralogic descriptions available of the Ned's Beach Calcarenite are from Standard (1963, p. 113): "The calcarenite is composed largely of fragmental detritus from *Lithothamnion* and *Halimeda* with pulverized coral, foraminifera, fragmented mollusca shells, etc. comprising only a small portion of the total composition of the rock." Unfortunately, the source rock, eolianite or marine, is not mentioned.

Bermuda is probably the most intensively studied example of Pleistocene coastal calcarenites and the many similarities between Bermuda and Lord Howe Island invite a comparison between them. (See Bretz, 1960; Harmon, Schwarcz, and Ford, 1978; Land, Mackenzie, and Gould, 1967; Mackenzie, 1964; Ruhe, Cady, and Gomez, 1961; Sayles, 1931; Vacher, 1973; Verrill, 1905, for data on Bermuda.) Bermuda and Lord Howe Island are both situated at about the same latitude (32°) in a tectonically stable region, some hundreds of kilometers from a continental

landmass. Both islands lie on truncated (or nearly truncated, in the case of Lord Howe Island) volcanic seamounts which were formed over a late Tertiary hotspot. As far as can be determined the controlling factor in sedimentation on both islands is sea level. Bermuda and Lord Howe Island have extensive calcarenite deposits consisting of variably cemented biogenic particles originally derived from marine organisms. The bulk of the sediment in both places is characterized by high-angle, cross bedded eolianites with interbedded marine and soil horizons. The marine units are intertidal shoreline deposits, whereas the soils consist of true soils of the terra rossa type and "soils of accretion" or poorly bedded sands with only incipient soil horizon development. On both islands fossil land snails are common in the soils and marine fossils occur in the beach deposits. The problems of stratigraphic analysis are common to both localities, i.e., there are no consistent lithologic or biostratigraphic parameters that allow unambiguous identification of time parallel horizons other than lateral continuity. Absolute dating is considered to be the key to unraveling the stratigraphic problems on both islands, but even in Bermuda, where absolute dating is far advanced over that of Lord Howe Island, the general absence of material suitable for dating has precluded the development of anything but a rudimentary time scale for the calcarenites.

There are, of course, important differences between Bermuda and Lord Howe Island, not the least of which is the great disparity in the quantity and extent of calcarenite. Subaerial Bermuda consists entirely of calcarenite and has an area of 7575 hectares, whereas Lord Howe Island has an area of about 1455 hectares, of which roughly 25 percent is calcarenite (about 366 hectares). The thickness of the calcarenite cover and its extent over the submerged portions of the seamounts of both islands is not well known, although on Bermuda there is good evidence that present topographic features are the result of accretionary dunes and are unrelated to the shape of the volcanic basement. On Lord Howe Island volcanic rock dominates the landscape and much of the calcarenite lies very close to volcanic exposures and its deposition presumably has been affected by volcanic topo-

graphy. Nonetheless, with the exception of the apparently thin deposits on North Ridge and Big Slope, the calcarenite deposits could be relatively thick, as indicated by the 40 m. exposures on Ned's Beach. The volcanic influence on the Lord Howe calcarenites can be seen in the volcanic cobbles present in beach deposits on Ned's Beach, Old Settlement Beach, Johnson's Beach, and Middle Beach, as well as in heavy mineral stringers in various sand laminae. Nonetheless, the strong similarities between the lithology and sedimentology of the calcarenite deposits on the two islands suggests that the same general processes may have been responsible for both. The Bermuda calcarenites have been studied more intensively and over a longer period of time than those on Lord Howe Island and it will be useful to summarize those investigations.

Sayles (1931) was the first to correlate dune-soil cycles with sea level fluctuations due to glacial control. He identified eolianites with low sea level (glacial stages) and soils with high sea level (interglacial stages) and hypothesized vast areas of the Bermudan sea mount exposed during glacial stages providing a source of sand for a succession of dunes blown across the subaerial portions. The soils would be formed during high sea level periods when the sand source was cut off. Sayles also recognized four eolianites separately by three soils and correlated the four eolianites with the four glacial stages of the Pleistocene. Subsequent workers, beginning with Bretz (1960) have developed a modified version of Sayles's general explanation by developing evidence in favor of dune formation during high sea level and soil formation during low sea level while revising Sayles's chronology to include just the late Pleistocene. The evidence for this idea of dune generation close to the beach on Bermuda is as follows:

(1) The primary source for the generation of particles found in modern coastal dunes is the beach (Fairbridge and Teichert, 1953; Bretz, 1960; Goldsmith, 1978).

(2) Lateral facies changes can be traced on three separate places in Bermuda from marine limestone to eolianites (Bretz, 1960).

(3) Bermudan eolianites have the structure of transverse dunes with long axes parallel to the coast and the direction of dune

accretion is inland. The strike and dip relations of eolianite foresets show lineation with the beach not with storms or prevailing winds (Mackenzie, 1964).

(4) Geomorphology and geochronology of the dune system of Bermuda suggests formation by accretion, with the older dunes inland of later dunes (Land, Mackenzie, and Gould, 1967).

(5) "Organisms provided the tremendous volume of carbonate detritus incorporated in the calcarenites and those organisms must have lived on the extensive submerged platform, not in a fringe around the edge of a pinnacle several hundred feet high" (Land, Mackenzie, and Gould, 1967).

(6) "The red soils, which can be traced below sea level, represent solutional unconformities developed on limestones without regard to elevation, facies or present sea level and are persistent island-wide horizons. They record periods of nondeposition and freshwater diagenesis of the underlying calcarenites" (Land, Mackenzie, and Gould, 1967).

(7) "Absolute age determinations demonstrate that deposition of rocks between red soils was nearly contemporaneous but that rock units separated by soils differ greatly in age" (Land, Mackenzie, and Gould, 1967, p. 997).

Of these points, 1 and 5 are general and apply to Lord Howe Island as well as Bermuda. Points 4 and 7 require geochronologic data not available for Lord Howe and point 6 requires subsurface information which is also unavailable for Lord Howe Island. The remaining points, 2 and 3, can be determined for Lord Howe and they agree with the situation on Bermuda. Although we have not made extensive measurements or vector analyses of eolianite foresets on Lord Howe Island, it seems clear to us that many of the eolianites, even those on the lagoon side, dip inland from the coast and fit the conditions described on Bermuda, but Lord Howe is so dominated by the volcanic topography that local wind conditions would have been modified.

We also think that on Lord Howe Island there is evidence for a facies change from beach to dune deposition, although alternative explanations are certainly possible in view of the limited sedimentologic and strati-

graphic work completed to date. Nonetheless, we think that the Old Settlement Beach *Meiolania* locality is at present best interpreted as an example of such a beach/dune facies change. In a localized area, just covered by high tide, is an apparently unbedded, or massively bedded, unit with volcanic cobbles in it indicating beach deposition. About 1 to 2 m. above this unit but exposed about 10 m. inland, is a *Meiolania*-bearing unit that can be interpreted as a backbeach/overbeach deposit which seems to grade into dunes with high-angle foresets only 10 m. or so along the present exposure. The outcrop is not perfectly continuous and the eolian deposits are not necessarily contemporaneous with the beach units but there is no evidence of a discontinuity or unconformity. The Ned's Beach Cliff exposure also has a beach unit overlain by backbeach/overbeach deposits but in this case the eolian unit possibly contemporaneous is about 15 m. northeast along the coast and separated by variously bedded calcarenites (although it is a continuous exposure).

The evidence against near beach deposition of eolianite as advocated by the model presented above is primarily the presence of eolianite deposits at a much higher elevation than beach deposits. On Lord Howe Island eolianites extend locally up the southern slope of North Ridge to an elevation of about 100 m. while known beach deposits are all within present tide range. The parallel with Bermuda still holds, however, and eolianites there are known at an elevation of 80 m. If these deposits were made during sea level stands higher than at present, we must argue that contemporaneous beaches either left no deposits or that such records have been destroyed in the interim. Modern coastal dunes are known more than 50 meters above present sea level (Bretz, 1960) and one could adopt a model with most of the eolianite originating on the beach but with some of it being blown to greater elevations due to some local wind situation.

Although absolute dates for the Lord Howe Island volcanic series provide a useful chronology for the origin and early history of the island, a similar chronology for the more recent Ned's Beach Calcarenite has not yet been constructed. The only dates available at the present time are two carbon-14 analyses pub-

lished by Squires (1963). He collected his specimens in 1959 and one of his dates was taken from a piece of coral in the marine deposit at the base of Ned's Beach Cliff "about four feet" (Squires, 1963, p. 412) below a *Meiolania* skeleton that Squires identified as having been collected by Raymond Missen. This *Meiolania* specimen is almost certainly AM F. 49141 (see History of *Meiolania* Collecting on Lord Howe Island). Unfortunately, the coral sample was older than maximum age determinable using carbon-14 (greater than 38,500 years in Squires's paper). The other date obtained by Squires was taken from land snail shells in a soil layer at Middle Beach. This date was within the carbon-14 range and was determined to be  $20,700 \pm 700$  years. Although *Meiolania* bones have been found in a soil layer that is at about the same elevation as the Middle Beach soil and only one-half mile north of Middle Beach, efforts to trace any physical connection of the two soils have been unsuccessful. Elevations are poor indicators of contemporaneity under the calcarenite accretion model developed for Bermuda and so must be suspect for Lord Howe Island. Therefore, there are no "hard" dates for *Meiolania* specimens. The volcanics provide maximum age for the Ned's Beach Calcarenite of 6.4 million years, and considering that the present subaerial exposures of calcarenite are lying on the greatly reduced remnants of this vulcanism, it is likely that these exposures are much younger. But how much? Is any of the calcarenite Pliocene? Is it all Late Pleistocene? The possibility that some of the specimens identified in this paper as *Meiolania platyceps* are separated by one, two, or more million years cannot be excluded at the present time.

However, if we accept the model of calcarenite accretion that would have dune and beach sediments roughly contemporaneous with high water stands and soil development occurring during low water periods we can at least present the hypothesis that the Ned's Beach *Meiolania* specimens found in the beach deposit that is now intertidal were buried there the last time that sea level was the same as it is now. This would presumably have been during the last interglacial, the exact date of which is a science unto itself, but has variously been placed in the vicinity of

100,000 to 120,000 years ago. Subsequent high sea levels have come to within 20 m. or less of present sea level with a maximum lowering around 18,000 years ago (see John, 1979, and references). If Lord Howe Island has been stable tectonically over the past 200,000 or so years, then, using the above assumptions, the *Meiolania*-bearing beach deposits might be around 100,000–120,000 years old (Phipps, 1981, also seems to have suggested this age for this deposit but an apparent typographic error left his date at 12,000

years). A lot of things could be wrong with this, including the probability that earlier shoreline deposits as well as more recent ones are preserved.

In summary, *Meiolania platyceps* bones are found in shoreline and soil deposits that are probably late Pleistocene in age but may be as old as Pliocene. Etheridge (1889b, p. 112) said it all: "The general geology of Lord Howe Island is extremely simple, but the details are more complicated."

## A HISTORY OF *MEIOLANIA* COLLECTING ON LORD HOWE ISLAND

The history of *Meiolania* and the history of Lord Howe Island are tightly interwoven. The earliest records of *Meiolania* discoveries are contemporaneous with the earlier island settlements, and the past 100 years shows a pattern of interest and awareness by the islanders in their prehistoric predecessor that has often exceeded the interest shown by museum authorities.

At present there is only limited published material available on Lord Howe Island history, some of the published works are contradictory, much is anecdotal. I have relied primarily on Rabone (1940), Nicholls (1952), Finch and Finch (1967), plus primary sources indicated.

There is no evidence that Lord Howe Island was settled, or even seen by humans before it was sighted by Lieutenant Henry Lidgbird Ball on February 17, 1788, commander of the ship *Supply*. The *Supply* was on its way to support the establishment of a settlement on Norfolk Island and did not actually send men ashore on Lord Howe until March 13, 1788. Lieutenant Ball named the island for the first Sea Lord of the Admiralty and named a mountain on Lord Howe (Mt. Lidgbird) and a nearby islet (Ball's Pyramid) for himself. The following four decades saw ships of various sorts, particularly whalers, use Lord Howe for provisioning and anchorage but the first recorded attempt at permanent settlement was not until 1834.

The *Meiolania* story, however, begins in 1844 with the arrival of John Foulis, M.D.

and his family who settled in an area of the island now occupied by the guest house "Pinetrees." Foulis stayed only three years but in 1853 he contributed to a report urging the development of a penal colony on the island (because of the difficulty of gaining access to copies of this report and because it is one of the earlier descriptions of this island, I have reproduced it here as Appendix 1). His report greatly overestimates the resources of the island, saying that it could "support a population of 5,000 souls if under control . . ." (Appendix 1). One wonders what the controls might be. Nonetheless, Foulis goes on to say (*ibid.*): "The higher hills of Howe's Island are all volcanic, and in some parts form perpendicular basaltic cliffs, many hundred of feet above the level of the sea. The middle and lower parts consist of soft sandstone hills and cliffs composed of granulated coral, which seems to have been stratified under water, as the bones of turtle and sea shells are found embedded in them." Edgcombe and Bennett (1978, p. 14) say of Foulis: "It was he who sent back the first specimens of the extinct Giant Horned Turtle to the Museum." What museum is not indicated nor is the source of this information, and I have been unable to substantiate the statement by examination of records in the Australian Museum, Mining Museum, and British Museum (Nat. Hist.). There is good evidence, however, that Foulis found *Meiolania* bones, the only form of fossil turtle yet known from Lord Howe Island. Fortunately





FIG. 7. Members of the J. B. Wilson *Thetis* expedition of 1882 shown at the Commissioner's Camp near Johnson's Beach. Although the primary purpose of the trip was the investigation of administrative problems, most of the expedition members were scientists. *Meiolania* specimens were collected by this expedition and are probably housed in the Mining Museum in Sydney or the British Museum (Natural History). However, it is no longer possible to identify these specimens as such. Photograph by J. Sharkey, from Wilson (1882).

the penal colony efforts never took hold and Lord Howe Island was spared that form of economic development.

In 1869 The New South Wales Government took notice of a report that someone on Lord Howe Island had been murdered and sent the government steamer *Thetis* with P. L. Cloete, Water Police Magistrate, in charge. Cloete was accompanied by a group of scientists who produced the first scientific report (Hill, 1870) on the natural history of the island. The group consisted of Edward H. Hill (apparently without institutional affiliation at that time, who acted as editor); Charles Moore, Director of the Botanic Gardens in Sydney; his assistant, Carron; Master, collector for the Australian Museum; and Robert D. Fitzgerald, Surveyor General's Office of New South Wales. Fitzgerald is known for his work on Australian orchids but also dealt

with the geology. The trip lasted three days, during which time the murder was judged to be self-defense (see Hill, 1870; Nicholls, 1952; and Finch and Finch, 1967). In common with many of us, Fitzgerald was enchanted by Lord Howe Island and it is his informal accounts (in Hill, 1870) of trying to climb Mt. Gower, hunting goats, and finding the rare flightless rail, the Woodhen, that have been repeated in most histories of Lord Howe Island. He returned to Lord Howe in 1871 and did further botanical work. In addition to finding land snails and palm tree imprints in the "stratified coral," the 1869 *Thetis* expedition apparently found *Meiolania* bones, because Clarke (1875, p. 200) refers to them (see below) and another collection made by a Mr. Leggatt, neither of which I have been able to trace:

An expedition to Howe's Island made known

in 1869 the existence of bones of birds and turtles embedded in the beach rock of the island. Afterwards, a collection of them was sent to me by Mr. Leggatt, of Fiji. I forwarded them to Professor Owen, who informed that he was unable to determine to what they belong, owing to their imperfect state; but they undoubtedly belong to some period near to the present, as the rock is coral limestone, common to the coasts of the Pacific Islands; and that deposit also contains a *Bulimus* scarcely distinguishable from a living shell of the same genus off the Island, and eggs of Turtle also embedded as in Raine Island in the Barrier Reef.

On March 15, 1880, Fitzgerald wrote (letter in BMNH Library, Owen Correspondence) to Sir Richard Owen of the British Museum, then the world's leading expert on Australian paleontology, that he had been to Lord Howe Island twice (presumably in 1869 and 1871) in order to study the plants and birds, and that he had looked for bones but did not find any. However, someone later sent him a bone that looked "like a moa."



FIG. 8. The white-bearded gentleman, left of center, is William Nichols one of the first and most prolific collectors of *Meiolania* bones. For more than 20 years he collected and sent specimens to Robert Etheridge at the Australian Museum. Nichols lived in a house near the present location of "Trader Nick's" (figs. 11, 14), one of the primary localities for *Meiolania*. Photograph enlarged from a view of a group of islanders taken by Sharkey during the *Thetis* expedition, from Wilson (1882).

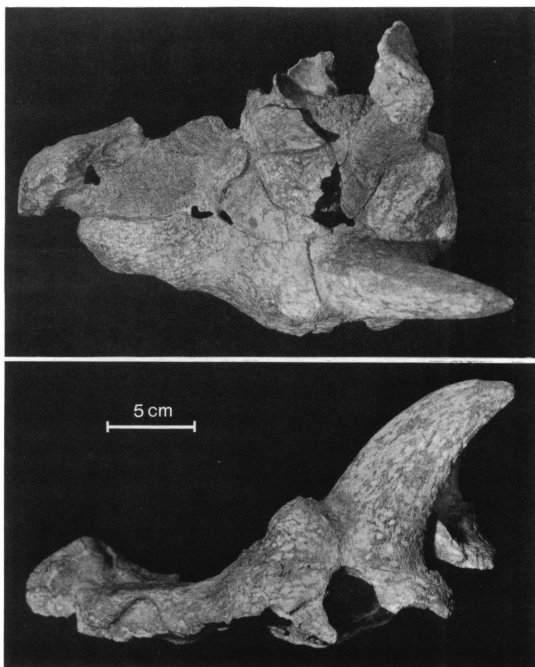


FIG. 9. Type specimen of *Meiolania platyceps* Owen, BMNH R675, figured in Owen (1886b, pl. 30, fig. 1; pl. 31, fig. 1). Upper, dorsal view of skull; lower, left lateral view of skull. This specimen obtained by Fitzgerald in 1884 was sent to Owen in 1885. It is possible that it was collected during the *Thetis* 1882 expedition.

Fitzgerald did not send the bone to Owen nor did he say where the bone was at that time. On August 9, 1880, Fitzgerald again wrote to Owen (letter in BMNH, Owen Correspondence), saying that he was sending Owen a drawing of a bone from Lord Howe Island (the drawing is lost) and that the "original of drawing" is in the Sydney Museum (which, from other Fitzgerald correspondence clearly means the Department of Mines, now the Mining Museum, in Sydney, not the Australian Museum). Unfortunately, I have not been able to identify these specimens, but they do not seem to be any of the Owen figured material now in the Mining Museum (discussed below).

Edward P. Ramsay, Curator of the Australian Museum, wrote a few pages on the Lord Howe Island fauna, primarily avian, in 1882 (but before the return of the Wilson



FIG. 10. Pit dug on Ilma Sainsbury's property adjacent to "Trader Nick's" in June 1980, showing soil overlying calcarenite. This area (loc. 2 in fig. 4) has yielded many *Meiolania* bones, particularly through the efforts of Max Nicholls and Reginald Hines in the 1920s. The calcarenite here is without apparent bedding (although the exposures that could be examined were very limited) and varies from unconsolidated sand to indurated sandstone. The work of the 1980 AMNH-AM expedition substantiated earlier reports that the bones were found in the dark brown soil layer. This soil may represent a "lag deposit" of bone that has survived weathering of the calcarenite to become concentrated in the soil layer. Photograph by Gaffney, June 1980.

*Thetis* expedition discussed below). Ramsay's paper contains the following:

Among some Geological specimens received from Mr. Berry, who has, I believe, recently returned from the Island; I found a portion of the pelvis of a Turtle, the fossil was much waterworn and encrusted with carbonate of lime, upon my making this known, further search was made by other parties and I believe other bones found, which I regret I did not see before they left the colony. I believe the bone above referred

to will prove to belong to a large sea turtle, but from the only fragment I have seen it would be very risky to draw any definite conclusions respecting its genus.

The earliest catalogued Lord Howe Island fossil turtle in the Australian Museum register is AM F. 182, found in 1888 by Robert Etheridge; there are no pre 1888 catalogued fossils from Lord Howe Island. "Mr. Berry" does not seem to have been an island resident and no further reference to him has turned up. It is possible that the bones Ramsay refers to as leaving the colony (New South Wales) could possibly mean material sent to Owen.

In 1882 the durable *Thetis* again carried a group of government officials and scientists (fig. 7) to Lord Howe Island, this time to investigate charges of mismanagement by Captain Richard Armstrong, the resident magistrate. The island population, 16 in 1853 (Foulis, 1853) and 35 in 1869 (Hill, 1870)



FIG. 11. Although the tropical beaches of Lord Howe Island did yield *Meiolania* bones, most of the AMNH-AM 1980 expedition's effort involved earth moving in backyards. This spot, adjacent to the water tanks of "Trader Nick's" store (loc. 2 in fig. 4) was identified by Ilma Sainsbury as the site of Nicholls's and Hines's excavation in the 1920s. Digging in this area in 1980 resulted in the collection of many *Meiolania* and bird bones. The 1980 AMNH-AM field crew is (from left to right): Ed Wilson, then of the Australian Museum, Robert Jones and Alex Ritchie, both of the Paleontology Department, Australian Museum; Steven Barghoorn, and Paul Sereno, both of the Department of Vertebrate Paleontology, American Museum of Natural History. Photograph by Gaffney, June 1980.

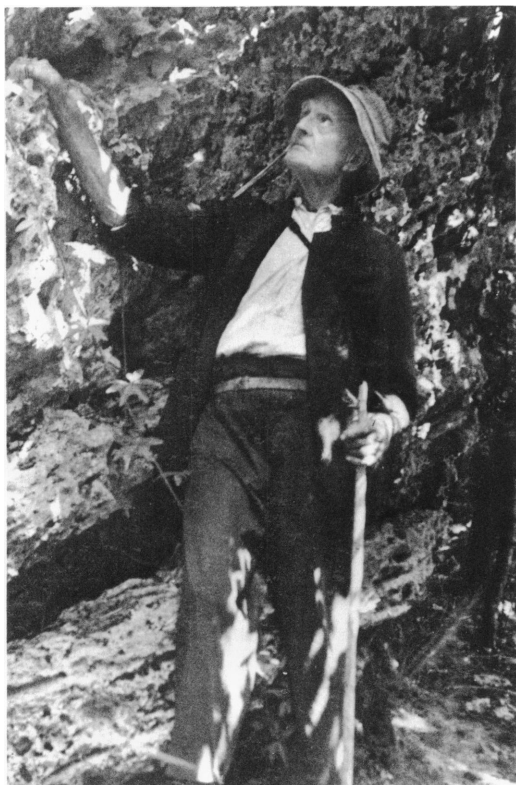


FIG. 12. Max Nicholls (unrelated to William Nichols), a Tasmanian who taught school on Lord Howe Island for many years and teamed up with Reginald Hines to sell *Meiolania* bones to the Australian Museum in the 1920s. Photograph courtesy Lord Howe Island Museum.

would grow to 61 by 1890 (Spencer, 1979), required some sort of formal administration and Armstrong was appointed in 1878. J. Bowie Wilson, appointed as Commissioner, led the 1882 *Thetis* group to investigate Armstrong. His investigations led to Armstrong's removal, but later hearings cleared Armstrong, although his petitions for redress failed (see Rabone, 1940; Nicholls, 1952; Finch and Finch, 1967, for discussions of the Armstrong affair). The scientists accompanying Wilson represented much the same institutions as the *Thetis* group of 1869 but the people were different; H. Wilkinson, Department of Mines; W. J. Conder, Superintendent of Trigonometrical Survey (Conder's trip was a preliminary one to find a location



FIG. 13. Reginald Hines, resident of Lord Howe Island, who collected *Meiolania* bones with Max Nicholls. Photo courtesy of Mrs. Ilma Sainsbury.

to observe the transit of Venus; he returned in December 1882 for that observation); J. Duff, Botanic Gardens; A. Morton, Australian Museum; and J. Sharkey, photographer, Government Printing Office. The results of the trip, along with Sharkey's excellent photographs, can be seen in Wilson (1882).

Wilkinson's contribution to the geology of Lord Howe Island includes this description of the "coral sand rock": "It consists almost entirely of fine rounded grains and comminuted fragments of corals and shells, occasionally it encloses land shells of the genus *Bulimus divaricatus*, and, when it occurs near the coast, fragments of bones, which Mr. E. P. Ramsay, Curator of the Australian Museum, has determined to be remains of turtles" (Wilson, 1882, p. 18). From this it is apparent that Wilkinson collected *Meiolania* bones in 1882, because Ramsay did not trav-





FIG. 14. Hines's residence (now site of "Trader Nick's" Department Store) as it appeared in the 1920s. Gardens and cultivated parts of this property (loc. 2 in fig. 4) have yielded more *Meiolania* specimens than any other single site on Lord Howe Island. Photo courtesy of Mrs. Ilma Sainsbury.

el to Lord Howe at this time (if ever). The disposition of this material is presumably also in the Mining Museum, but could not be located as such.

At about this time parallel developments were going on in Queensland and London that would greatly affect understanding of the Lord Howe Island fossil turtle (see Previous Work). In 1879 and 1880 a skull and tail club were found in the Pleistocene deposits of the Darling Downs in Queensland that Owen (1880) identified as a giant horned lizard, *Megalania prisca*. In Owen's defense one must say that the specimens came from a locality that had previously yielded giant lizard vertebrae and the skull was quite unlike any then known turtle (or anything else for that matter). Nonetheless, George F. Bennett, discoverer of the Queensland fossils and lifelong collaborator of Owen's thought it was a turtle, and Ramsay of the Australian Museum in 1882 had identified Wilkinson's Lord Howe Island specimens as turtles, so when Owen was sent a relatively good collection of Lord Howe fossils in 1884 he should have been at least receptive to the possibility that these were turtles and not lizards.

It is ironic that we have good published reports and narratives of expeditions that produced little or no *Meiolania* material,

while hundreds of specimens, including material destined to be types and figured specimens, seem to simply appear. On October 21, 1884, Fitzgerald wrote to Owen (letter in BMNH Library, Owen Correspondence) "I have been sent two boxes of specimens and a block of stone . . ." from an unidentified person on Lord Howe Island. The material included several horns from two inches to four inches long. Fitzgerald took his cue from Owen's *Megalania* paper (1881) and suggested that the material may belong to "possibly some large lizard . . ." Fitzgerald sent this material to the British Museum (Nat. Hist.) where it was accessioned in 1885 and described by Owen (1886b). All the British Museum *Meiolania platyceps* apparently came from this shipment of Fitzgerald's (see Lydekker, 1889, for a list), including the type skull (BMNH R675; Fig. 9).

In 1887 the New South Wales Department of Mines again sent Owen Lord Howe Island *Meiolania* material, this time from Wilkinson (Owen, 1888), but as Fitzgerald and Wilkinson worked for the same government department the significance, if any, of this distinction is not clear. It is known that the material came from Lord Howe Island but it is not known who collected it and when. In view of Fitzgerald's letters of 1880 and 1884 it is unlikely that this second collection (1887) was brought to his attention before 1885. It is apparent that some time during the mid-1880s one or more individuals were very active on Lord Howe Island making the first significant collections of *Meiolania* material amounting to hundreds of specimens. This 1887 collection (the Wilkinson material) remained the property of the Department of Mines (and is now in the Mining Museum in Sydney) and was returned by Owen after being described and cast. Included in this collection was the best known skull to that date (MM F:13825a), a nearly perfect tail club, limb bones, cervicals, and other useful material described and figured by Owen (1888).

The Australians, however, were busy at this point collecting more material from Lord Howe Island. The Australian Museum had sent Masters in 1869 and Morton in 1882 on the two *Thetis* expeditions and had main-



FIG. 15. Upper, excavation for Ocean View Guest House swimming pool (loc. 3 in fig. 4) in 1971, when a skeleton of *Meiolania platycephs* was discovered. This specimen, AM F:57984, was found in the deep end of the excavation (on right) in calcarenite that was partially unconsolidated. View is approximately toward northeast. Lower, *Meiolania platycephs*, AM F:57984, skull and anterior margin of carapace soon after discovery in the pool excavation. Specimen does not appear to be in place although it may have been returned to the spot where it was found for the photograph. In addition to the skull and jaws, large parts of the shell, cervicals, both right limbs, and other elements belonging to the specimen were found, making it the most complete *Meiolania* skeleton known to date. AM F:57984 was used as the basis of the American Museum of Natural History skeletal reconstruction (fig. 1; see also Gaffney, 1982). Both photos courtesy of Mr. James Dorman, Curator, Lord Howe Island Museum.



FIG. 16. Ned's Beach from Malabar. Numbers are the same as in figure 4, beach exposures (loc. 4) are largely covered by high tide in this view but extend from the boat jetty along the beach in the direction of the viewer for about 100 m. The Ned's Beach cliff exposures (loc. 5) are the type section of the Ned's Beach Calcareenite of Standard (1963). Photograph by Gaffney, December 1979.

tained a continued interest in the island's natural history. By 1887 that interest had become more ambitious and a group of Australian Museum scientists went to Lord Howe Island, independent of any strictly governmental purpose, in order to "investigate the general zoology, geology and palaeontology . . ." (Etheridge, 1889b). The party consisted of J. A. Thorpe, T. Whitelegge, and, most importantly for *Meiolania*, Robert Etheridge, paleontologist for the Australian Museum (fig. 20). The collections and observations of the expedition were written up in a special volume edited by Etheridge (1889b) which still stands as one of the primary scientific works on the fauna and geology of Lord Howe Island.

Etheridge contributed the first relatively detailed description of the island's geology and produced a geologic map that was the best available until Standard (1963). Etheridge collected *Meiolania* specimens and made

contacts among the islanders (particularly William Nichols) to insure that new material would continue to come to the Australian Museum. Etheridge began a research project on *Meiolania*, as noted by Ramsay (in the introduction to Etheridge, 1889b): "A description of the remains of the extinct *Meiolania* is also for the present postponed. The Museum is gradually acquiring an extensive series of its bones, and it is intended, at a future date, to issue a separate Memoir dealing with this interesting Reptile." Although Etheridge published a few notes on *Meiolania* (1889a, 1893), his projected monograph based on the Lord Howe Island material never materialized; as time went on, his interests became more ethnologic and the work on these specimens was actually done by Anderson in 1925.

During the late 1880s the Australian museum paid a collector, E. H. Saunders, to obtain various types of natural history material

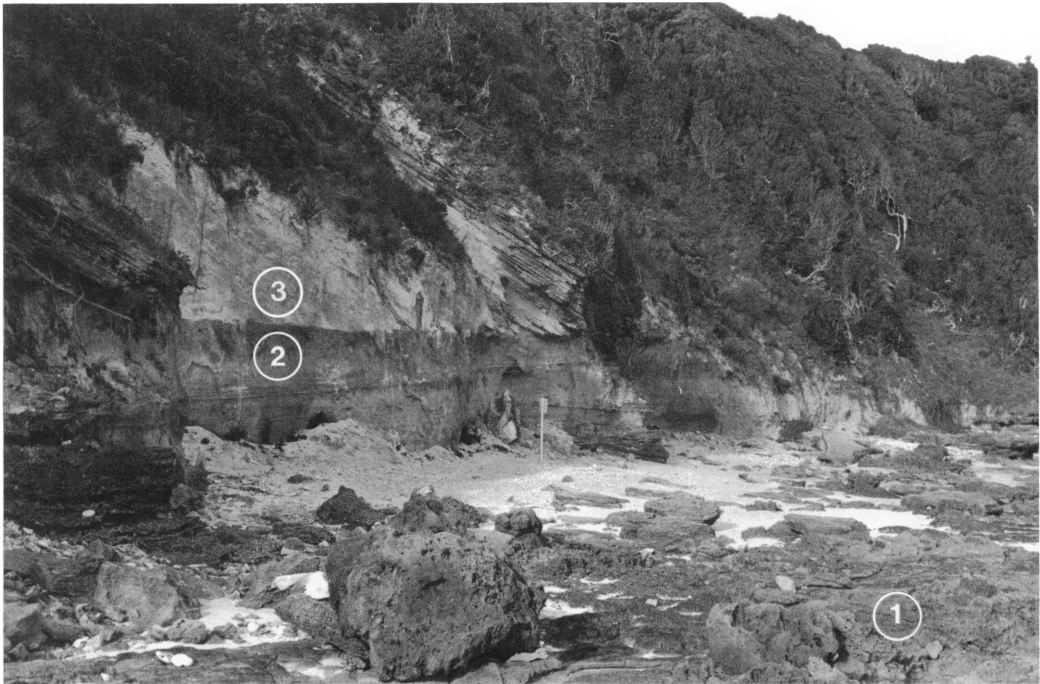


FIG. 17. Ned's Beach cliff (loc. 5 in figs. 4, 16) exposures of the Ned's Beach Calcarenite. Three depositional units can be tentatively recognized in this view: (1) A beach deposit containing marine invertebrates at this locality and volcanic cobbles and *Meiolania* bones farther west (loc. 4 in figs. 4, 16). Calcarenite talus and Recent beach sand covers much of this unit which extends vertically from low tide to above high tide. (2) Aqueous or low angle cross-bedding characterizes this unit which tentatively may be interpreted as a supratidal beach or backbeach deposit. A *Meiolania* skeleton (AM F:49141) was excavated in 1959 from this unit, about 1 m. below the contact with unit (3) just behind the signpost in the middle of the figure (the signpost is 6.5 ft. or about 2 m. in length). (3) Eolianites characterized by high angle cross-bedding produced by wind. *Meiolania* bones have not been recovered from this unit. Photograph by Gaffney, June 1980.

from Lord Howe Island (see Ramsay's introduction in Etheridge, 1889b). Among his collections (often conveyed to the museum by Captain Garth, of the schooner *Mary Ogilvie*), is a good suite of *Meiolania* bones. The following letter to Saunders shows that the practice of withholding taxes is not a recent innovation:

Sir, in reply to your request for a further advance on account of specimens received from you, I am desired by the Curator [Edward P. Ramsay] to say that the value of what has been selected for the Museum is about £ 13 - 8 - 6, from this has been deducted:

cash advanced	£ 5 - 0 - 0
paid freight	2 - 0 - 0

paid freight	2 - 16 - 0
value of stores	
supplies (not including gun)	5 - 0 - 0
Total	£ 14 - 16 - 11

So there is really no balance due to you at present. Probably, however, you will have left the Island before this reaches you[.] If it is your intention to return by the *Mary Ogilvie*, and if you have more specimens of value to the Museum accounts can be settled on your arrival. [Letter, 14 February 1888, from Sutherland Sinclair, Secretary, Australian Museum to E. H. Saunders, Lord Howe Island.]

Sir, I take the opportunity of mail leaving today to send a copy of my last letter—and to explain

what I have made quite clear in it, viz: that the specimens valued are only those that have been selected for this museum. The duplicates, which form the bulk of your collections have not been taken into account and lie here at your disposal. If you have specimens to send Dr. Ramsay will [be] pleased to receive them and to give you full value for what he selects—the balance will be taken care of for you. [Letter, 16 March 1888, from Sutherland Sinclair, Secretary, Australian Museum, to E. H. Saunders, Lord Howe Island.]

Presumably the gun was just in case he found a particularly recent specimen of *Meiolania*. Sinclair was involved in a power struggle with Ramsay at this time (see Strahan, 1979, for a fascinating history of the Australian Museum), as the positions of secretary and curator had not been clearly defined. It is possible that Saunders had the misfortune to get caught in the crossfire.

The most important single contributor to the nineteenth-century collections of *Meiolania* was William Nichols (fig. 8), a Lord Howe Island resident. Nichols, a Tasmanian, and his half-brother, Thomas, came to Lord Howe Island in 1862 (Nicholls, 1952, p. 140). William settled on land south of Old Settlement Creek, a locality that is one of the most fossiliferous on the island. The Wilson expedition of 1882 utilized William Nichol's services as guide, and he aided the Australian Museum for decades as a collector and informal agent for all sorts of natural history material from Lord Howe Island. He sold hundreds of *Meiolania* specimens to the Australian Museum and virtually doubled the number of specimens in the collection. The plastron (AM F:1208) with associated pelvis and shoulder girdle, described and figured by Anderson (1925) was obtained by Nichols and was the first sizable portion of a *Meiolania* shell ever collected. There is no locality data (other than Lord Howe Island) for Nichols's specimens but his collections contain specimens with matrix and soil indicating beach as well as inland sources. Nichols lived right on one of the *Meiolania* localities (now referred to as "Trader Nick's," see Nicholls and Hines letters, below; figs. 4, 10, 11, 14) and was very near Old Settlement Beach—Wilson's Landing, another source area. Nichols's relations with the Australian Museum curators were cordial and the following letter

gives a brief but fascinating glimpse of this *Meiolania* hunter's personality.

Dear Sirs, According promise [*sic*] I write you these few lines and [I am] sending you those things I promised to you gentlemen. I am happy to state that I arrived safe after 5 days passage, and I am almost over my complaints. The asthma is leaving me but I am still coughing badly. dear Sirs, I am sending a box containing Birdskins, shells and a few fresh nuts and 1 bundle palmplants trusting you gentlemen are all well I now conclude with best wishes and remembrance of Mrs. Nichols, Yours faithfully W. Nichols.

P.S. Please remember me to Mr. Whitelegge [then in charge of marine invertebrates, Aus-

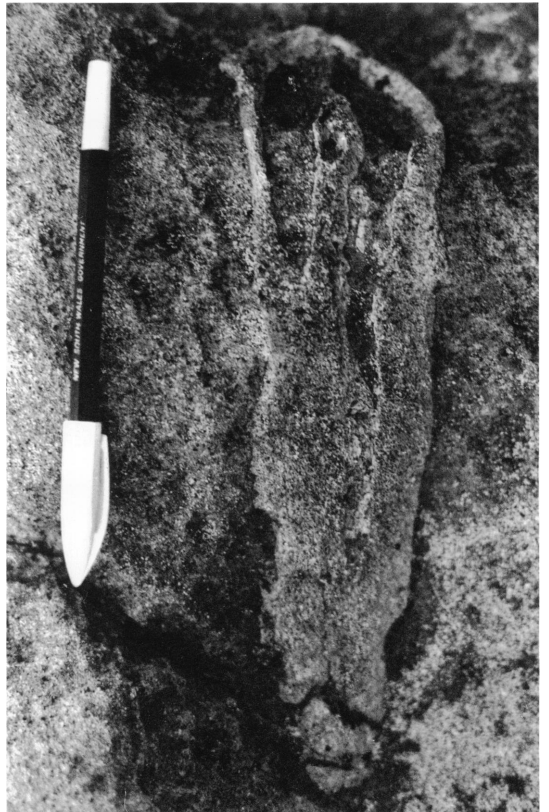


FIG. 18. Tail club of *Meiolania platyceps* (AMNH 20980), in situ before being collected in 1980 from the intertidal beach deposit at Ned's Beach locality 4 (figs. 4, 16). The calcarenite in this unit is very indurated and required a jackhammer and rock drill to collect specimens. Photograph by Gaffney, June 1980.





FIG. 19. Old Settlement Beach *Meiolania* localities. Barghoorn (left) is standing on the spot where Ritchie of the Australian Museum collected a skull and carapace of *Meiolania* (AM F:61110, figs. 14–17, 20, 21) in 1977 while the person on the right (Serenio) is standing on the spot where the AMNH–AM 1980 expedition collected a tail club (AM F:64435) and a plastron (AM F:64434) of *Meiolania*. The calcarenite at this locality is within 3 m. of high tide and has barely perceptible, roughly horizontal, bedding that appears to be comparable to unit (2) at Ned's Beach cliff (fig. 17), and may be interpreted as a supratidal beach deposit. This unit at Old Settlement Beach appears to grade into an underlying beach deposit presently exposed at low tide containing volcanic cobbles and pebbles; again apparently similar to the situation at Ned's Beach. Photograph by Gaffney, June 1980.

tralian Museum] I will always endeavor to look well after all things concerned, if any thing is wrong with the skins please let me know. I have not been able to go about much yet and my oldest son Fred met with an accident by falling from the old settlement bank with a load of palm seed he has been laid up for 14 days, but he is now getting better his leg is bad still but I trust both he and myself will soon be about again, so no more at present. W. Nichols. [Letter, 13 June 1898, from William Nichols, Lord Howe Island, to Robert Etheridge, Curator, Australian Museum; also addressed to Thorpe.]

Dear Sir, I forward you per 'Dewdrop' 2 cases containing fossils, viz: sea eggs, bonefish, stuffed birds, etc. trusting they will arrive in good condition and meet with your approval. We are I am happy to state all well trusting you and yours

are the same. Mrs. Nichols wishes to be remembered to you and joins me in wishing you a merry Christmas and happy new year. Kindly remember me to Mr. Thorpe, Mr. Whitelegge and family. I hereby conclude with best wishes from yours, Faithfully, Wm. Nichols. 19 fossil fragments [Letter, 5 November 1898, from William Nichols, Lord Howe Island, to Robert Etheridge, Curator, Australian Museum; this was received on 10 November 1898.]

In 1898 Robert Etheridge and E. R. Waite made or obtained from the residents on Lord Howe Island a collection of about two dozen *Meiolania* bones, but the period from 1906 to 1922 was one of no new *Meiolania* accessions at the Australian Museum. During that time, however, Charles Anderson, Director

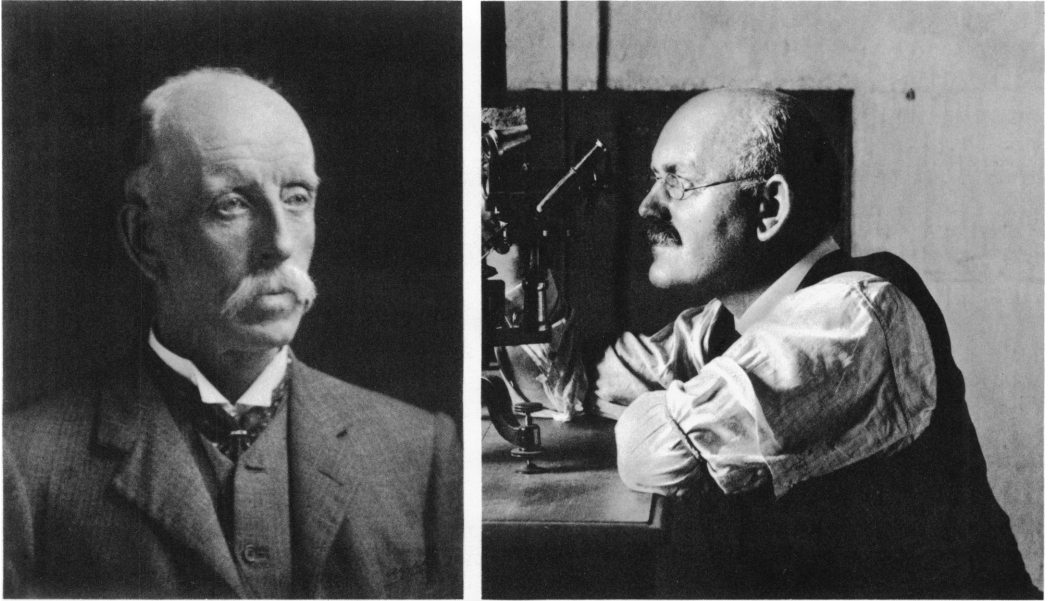


FIG. 20. Two prominent figures in the study of *Meiolania platyceps*. Left, Robert Etheridge, Curator and Paleontologist of the Australian Museum. He was instrumental in early geologic and paleontologic work on Lord Howe Island and acquired a large collection of *Meiolania platyceps* for the Australian Museum. Right, Charles Anderson, Director of the Australian Museum, described the Lord Howe Island *Meiolania platyceps* material (Anderson, 1925, 1930) even though he was primarily trained as a mineralogist. Photographs courtesy of Dr. Alex Ritchie and the Australian Museum.

of the Australian Museum, was adding *Meiolania* to his speciality of mineralogy. In 1925 his paper appeared, based on the collections accumulated by Etheridge. Anderson's paper is the most detailed and thorough study of *Meiolania platyceps* published to date and includes the description of another species of *Meiolania* (*M. mackayi*) from Walpole Island, New Caledonia.

Anderson also published in this paper the first account of the distribution of *Meiolania* fossils on Lord Howe Island and the only map published to date showing this distribution. Anderson did not visit Lord Howe, instead he obtained his information from another Australian Museum colleague, Allan R. McCulloch, an ichthyologist who was very familiar with the island. McCulloch (quoted in Anderson, 1925, p. 226) has this to say about the distribution of *Meiolania* fossils:

Disintegration of the rock, as a result of water action, accounts for the fact that outstanding portions of bones have been most commonly

found in "runs" or creek beds, but, as the bones are found equally plentifully in neighbouring rock excavated during gardening operations, it is reasonable to suppose that they are fairly evenly disposed throughout much of the rock in the area marked on the map. Other bones, particularly horn cores, are frequently found lying loose in rich patches of loamy soil, which consists of decomposed basalt, coral sand, and decayed vegetable matter. These have undoubtedly become detached from the coral-sand rock during the process of disintegration.

Based on McCulloch's report of *Meiolania* being restricted to two comparatively small areas of the exposed "coral-sand rock" (Etheridge's terminology, 1889b), Anderson suggested that this supported the idea that *Meiolania* was marine, the two localities represented nesting beaches. Although McCulloch is recorded as contributing only a few *Meiolania* specimens to the Australian Museum collections, his interest in the turtle is shown by one of his notebooks in the Lord Howe Island Museum, which contains two

*Meiolania* reconstructions as well as a few of his beautiful water colors of marine life. McCulloch loved Lord Howe and its people and evidence of their reciprocity is the 12-foot-high monument containing his ashes which was erected on a prominent headland following his suicide in 1925 (Strahan, 1979). One can only comment, at a distance of 50 years, that the islanders and his other friends were more perceptive than the president of the Australian Museum's Board of Trustees who ended his eulogy: "... Mr. McCulloch suffered from an intense devotion to his work and was a martyr to his own enthusiasm" (Anon., 1925, p. 275).

In 1922 and 1924 Reginald V. Hines (fig. 13), William Nicholls's son-in-law, sent the Australian Museum a total of about four-dozen *Meiolania* specimens, most of them having been dug out of soil from the area around Hines's property (now "Trader Nick's"). Early in 1924, a new school teacher was appointed to Lord Howe, Max Nicholls (unrelated to William Nicholls, spelled with one l instead of two ls) from Tasmania (Spencer, 1979). Nicholls (fig. 12) had a long association with Lord Howe Island and wrote the most extensive history of the island to date (Nicholls, 1952). Hines and Nicholls were both interested in *Meiolania* and teamed up to do some serious excavating. They very quickly became aware of Anderson's work and within a few months of the publication of his *Meiolania* paper the following letter was sent:

Dear Sir, I read your article on the *Meiolania* question and being interested in that sort of thing I have been doing a lot of fossicking in conjunction with Mr. Hines of this island. Our investigation resulted in the unearthing of a great quantity of bones. Many of them being quite unbroken. In a patch of ground about 10 sq. yards we found enough to 3 parts fill a kerosene box. The remains are very mixed and include 5 tail sheaths, one of them being practically perfect and about  $\frac{3}{4}$  of a skull (probably AM F:18668, fig. 44) with part of lower jaw, but horns are missing. There are also a great number of vertebrae, some 1 inch in diameter, and many others which I am unable to specify. I think if the matter was taken up and carried out methodically the question could soon be solved as there appear to be great quantities of remains about 18 in or 2 ft under the surface. Yours

faithfully, M. Nicholls, Public School, Lord Howe Is. [Letter, 14 July 1925 from Max Nicholls, Public School, Lord Howe Island, to Charles Anderson, Director, Australian Museum.]

The 10-square-yard spot referred to by Nicholls was pointed out to me by Reginald Hines's daughter, Mrs. Ilma Sainsbury, in 1979, and it is directly behind Trader Nick's water tanks (fig. 11). This area was excavated by the American Museum-Australian Museum field crew in 1980 up to the present building foundations, and although about three dozen *Meiolania* bones and hundreds of bird bones were found, there was no sign of another concentration of the sort described by Nicholls.

The actual acquisition of the material required some effort on the part of the Australian Museum's mammalogist, Ellis Troughton (see also Strahan, 1979), another scientific visitor to Lord Howe Island:

Subject—Collection of *Meiolania* bones offered for purchase by Messrs. M. Nicholls and R. V. Hines of Lord Howe Island.

While on annual leave at Lord Howe Island recently, I made an examination of a large and, apparently, valuable collection of *Meiolania* bones which were secured by the joint efforts of Mr. Max Nicholls (Public School Master) and R. V. Hines (Storekeeper) of Lord Howe. I approached Mr. Nicholls regarding the possibility of the specimens being lodged in the Australian Museum, my impression being that you had written him upon the subject and received no reply to date, whereupon he agreed to consider the matter. Subsequently I persuaded both gentlemen that our museum was the most fitting institution to receive the specimens but they were reluctant to make a definite decision, evidently desiring some payment for the specimens but in doubt as to prospective purchasers.

With a view to securing the first offer for the Museum it was agreed that I bring the specimens up on my return and I packed and consigned two cases for which a bill of lading was handed to the office on the 18 inst. In view of the heavy work of excavation entailed the vendors suggested a sum approximating to £ 12, and an absolute minimum of £ 10. I felt that the partially unique material was in danger of going elsewhere and that its acquisition would greatly enhance the present collection and therefore hope that my actions in the matter will prove entirely satisfactory. [Signed] E. Le G. T.

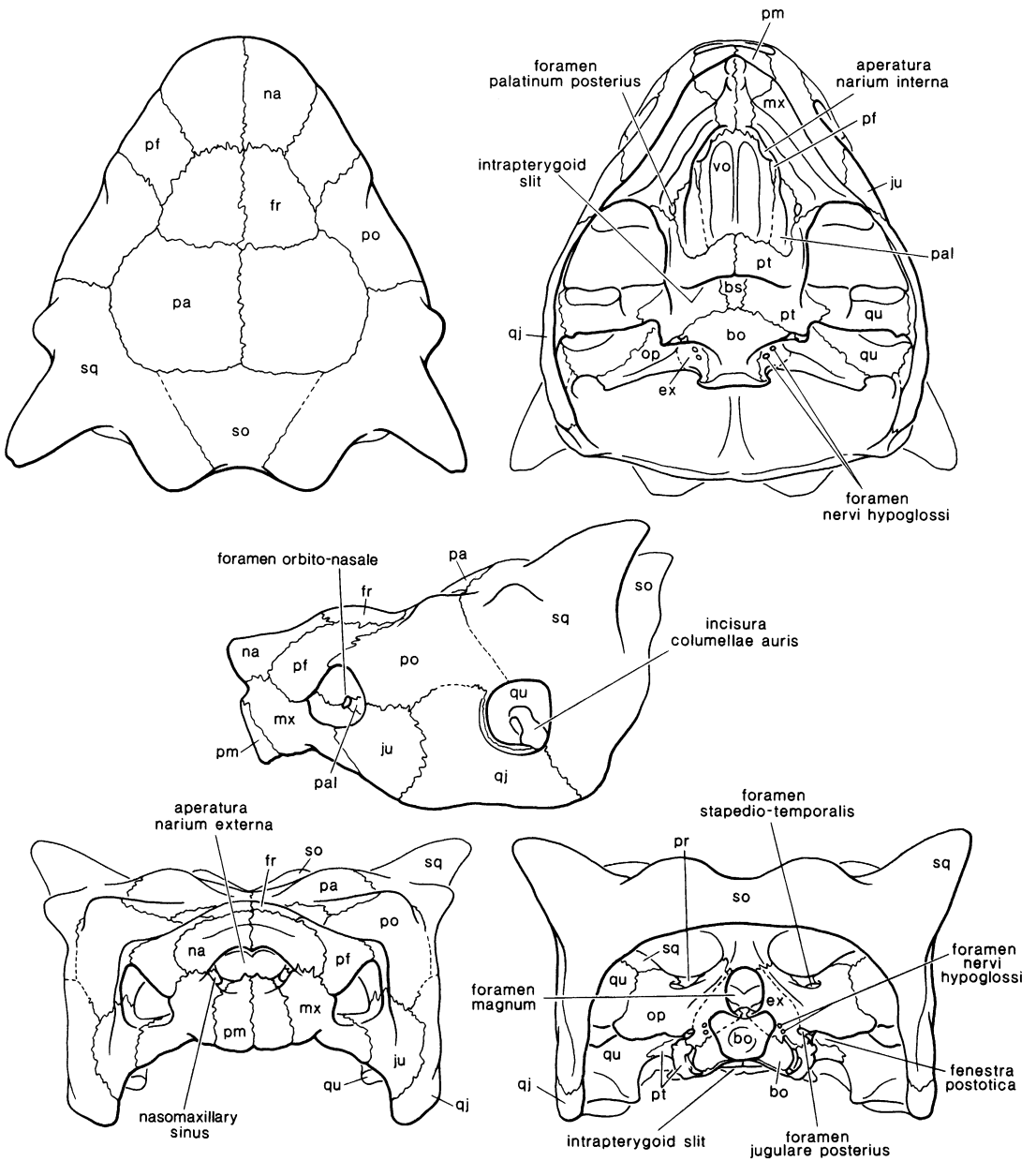


FIG. 21. *Meiolania platyceps*, AM F:57984, partially restored, with squamosal sutures from AM F.18668 and AM F:64471. See abbreviations.

[Memorandum, 20 January 1926, from E. Le G. Troughton, Curator of Mammals, Australian Museum, to Charles Anderson, Director, Australian Museum.] [The boxes were received on 25 January 1926.]

Dear Sir, on behalf of the Trustees I acknowledge your letter of the 14th instant, which has been read with interest. The recent find seems to be of some importance, and I should much like to examine the bones if you would be so



FIG. 22. *Meiolania platyceps*, AM F:57984.

good as to submit them for that purpose. After they have been inspected the question of systematic search could be considered.

I am particularly interested in the skull and lower jaw, and trust that you will send these on at any rate.

I have no doubt my Trustees would be prepared to pay expenses and also recompense yourself and Mr. Hines. Your faithfully, Director. [Letter, 22 July 1925, from Charles Anderson, Director, Australian Museum, to Max Nicholls, Public School, Lord Howe Island.]



Dear Sir, on behalf of the Trustees and following upon a letter addressed to you by the Director relating to remains of *Meiolania*, I am now directed to inform you that after examination of the specimens the Trustees are prepared to purchase the collection for the sum of £10.

I shall be glad if you will let me have early intimation of your acceptance of this offer. Yours faithfully, W. T. Wells, Secretary. [Letter, 9 March 1926, from W. T. Wells, Secretary, Australian Museum, to Max Nicholls, Public School, Lord Howe Island.]

Dear Sir, Yours to hand re offer of £10 for *Meiolania* remains. I told Mr. Troughton I would accept this amount I think, so will be pleased to accept your offer. If any more remains wanted please let me know as there is a great quantity to be got there. If Mr. Hines calls you may do business with him as he is in Co. with me, re the bones. Yours faithfully, M. Nicholls. [Letter, 3 April 1926 from Max Nicholls, Lord Howe Island, to Australian Museum.]

According to Australian Museum records Hines came and was given £10 on 23 April 1926. Although Anderson apparently wrote to Nicholls (no copy of letter available) asking for more specimens, there is no record of further transactions. The Nicholls and Hines's collection was the most important single acquisition of *Meiolania* material to that date and consisted of over 200 specimens including a skull, many braincases and skull elements, a plastron (used in the American Museum *Meiolania platyceps* reconstruction, fig. 1), and an articulated hind foot described by Anderson (1930). This hind foot was considered to be of some importance by Anderson because he felt it demolished his idea that *Meiolania* was marine (I agree) and supported the idea that *Meiolania* was terrestrial, like modern tortoises.

In his "History of Lord Howe Island" first written in 1938, with subsequent editions in 1952 and 1975, Nicholls (p. 122) said: "An almost complete head was got out of the same cliff at Ned's Beach, but the chief locality is the sandy soil near Hines' garden; as many as five tails have been got out of one hole." Troughton brought in some bones he had collected and/or been given in 1941 but the tide had changed for Hines's garden, subsequent discoveries would be comparatively spectacular, but would come from other localities.

One of the best *Meiolania platyceps* skulls known (AM F:43183) came to the Australian Museum in 1947 when the museum purchased it from Mrs. Phyllis M. Ross. Although no locality information accompanied the skull, Mrs. Ilma Sainsbury gave me a photograph of it which had inscribed on the back "Skull of extinct reptile known as '*Meiolania*.' Found in cliff at Ned's Beach. Sold to Sydney Museum for £5. Head was 10 inches long." Other details of this specimen's discovery are unknown.

It was not until 1959 when another find of any significance was recorded. It was reported in the local newspaper, the *Lord Howe Island Signal* (vol. 2, no. 8, 5 August 1959), and as I cannot improve on it, I repeat it here:

#### "Important Fossil Find at Ned's Beach"

When Mr. Ray Missen, of the Meteorological Radar Station, was jokingly challenged by Miss Elizabeth Pope, of the Australian Museum, Sydney, to show her where fossil bones of the extinct turtle, *MEIOLANIA*, could be found, Ray brought off a 'million to one' chance. On Monday, 20th July, he took Miss Pope to the north eastern end of Ned's Beach, and where the sand cliff face is bare, uncovered what is believed to be the only 'shell' or CARAPACE that has ever been found of this extinct turtle. After two days of patient and careful digging, the great importance of the find was recognized. However, shortly after some photographs had been taken to record the progress of 'the dig' the whole block of sandy rock and the fossil bones collapsed. In spite of this 'tragedy' important scientific information will result from the find. Interest in this reptilian species centres on the fact that it is believed to have been confined to fresh water when alive and its appearance on present-day isolated Lord Howe Is. points to previous land connections between the island and other parts of the world and interesting speculations arise as to how such a species could have migrated here."

This specimen, AM F:49141, has yielded articulated neck and limb bones but no skull.

In 1960 soon after the Ned's Beach discovery, Pastor Donald H. Watson, who had become interested in *Meiolania*, brought to the Australian Museum some *Meiolania* bones and a nest of eggs.

The most remarkable accidental discovery was made during excavation of the Ocean

View Guest House swimming pool in 1971 (fig. 15) by residents helping with the excavation being done under the direction of Mr. Cec Tompkins of Mutual Pools, Sydney. Mr. Alan Wilson, Ocean View proprietor of the Ocean View, saved all the fragments he could find and sent them to the Australian Museum where some were prepared in acid and all were piece-fitted together. Despite its collection by means of a jackhammer, this skeleton (AM F:57984; figs. 21, 22) is the best one known to date and is the basis of the reconstruction made at the American Museum of Natural History in 1980–1981 (fig. 1).

Because nearly all the missing parts of AM F:57984 are represented by freshly broken edges, it was hoped that more of the specimen could be found. The Australian Museum–American Museum of Natural History 1980 expedition uncovered the swimming pool backdirt heap in 1980 (with the aid of Mr. Garth Nichols and the Lord Howe Island Board backhoe). A number of residents who were present at the original excavation showed us the part of the pile where the calcarenite from the vicinity of the skeleton was dumped. Examination of this material revealed only one bone fragment, and we suspect that the missing parts may still be in the ground by the pool.

The best carapace of *Meiolania platyceps* (AM F:61110) was found on Old Settlement Beach on October 5, 1977 along with an excellent associated skull (figs. 34–37, 40, 41)

and numerous other skeletal elements. Alex Ritchie of the Australian Museum was unable to visit Lord Howe when the 1971 “swimming pool” skeleton was jackhammered into pieces, but in September 1977 when James Dorman, Curator of the Lord Howe Island Museum, informed Ritchie that bones were exposed on Ned’s Beach, Ritchie flew to the island (Ritchie, 1978). The bones turned out to be comparatively insignificant, but on October 5 Ritchie found a nearly complete carapace and skull of *Meiolania* (AM F:61110). He collected it with the help of some residents, including Hans Rueckert, proprietor of “Trader Nick’s.” Ritchie was also lucky in being able to arrange return transport for his hundreds of pounds of rock on a DC 3 that was going to Sydney.

In June 1980, a combined Australian Museum–American Museum of Natural History expedition prospected for *Meiolania* bones on Lord Howe Island by opening a number of pits in the area of “Trader Nick’s” and by collecting specimens at Ned’s Beach and Old Settlement Beach. An American Museum of Natural History expedition worked on Lord Howe in July–August 1982, and the results of both of these trips are the subject of a forthcoming paper once the specimens are fully prepared. During both trips, the emphasis was placed on making stratigraphically controlled collections as well as obtaining new specimens.

## PREVIOUS WORK ON THE MEIOLANIIDAE

The first meiolaniid skull described in the scientific literature was found in Queensland in 1879 by G. F. Bennett and sent to Sir Richard Owen in the British Museum who identified it (Owen, 1881) as an extinct horned lizard, *Megalanian prisca*. *Megalanian* is a gigantic varanid that Owen had named earlier on the basis of vertebrae and is now known to be a relatively “normal” looking varanid lizard, lacking horns or other protuberances. The Queensland material sent to Owen consisted of varanid vertebrae and a braincase, all diagnostic; as well as the partial turtle skull which did not present any overwhelmingly chelonian features. However, the skull was

edentulous, did depart strikingly from any known lizard, and was thought by its collector to be a turtle. Owen described this skull, BMNH R391, in detail in the 1881 paper and published excellent lithographs of it (Owen, 1881, pls. 37, 38), which should be referred to by the reader for comparison with the figures of *Meiolania platyceps* in this paper. In 1882 Owen published a description of a tail club (BMNH R392) of the Queensland meiolaniid but still identified it as *Megalanian prisca*, and later confused the situation further by referring footbones of the marsupial *Diprotodon* to *Megalanian* in 1886 (Owen, 1886a). Then, later in 1886, understanding

of this enigmatic turtle took a new but very significant turn with the first description of meiolaniid material from Lord Howe Island (Owen, 1886b). The significance of the Lord Howe specimens lies in the fact that over the past 100 years Queensland (as well as other localities on the Australian mainland) has yielded only a few, fragmentary meiolaniid specimens, whereas Lord Howe Island has been the source of most of the material on which knowledge of the group is based. Owen figured skulls from three individuals and erected one new genus, *Meiolania*, and two new species, *M. platyceps* and *M. minor*, for this material. Woodward later (1888) synonymized the two species and chose *M. platyceps* as the species name, actions that have been accepted by subsequent authors. Owen did not clearly identify types, use specimen numbers, or otherwise delimit material to aid future workers; so there are still some uncertainties. The name *Meiolania platyceps* appears first on page 474 of Owen (1886b), whereas *Meiolania minor* appears first on page 475; however, it is Woodward's (1888) actions as first reviser rather than page priority that have legal significance according to Article 24(a) of the *Code of Zoological Nomenclature* (1961). In any case, both conditions are in agreement. The current disposition of the *Meiolania minor* material is unclear. The specimen that was designated as the type of *Meiolania platyceps* (BMNH R675) by Lydekker (1889, p. 161) is readily identified as such in the British Museum, but the material described by Owen (1886b, pl. 29, figs. 1–6) as *Meiolania minor* has not been located. Owen refers to everything in that paper as “transmitted by the Government of New South Wales (Department of Mines) . . .” (1886b, p. 471), but I have been unable to find a close match for plate 29 in the Mining Museum, Sydney, the Australian Museum, or the British Museum (Nat. Hist.). Similarly, the anterior skull fragment identified in plate 31, figure 2 as *Meiolania platyceps* (a ventral view of the premaxilla-maxilla rather than a dorsal view of a mandible as stated in the caption) has not been located. There is no reference to this material in Lydekker (1889) and these specimens may have been returned to Australia. The right horn core (BMNH R675a, Owen, 1886b, pl. 30, fig. 2) figured

with the type skull of *Meiolania platyceps* (BMNH R675) probably was associated with it and removed during preparation; although the contacts between the two specimens available at present are ambiguous.

Following Owen's description of the new material from Lord Howe, Huxley (1887) argued that the specimens belonged to a cryptodiran turtle rather than a lizard. It was hard for him not to take a jab at Owen: “The specimens have been for some years in the palaeontological collection of the British Museum; and, for the most part, they have not yet been submitted to careful examination. But I learn that the greater number of them were long since rightly determined to be Chelonian by Mr. Davis (an assistant), and set aside as such . . .” (Huxley, 1887, pp. 232–233). Huxley used the caudal vertebrae and skull of *Meiolania platyceps* and compared them directly with *Chelydra*. The skull he figured (1887, fig. 3) is BMNH R675, the type specimen, and it was placed directly above *Chelydra* figures to show the close similarity of orbital and tympanic openings, despite the addition of horns in *Meiolania*. Huxley also renamed the turtle *Ceratochelys sthenurus*, appropriate but unfortunately junior to *Meiolania platyceps*.

Hard on the heels of Huxley's identification of *Meiolania platyceps* as a cryptodire was a short paper by the British Museum herpetologist G. A. Boulenger (1887) arguing that *Meiolania* (“corrected” to *Miolania* by Boulenger, *ibid.*, and Lydekker, 1889) was a pleurodire. The specimen used primarily by Boulenger appears to have been the one described by Owen in 1888, the nearly complete skull and jaws on loan from the Mining Museum in Sydney, MM F:13825a. Owen described and figured this specimen (1888, pls. 31, 32) and the posterior half of the skull (1888, pls. 33, 34) also in the Mining Museum, MM F:13827. There is no reference in this paper to either Huxley's or Boulenger's identification of *Meiolania* as a turtle and Owen denied that *Megalania* (at this point still consisting of Owen's combined varanid-meiolaniid, and *Diprotodon*) and *Meiolania* could be turtles. However, he agreed that the edentulous jaws were a chelonian feature and proposed the suborder Ceratosauria to contain *Megalania* and *Meiolania* as a group in-

intermediate between turtles and other reptiles. Owen also used the "palatal nostril" as a lizard character (1888, p. 189) but this is the intrapterygoid slit (see Pterygoid section below), which he incorrectly identified. This paper was Owen's last word on the horned whatevers and the ink wasn't even dry before Woodward (1888) wrote a paper sorting out lizard, turtle, and marsupial with a corrected system of nomenclature largely followed to this day. Woodward sunk *Meiolania minor*, showed that Huxley's *Ceratochelys* was junior to *Meiolania*, and referred the Queensland turtle material to a new species, *oweni*, and placed it in *Meiolania*.

Early in 1889, George Baur (1889a), a German paleontologist who had worked for O. C. Marsh, wrote a paper disputing Boulenger's assertion that *Meiolania* was a pleurodire. Baur was more knowledgeable about turtle skulls than Boulenger and identified (among other features) the following derived characters (in current terminology) of cryptodires that occur in *Meiolania*:

(1) Descending processes of prefrontals reach vomer.

(2) Processus trochlearis oticum present. In 1889, Boulenger replied to Baur by throwing doubt on various characters and their distributions and accusing him of relying on casts rather than actual specimens, standard operating procedure for systematic arguments. Baur soon replied (1889b) to Boulenger but no new information came to light. The British Museum views, however, prevailed, Lydekker (1889) and most later authors of the texts and classifications of turtles adopted meiolaniids as pleurodires. The Baur-Boulenger fracas was summarized by Simpson (1938). Another useful paper of this period is Lydekker's catalogue (1889) in which all the British Museum meiolaniids are listed and the literature to that date is summarized.

Etheridge (1889a) announced the discov-

ery of meiolaniid fragments from possible Tertiary deposits in Gulgong, New South Wales, that included a cranial B horn core (pl. 26, fig. 4, MM F:13841) and in 1893 he described tail club fragments found near Coolah, New South Wales.

In 1901 Woodward described and figured a meiolaniid from pre-Oligocene rocks of Argentina that he called *Miolania argentina* however, this specimen is generally called by its Ameghino name, *Niolamia argentina*). The discovery and naming of this form is confusing and the reader is referred to Woodward (1901) and Simpson (1938) for further information. It will be useful to have available both of these papers for comparison of the South American material with *Meiolania platyceps*; the only figures that convey any information are in these publications.

*Meiolania platyceps* material from Lord Howe Island accumulated over the years in the Australian Museum in Sydney; the paleontologist Robert Etheridge planned to do a monograph on the turtle but it was Charles Anderson, a mineralogist at the Australian Museum, who actually did it (for an interesting history of the Australian Museum see Strahan, 1979). Anderson (1925) did a good job of describing the available material and he accompanied it with well-executed figures that are useful to this day. He concluded that *Meiolania* was an amphichelydian, a member of that waste-basket group of "slightly ancestral" turtles that I (Gaffney, 1975) discarded in favor of monophyletic groups. At that time, I suggested that meiolaniids, based on *Meiolania platyceps* and *Crossochelys corniger* were members of the Eucryptodira. Since that date, I have published a new palatal view of *Meiolania platyceps* (1979b), a short paper with dorsal views of skulls (1981a), and a review of the known distribution (1981b).

## DESCRIPTION

### HORNS AND SCALE AREAS

Figure 23

Simpson (1938, fig. 10) adopted a system of letters for the scale areas on meiolaniid

skulls, possibly using the labels of Owen (1881, pls. 37, 38) for "*Meiolania*" *oweni* as a source. Owen's labels are lower case letters, whereas Simpson's are capital letters for the paired scales and lower case letters for the midline scales. I use Simpson's capital letters

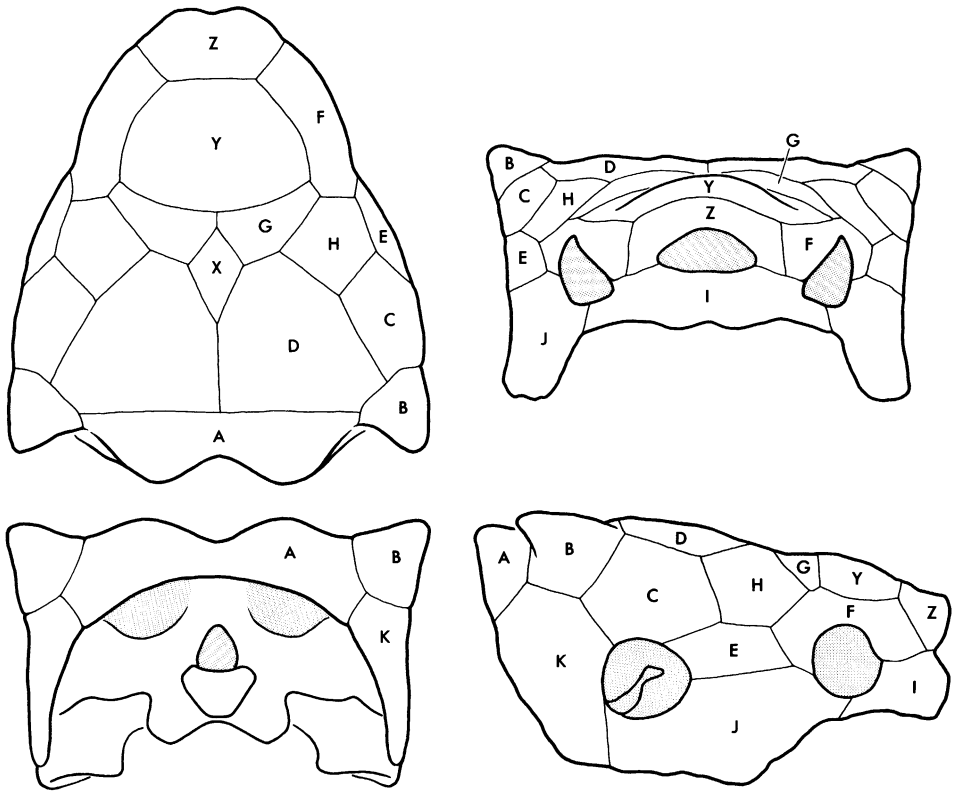


FIG. 23. *Meiolania platyceps*. Generalized illustration of scale distribution. Skull based on AM F.43183, scale pattern based on AM F:61110 and other specimens.

beginning with A as he did, but replace his lower case letters (a, b) with capital letters from the other end of the alphabet (X, Y, Z) to eliminate confusion of duplicate letters.

Simpson's purpose in naming the scale areas was to compare *Crossochelys*, *Niolamia*, and *Meiolania platyceps*. Simpson found *Crossochelys* and *Niolamia* to be very similar but both were so different from *Meiolania platyceps* that he identified the scutes in *Meiolania platyceps* with prime signs (A', B', etc.) apparently to suggest a somewhat greater level of uncertainty. However, Simpson based his *Meiolania platyceps* on a cast of the Kingsley model (Anderson, 1925), which, was just that, a model and not an actual specimen. New material, particularly AM F:61110 (figs. 34–36) shows that Anderson erred in reconstructing the scale pattern in the Kingsley model because he lacked the necessary material. The scale pattern shown by AM

F:61110 is much closer to that of *Crossochelys* and *Niolamia*. Although Simpson used only *Meiolania platyceps*, I have extended the comparison to "*Meiolania*" *oweni* with interesting results (a complete restudy of "*Meiolania*" *oweni* and *Crossochelys* is in preparation).

As noted by Anderson (1925) and Simpson (1938) the scale margins of *Meiolania platyceps* are usually raised ridges rather than the grooves found in *Niolamia* and *Crossochelys*. In fact, I have been unable to find another example of raised scale margins in any turtle. "*Meiolania*" *oweni* has neither raised ridges nor particularly distinct grooves but the bosses and horns are sufficiently distinct to allow comparison with the scale areas of *Meiolania platyceps*. On AM F:61110 the center of each scale area tends to be slightly raised (if not developed into a horn) and has more vascular openings than the bone surface



toward the edge of the scale area, suggesting that the scale itself was thicker in the center. The following description is based primarily on AM F:61110 and emphasizes *Meiolania platyceps* with comparisons with the other meiolaniids.

The anteriormost scale area is scute Z (unnamed in Simpson, 1938), covering the anterior margin of the skull and part of the nasal region. The posterior border of scute Z is scute Y and it is marked by a raised ridge but the lateral margins of scute Z extend ventrally between the orbit and the apertura narium externa. This scale margin is a raised ridge dorsally but as it extends ventrally it becomes a trough. The scale marking that is the ventral limit of scute Z and scute F runs between the orbit and apertura narium externa and is also a trough. Scute Z is not clear in *Niolamia* and the area is not preserved in *Crossochelys*, but it seems quite similar to *Meiolania platyceps* and "*Meiolania*" *oweni*.

Scute Y (b' in Simpson's, 1938, terminology) is another unpaired midline scale as is scute Z, but much larger, covering most of the internarial area of the skull. Its center is a distinctive convexity found in all the *Meiolania platyceps* material having this area preserved. In *Niolamia* and *Crossochelys* this scute area is relatively much smaller with "*Meiolania*" *oweni* being much larger than the South American forms but slightly smaller than *Meiolania platyceps*.

Lateral to scute Y is the paired supraorbital scute F, which surrounds the dorsal half of each orbit. Scute F, to the extent it is determinable in *Niolamia* and *Crossochelys*, is much smaller than in *Meiolania platyceps*. In "*Meiolania*" *oweni* scute F is smaller than in *Meiolania platyceps* but it still surrounds the dorsal half of the orbit.

Directly behind scute Y is the paired scute G which, along with the median scute X, Anderson omitted on the Kingsley reconstruction. Because of this, Simpson (1938, fig. 10) misidentified a more lateral pair (here identified as scute H) as G. Scute G of my terminology agrees closely in size, outline, and relations to other scutes in *Niolamia*, *Crossochelys*, "*Meiolania*" *oweni*, and *Meiolania platyceps*. In all the meiolaniid taxa scute G contacts scute Y anteriorly, scute F anterolaterally, scute H posterolaterally, and scute

D posteriorly, and scute X posteromedially. The principal difference between the scute G of *Meiolania platyceps* and that of other meiolaniids is the absence of a distinct boss or convexity in *Meiolania platyceps*.

Scute X is a small unpaired scale area that lies in the center of the skull roof and is slightly concave in *Meiolania platyceps* and "*Meiolania*" *oweni*. In *Meiolania platyceps* scute X partially divides the paired scute G but in other taxa this does not seem to be the case. Scute X in AM F:61110 has a few small tubercles along its midline but these do not seem to represent a division of this scale into two. Scute X is smallest in *Meiolania platyceps*, larger in "*Meiolania*" *oweni* and largest in *Niolamia* and *Crossochelys* where it reaches the size of scute D and entirely separates the paired D scutes.

"*Meiolania*" *oweni* and *Meiolania platyceps* have a scute pair H; in *Meiolania platyceps*, however, the scale area is marked only by a very slight convexity while the area is a distinct protuberance in "*Meiolania*" *oweni*. Scute H in AM F:61110 meets F anteriorly, G anteromedially, D posteromedially, C posterolaterally, and E laterally. Its contacts in "*Meiolania*" *oweni* are the same (with the exception of E which has not yet been determined). *Crossochelys* and *Niolamia* lack the H scute; at least I have been unable to identify one in the material available to me.

Scute D is a large paired scale area covering much of the posterior portion of the skull. The area is always distinctly convex in *Meiolania platyceps* and may have a large boss (AM F:57984, AM F:61110). Scute D in *Meiolania platyceps* meets the other D for about half its length along the midline, anterior to which it meets X and then G farthest anteriorly. Anterolaterally scute D meets H, laterally C, posterolaterally B, and posteriorly A. The scute markings D-A and D-B are the most persistent and usually recognizable even in fragmentary specimens, whereas many other scale ridges, especially those marking scutes X, G, H, D, and C, are absent. In "*Meiolania*" *oweni* scute D is somewhat broader than in *Meiolania platyceps*, presumably correlated with the fact that the whole posterior portion of the skull in "*Meiolania*" *oweni* is broader, but the scute contacts are the same except along the midline.

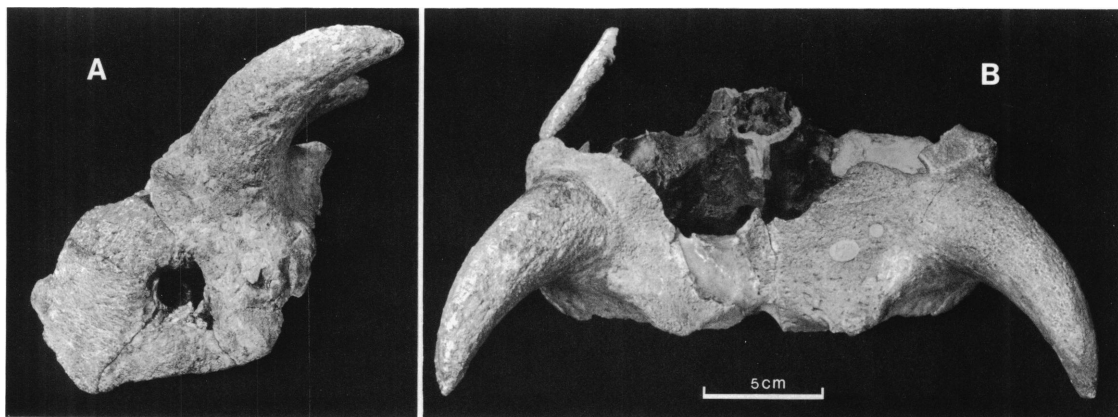


FIG. 24. *Meiolania platyceps*, AM F:1209. A, lateral view of left side; B, dorsal view.

In “*Meiolania*” *oweni*, as in *Crossochelys* and *Niolamia*, scute X separates scutes D and reaches A. However, there is some ambiguity in “*Meiolania*” *oweni* and it is possible that X does not entirely separate D at its posteriormost limits. In any case, “*Meiolania*” *oweni* is intermediate morphologically between *Meiolania platyceps* and the South American meiolaniids in that the latter have X and D scutes that are about the same size with scute X widely separating the paired D scutes. In “*Meiolania*” *oweni* scute X is smaller than in the South American forms but it still separates most, if not all, of scute D along the midline, whereas in *Meiolania platyceps* scute X is quite small, one of the smallest on the skull, allowing a broad median contact of the paired D scutes. Scute D of “*Meiolania*” *oweni* and the South American forms is developed into a protuberance. In *Meiolania platyceps* a protuberance often (but not always) occurs but it is not developed to the degree seen in “*Meiolania*” *oweni*.

Scute C is situated on the posterolateral margin of the skull just dorsal to the cavum tympani. It is a paired scute that is bordered anteriorly by H, anteroventrally by E, ventrally by the dorsal rim of the cavum tympani, posteroventrally by K, posteriorly by B, and medially by D. Scute C is always convex in *Meiolania platyceps*, and it usually bears a small hornlike protuberance but this is subject to considerable variation. For example, in AM F:43183 (figs. 38, 39), scute C is simply a rounded area of the skull conforming

to the change in the slope of the skull from skull roof to skull cheek. In AM F:61110 (figs. 40, 41) scute C has a definite protuberance which in MM F:13827 is more pronounced and in AM F:57984 (fig. 22) is conelike and similar to the horn cores. Scute C in “*Meiolania*” *oweni* and the South American forms is also a distinctive protuberance and has similar size and scute relations to *Meiolania platyceps*.

Scute B forms the most distinctive morphologic feature of *Meiolania platyceps*, the large cowlike horns at the posterolateral corners of the skull. The margins of scute B are nearly always distinct and determinable even in specimens like AM F:57984 which generally has very poor scute margin expression. Scute B contacts scute D anteromedially, scute C anteroventrally, and scute K posteroventrally, and scute A medially. The hornlike process is formed within scute B and the margins of the scute form the margins of the bony horn itself so that the raised scute ridges define the base of the horn. Presumably (as suggested by Owen, 1881), the horny scale that fitted over the bony protrusion exaggerated the outline and may have produced a larger horn in life. It would probably be appropriate then to refer to the bony protuberance of scutes B (and also A) as horn cores as Anderson (1925) does. There is a good deal of variation among the preserved cores (figs. 24, 25). The smallest and least developed in a well-preserved skull are found in AM F:43183 (figs. 33, 38); in this skull the B horn cores

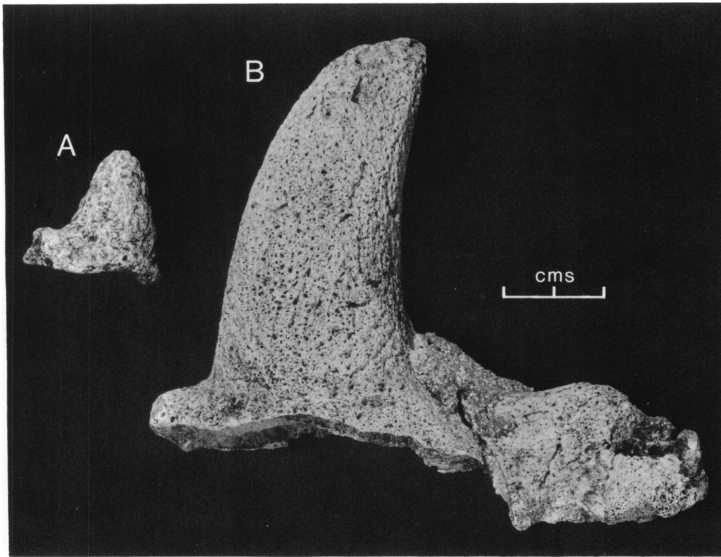


FIG. 25. *Meiolania platyceps*, medial views of right horn cores to same scale. A, AM F:18368, B, AM F:47544.

are no larger than the A cores. In MM F:13827 the B horn cores are larger, with AM F:61110 and AM F:5967 forming a series culminating in AM F:1209 (fig. 24; also in Anderson, 1925, pl. 34) which has the largest set. The *Meiolania platyceps* B horns are directed posterolaterally and may, as in AM F:61110 and AM F:1209, curve posteriorly resulting in a quite bovine appearance.

The possibility that sexual dimorphism is present and expressed by the horn core morphology has been tested by measuring a suite of 50 B horn cores (table 1). Two measurements, height from tip of bone surface on inside of skull, and width at greatest point at base, just above scute ridges were made. Most of the cores are separate fragments rather crudely measured with calipers to the nearest tenth of a millimeter. The length/width ratios (table 1) show no tendency toward bimodality. The measurements do show a skew at the long-narrow horn core end, showing that the distribution is not a normal one.

Comparing B horn cores among the meiolaniids is of considerable interest because it highlights the close similarities between "*Meiolania*" *oweni* and the South American forms in contrast to *Meiolania platyceps*. In the former taxa the B scute area consists of

a large projection that is somewhat flattened and is directed laterally rather than being rounded and directed posterolaterally as in *Meiolania platyceps*.

The A scute horn core area in *Meiolania platyceps* consists of a pair of large posteriorly directed protuberances that are separated by a trough rather than by the usual raised ridge and are probably not separate scales but were both covered by one scute. However, in the other meiolaniids the scale areas are separated by troughs or grooves and this may be the case in *Meiolania platyceps*. Nonetheless, I will treat the A scute area as one large, median scale in all the meiolaniids even though that may not be true for all of them. In *Meiolania platyceps* scute A is bordered anteriorly by a long, almost exactly straight transverse ridge marking the contact with the paired scutes D. Anterolaterally, scute A meets scute B and ventrolaterally it meets scute K in a comparatively short contact. The posteroventral margin of A is the posterior margin of the skull. The bone surface of scute A is the region where the skull slope changes from nearly horizontal on the skull roof to nearly vertical on the occipital margin. The paired protuberances (it will be convenient to refer to these as horn cores also) are not conical,

TABLE 1  
Width/Height Ratios of 50 *Meiolania platyceps*  
"B" Horn Cores

Width Height	Number of Horn Cores
0.40-0.49	3
0.50-0.59	16
0.60-0.69	15
0.70-0.79	10
0.80-0.89	3
0.90	3

as in the B horn core, but are flattened dorsoventrally with the apex pointing posterodorsally. There is some variation in size of A horn cores, the relatively small ones of AM F:61110 (fig. 41) can be contrasted with the relatively large ones of AM F:57984 (fig. 22), but it is interesting to note that, although no quantitative work has been done, the skulls with the largest or smallest B horn cores are not the ones with the largest or smallest A horn cores. Also the variation of A horn cores is much less in degree than that seen in the B cores.

The A horn core area in *Niolamia* is a broad sheet of bone that ends posteriorly in two irregular semicircular processes that can only be identified as the A scute area by an examination of *Crossochelys* and "*Meiolania*" *oweni*, which form morphologic intermediates with *Meiolania platyceps*, and by examining the close correspondence of the B, D, and X scute areas in the whole group. The ventral surface of these processes also shows their equivalence: the occipital margin of the skull lies at the base of the A horn cores even in *Niolamia*, which has the horn core apices drawn out posteriorly to such an extent that the post-occipital region of the skull forms a gigantic "frill," making up about 40 percent of the entire skull length.

The K scute area lies at the posteroventrolateral skull margin, meeting scute A posterodorsally, scute B dorsally, scute C anterodorsally, the cavum tympani anteriorly, and scute J anteroventrally. The posterior margin of scute K is the posterior margin of the skull. In the posterodorsal corner of the scute area, usually a moderate convexity facing posterolaterally that may be virtually

nonexistent as in AM F:43183, or well developed as in AM F:61110. The contact with scute J is a poorly defined, shallow trough seen in AM F:43183. It is quite possible that the J-K area was not covered by scales or scutes as the rest of the skull but perhaps just with skin as in many Recent turtles. However, the presence of this K-J trough in "*Meiolania*" *oweni* and the presence of a boss or convexity in the posterolateral corner suggests that this area is covered by scales like the rest of the skull.

The scute J area extends from the scute K margin posteriorly to the posteroventral margin of the orbit, where it presumably meets the horny material of the triturating surfaces that extends up to the sides of the skull to form a beak. The dorsal limits of scute J are the long ridge with scute E and the very short contact with F, whereas its ventral limit is the ventral margin of the skull. As with scute K, scute J may not have been covered by a scale.

The scute I area is labeled thus for convenience in comparison as it is the "beak," the portion of the skull usually covered by an extension of the horny rhamphotheca covering the triturating surfaces. In AM F:18668, AM F:43183, and AM F:61110 the contact between I and J is a poorly defined ridge that presumably marks the posterior extension of the rhamphotheca.

#### NASAL

Figures 21, 26, 46, 47

The nasal, although presumably present in all specimens with complete snouts, is delimited by sutures only in AM F:57984. The nasal is a very large element, relatively larger than in any other turtle except *Proganochelys*, and lies at the anterior margin of the skull. Both nasals in AM F:57984 are damaged along their posterior margin and their complete limits are not definitely known but the left nasal has enough of this posterior margin preserved to show that there is a roughly transverse suture with the frontal. Anterolateral to the frontal contact there is a relatively long suture between the prefrontal and the nasal which extends to the edge of the skull between the orbit and nares. Anteroventrally the nasal contacts the maxilla in a

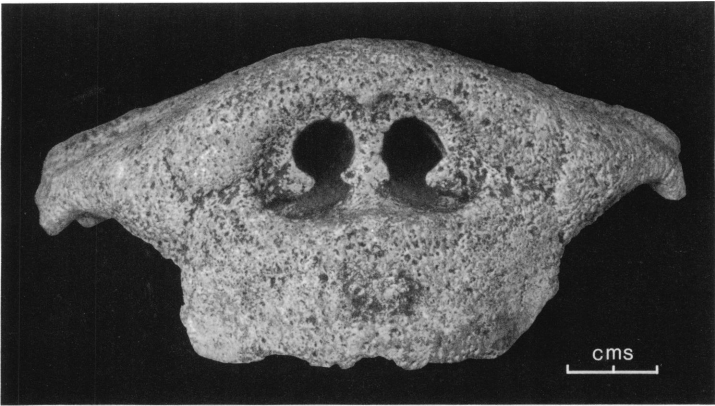


FIG. 26. *Meiolania platyceps*, AM F:398, anterior view of snout fragment.

nearly horizontal suture. The nasals are fused medially with no trace of a suture even along broken surfaces in AM F:57984.

The dorsal surface of the nasal is roughly pitted, as in the other skull bones with external exposure, and curved so that it is convex dorsally. The ventral surface is complex because it is involved in the formation of the apertura narium externa and the fossa nasalis, structures which in *Meiolania platyceps* have a number of unique features. The apertura narium externa of *Meiolania platyceps*

is unusual in having a septum dividing the apertura into two openings. In AM F:398 (fig. 26; also in Anderson, 1925, pl. 31), AM F:16860, AM F:43183, and MM F:13825a the septum is complete but in other specimens it is not. In AM F:61110 the lack of completion may be due to damage but in AM F:18668 and AM F:57984 the surfaces appear natural. AM F:57984 (figs. 21, 22) has the least developed septum, there is only a ventral ridge along the midline where the two nasals are fused. The premaxilla sends a pro-

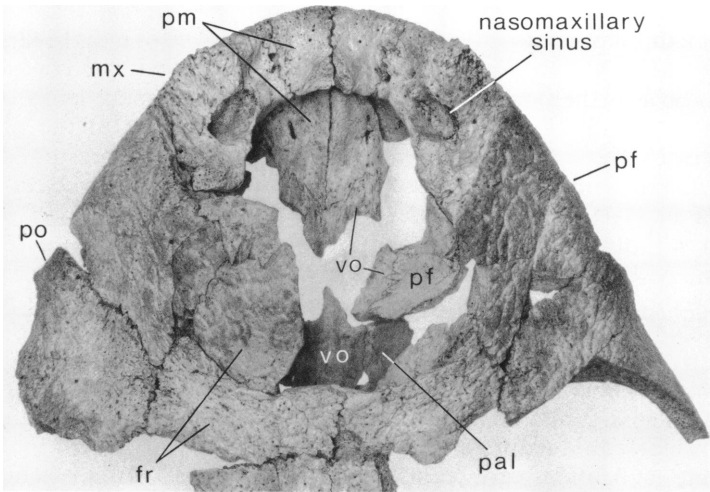


FIG. 27. *Meiolania platyceps*, AM F:57984. Dorsal view of snout (see fig. 21 for orientation) with nasal bones largely removed showing nasomaxillary sinus and floor of fossa nasalis. See abbreviations.



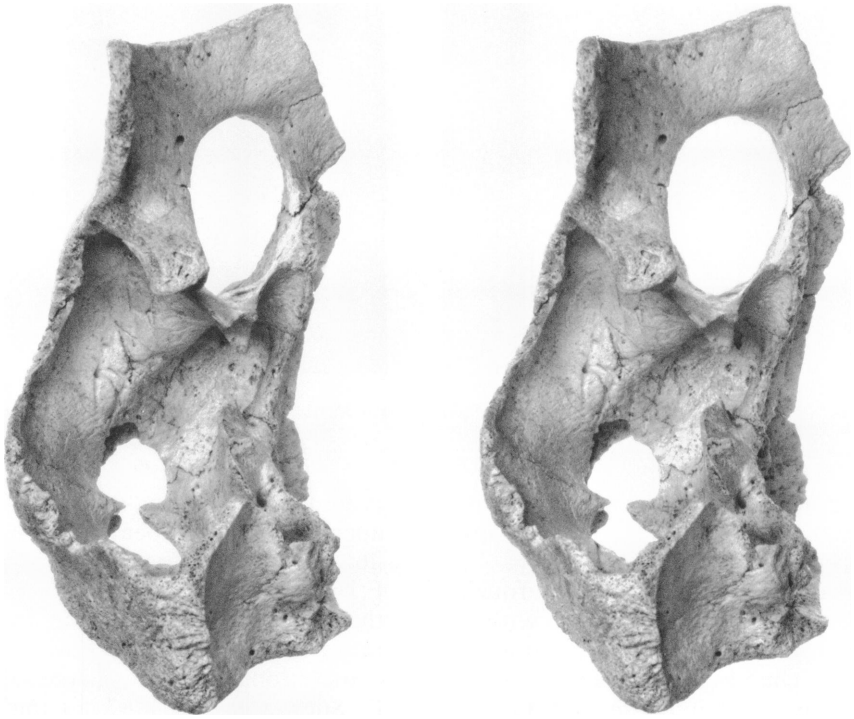


FIG. 28. *Meiolania platyceps*, AM F:18668. Stereophotograph of anterior portion of skull in oblique view with orientation such that the internal area of the right anterolateral part of the skull is exposed. In this view the anterior part of the skull is facing down and away from the viewer. See also figure 44 for other views of this specimen, and figure 29 for a different view of the same region.

cess dorsally to meet the nasal; however, in this specimen it is broken. AM F:18668 (fig. 44) would appear to be a further stage in the formation of a septum; there is a distinct ventral midline process from the nasal and a dorsal one from the premaxilla that nearly meet in the midline. AM F:61110 (figs. 36, 40) has this same condition, although here it is possibly due to erosion. AM F:43183 (figs. 36, 38) has the process completed but a suture remains. It is unlikely that this sequence is actually a growth series, since the respective sizes of the individuals is inconsistent with this hypothesis; nonetheless, it may represent growth stages for this feature. The differences among the available specimens are best ascribed to individual variation.

The only other turtles with an internarial septum are *Proganochelys* and *Kallokibotion*,

but the presence of a divided nares is a primitive amniote feature. The septum of *Proganochelys* is formed, as in other amniotes, by dorsal processes of the premaxillae that reach the nasals, the presumed primitive amniote condition (the structure of this area in *Kallokibotion* is unknown). *Meiolania platyceps* then may be considered to retain the primitive condition in the premaxillae to some extent but the ventral processes of the nasals are a feature unique to *Meiolania platyceps*.

The morphology of the apertura narium externa varies in other features among the available material. In AM F:57984 the dorsal margin of the apertura extends farther anteriorly, relative to the other specimens, and forms the anteriormost part of the skull, while in other skulls either the premaxillae form

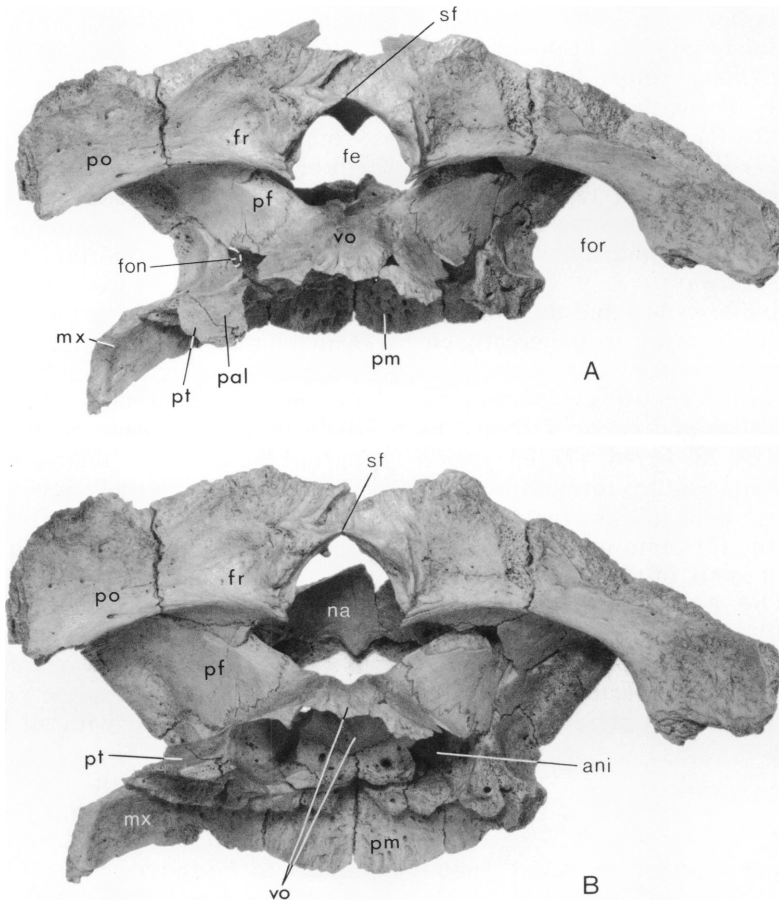


FIG. 29. *Meiolania platyceps*, AM F:57984. Posterior views of anterior portion of skull, in B skull is angled with the snout aimed more ventrally than in A. See abbreviations.

the anteriormost part of the skull or the premaxillae and nasals are at about the same position. The best snout available to Anderson was AM F:398 (fig. 26; Anderson, 1925, pl. 31) and he described the apertura narium externa of this specimen and used it in his plaster restoration. Both passages in the apertura of this specimen, however, have distinctive bony lips recessed slightly from the margin of the apertura that restrict the size of the passages and give them a circular shape rather than the irregular oblong of the more external apertura narium externa. The circular opening, however, is incomplete ventrally leaving a pair of spurlike processes pointing to the midline of each passage. Be-

cause AM F:398 has no visible sutures, it is very difficult to say what bones form these circular lips. Presumably the nasals and premaxillae are the dominant elements but because the maxillae enter the ventrolateral margins of the apertura narium externa they may also be involved in these curious structures. It is possible that these lips were cartilaginous in the other specimens indicating that their ossification was subject to individual variation.

Posterior to the external margin of the apertura narium externa (and to the circular lip of AM F:398) are paired cavities extending posterolaterally into the bone and opening in the lateral walls of the apertura (figs.

27, 28). Anderson (1925, p. 230) referred to this as the maxillary pocket but because of its relation to the nasal region I prefer to call it the nasomaxillary sinus. Each sinus is formed dorsally by the nasal bone and ventrally by the maxilla, as can be seen in AM F:57984 (fig. 27). The opening into the posterolateral margin of the apertura narium externa (fig. 28) is usually slightly smaller than the maximum size of the sinus which is reached about midway.

The nasomaxillary sinus and the internarial septum are all anterior to the greatly enlarged fossa nasalis proper. The fossa nasalis lies behind anterolateral walls formed by the nasals and maxillae and is partly roofed by the nasals (figs. 27, 28, 45, 46, 47). The region of the nasal-frontal suture forms a dorsally facing convexity on the midline that has thinner bone than the surrounding regions and is broken through in six of the seven available specimens. The unbroken skull is AM F:61110 (fig. 40) but AM F:57984 (fig. 22) is preserved in such a way that flipping the left side over to the right indicates that a symmetrical opening was not present.

### PREFRONTAL

Figures 21, 27, 28, 29, 47

The prefrontal is present in AM F:16860, AM F:43183, AM F:61110, MM F:13825a, but it is only in BMNH R9611, BMNH R9612, AM F:18668 (fig. 44) and particularly in AM F:57984 (fig. 22) that sutures can be seen. As in eucryptodires but in contrast to baenids, there are well-developed dorsal as well as vertical plates on the *Meiolania platyceps* prefrontal. The dorsal plates of the prefrontals do not meet in the midline as in nearly all eucryptodires because they are separated by the frontals. There is an anterolaterally trending suture with the postorbital that lies in the roof of the fossa orbitalis and reaches the margin of the skull in the dorsalmost part of the orbit. The dorsal plate of the prefrontal forms some of the roof of the large fossa nasalis, particularly the lateral concavities. Anteroventrally, the prefrontal broadly contacts the maxilla as in all turtles.

The morphology of the ventral plate (or descending process) of the prefrontal in *Meiolania platyceps* is difficult to determine

because none of the specimens are completely damage free in this area and sutures are usually absent. This description relies most heavily on MM F:13825a, AM F:18668 (fig. 28), and AM F:57984 (figs. 27, 29; left prefrontal is most complete of all specimens), all of which have significant portions of the ventral prefrontal plate preserved.

The ventral or descending process of the prefrontal is an important area of differentiation between pleurodires and cryptodires. Cryptodires have a well-developed process which broadly contacts the palatine ventrally where it participates in the formation of the foramen orbito-nasale, whereas ventromedially the prefrontal reaches the vomer to form part of the border of the fissura ethmoidalis. In pleurodires (with a few exceptions, see Gaffney, 1979b, pp. 74–75) the ventral process is absent medial to the maxillary contact; the palatine and vomerine contacts are absent, the foramen orbito-nasale is undefined by bone medially, and the fissura ethmoidalis is a broadly open area also undefined by bone. In *Meiolania platyceps* the process is broad and well developed with all the features of other cryptodires. There is an anteroventromedial contact with the maxilla and a broad ventral contact with the palatine. The foramen orbito-nasale is relatively small (similar in size to *Platysternon*; see Gaffney, 1979b, fig. 63) and is formed at the region of the palatine, prefrontal, and maxilla.

The entire foramen orbito-nasale is preserved on the right side of AM F:18668 (fig. 28) and, although the sutures are partly fused, it is clear that the maxillo-prefrontal suture runs into the foramen anterodorsally. A thin spur of bone from the maxilla extends along the ventral edge of the foramen to meet the prefrontal and exclude the palatine from the margin of the foramen. On the left side of the same specimen, the foramen orbito-nasale is not entirely preserved, nonetheless the maxillary spur still can be seen on the ventral edge of the foramen. The entire foramen orbito-nasale is also preserved on the left side of AM F:16860 (fig. 30) but no sutures are visible. The foramen is even smaller than in AM F:18668 and is circular rather than irregular.

Medial to the prefrontal-palatine contact is the suture with the vomer, a feature found only in cryptodires. Although portions of this

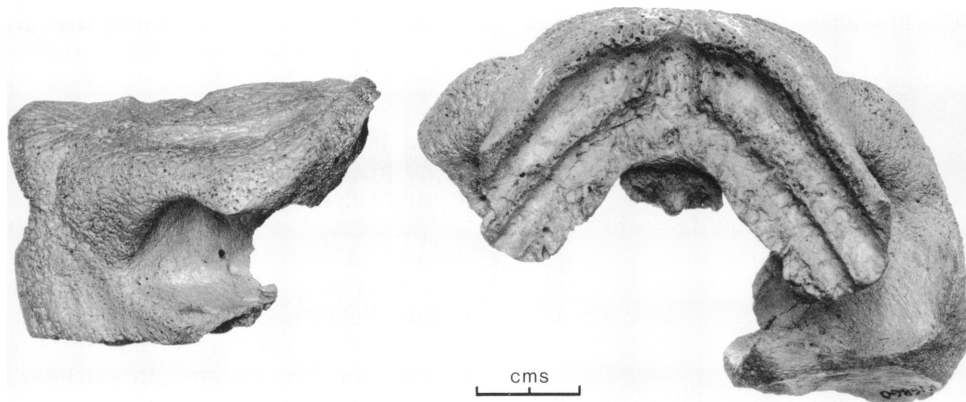


FIG. 30. *Meiolania platyceph*, AM F:16860. Left, lateral view of left side of snout fragment; right, ventral view of snout fragment. This specimen shows conspicuous supraorbital enlargements found in some but not all *Meiolania platyceph* specimens.

area are preserved in AM F:18668 and AM F:43183, only in MM F:13825a and AM F:57984 (fig. 27) are any sutures visible. In MM F:13825a the internal surface of the fossa nasalis remains obscured by matrix but the prefrontal-vomer suture on the posterior margin of the fissura ethmoidalis can be seen, while in AM F:57984, the entire prefrontal-vomer suture is visible. The vomer sends up a pair of short processes that articulate with the two prefrontals on either side of the fissura ethmoidalis. In AM F:57984 the prefrontal appears just posterior to the apertura narium interna and between the vomer and palatine (figs. 21, 32).

The anterodorsal margin of the orbit, formed by the prefrontal, has a variably developed swelling that is roughly hemispherical, convex outward. In specimens such as AM F:57984 (figs. 21, 22) and AM F:43183 (fig. 36) the swelling is barely noticeable, but in AM F:16860 (fig. 30) and especially in AM F:18668 (fig. 44), it is very well developed and distinctive. I am not aware of a similar situation in any other turtle.

#### FRONTAL

Figures 21, 29, 46, 47

The frontal, or portions thereof, are preserved in AM F:18668, AM F:16860, AM F:43183, AM F:1197, AM F:5473, AM

F:57984, AM F:61110, AM F:398, MM F:13825a and other skull fragments in the Australian Museum and British Museum collections. It is only on AM F:57984 (figs. 21, 22) that almost all the limits and contacts of the frontal can be seen; in the others the area is either broken or the sutures are largely fused and indeterminate. The left frontal of AM F:57984 is nearly complete, but it lacks most of the area along the midline.

The frontal of *Meiolania platyceph* is roughly triangular in dorsal view, contacting the nasal anteriorly, the prefrontal anterolaterally, the postorbital posterolaterally, the parietal posteriorly, and the other frontal medially. Frontal exposure in the orbital margin is prevented by broad contact of the prefrontal and postorbital.

The ventral surface of the frontal in *Meiolania platyceph* is relatively complex, in comparison with most turtles, because of the large fossa nasalis and its associated structures (figs. 28, 29, 46, 47). The anterior portion of the frontal along with the posterior portion of the nasal forms the roof of the fossa which is a simple concavity opening ventrally. Somewhat lateral to the midline, and formed by the frontal, is a low parasagittal ridge, which increases in size posteriorly where it joins the dorsal margin of the fissura ethmoidalis. Just anterolateral to the fissura is an anteriorly-

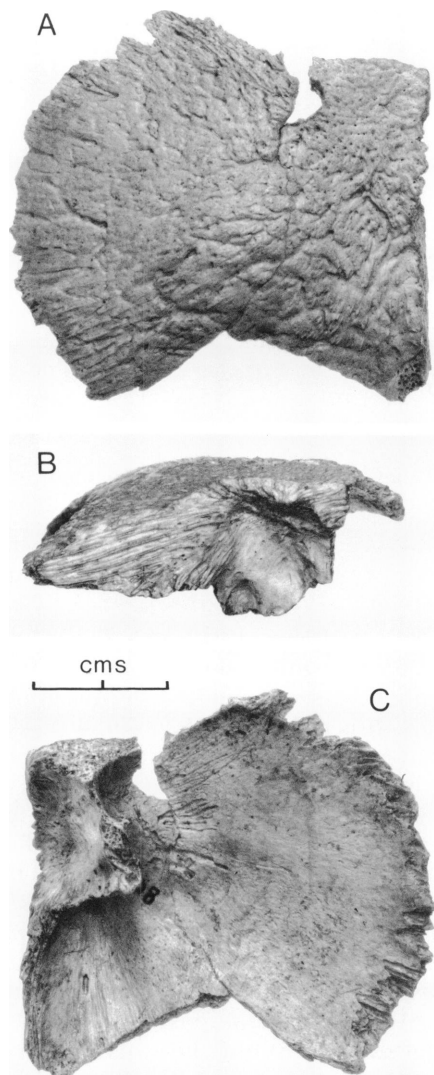


FIG. 31. *Meiolania platyceps*, AM F:61108. Left parietal; A, dorsal (anterior toward top of page); B, medial (anterior toward right); C, ventral (anterior toward top of page).

opening pocket which widens out to become continuous with the rest of the fossa nasalis. Anteroventrally, the frontal consists of a broad plate that reaches the prefrontal and forms the ventral portion of this pocket. Testudinids are the only other turtles having a nasal morphology similar to *Meiolania platyceps*. In testudinids the fossa nasalis is large

and roofed by the frontal; small pockets just anterior to the fissura ethmoidalis are also present as in *Meiolania platyceps* (see Gaffney, 1979b, fig. 6).

Due to the relatively huge fossa nasalis, the sulcus olfactorius is much reduced. In most turtles the sulcus is bordered by a long parasagittal ridge lying just lateral to the midline on the ventral surface of the frontal, but in *Meiolania platyceps* the fossa nasalis occupies most of this area on the frontal and the sulcus olfactorius is bordered by a short, thick ridge on the posterior portion of the frontal (fig. 29). In anterior view the sulcus is broad and semicircular in transverse section, as in testudinids, and forms the dorsal margin of the fissura ethmoidalis. Short projections, similar to the single one seen in testudinids, extend ventromedially from each side of the sulcus. Laterally the frontal supports a thick, transverse ridge that is continuous with one on the postorbital and separates the fossa orbitalis from the fossa temporalis superior.

#### PARIETAL

Figures 21, 31, 46, 47

The parietal is preserved in AM F:1209, MM F:13827, MM F:13825a, AM F:43183, AM F:57984, and AM F:61110, whereas AM F:61108 is a disarticulated partial left parietal (fig. 31). The dorsal plate of the parietal is relatively smaller in *Meiolania platyceps* than in most other turtles and, in the absence of any temporal emargination, is entirely surrounded by bone. Although nearly all the limits of the parietal can be seen in either AM F:57984 or AM F:61108 the contacts posteriorly are in doubt. The lateral and posterior sutures between the parietal and other elements are absent in all articulated specimens, as are sutures between the other posterior bones. AM F:61108, the disarticulated left parietal, shows the lateral margins but does not indicate what bones were sutured there. It is most likely that the posterior contact is with an expanded supraoccipital and that the posterolateral contact is with the horn-bearing squamosal. The lateral margin almost certainly meets the postorbital; AM F:18668 (fig. 44) shows that the postorbital extends back at least to the quadrate at the level of tympanic opening, and AM F:57984

(figs. 21, 22) shows the postorbital trending in the direction of the parietal margin. Restoring AM F:61108 on AM F:57984 (fig. 21) gives a good idea of the extent of the parietal (except posteriorly where AM F:61108 is broken), although it does not aid in determining the position of the postorbital-squamosal contact.

Two of the best preserved skulls, AM F:43183 (fig. 38) and AM F:61110 (fig. 40) have fenestrae with apparently natural edges. *Crossochelys* was described by Simpson (1938) as having temporal fenestrae in roughly these positions and it would be useful to explore the possibility that the fenestrae in *Meiolania platycephs* are the same as those in *Crossochelys*. In AM F:43183 the fenestrae are irregular in size and shape and may have been enlarged by postmortem damage. On the left side of AM F:43183 there are actually two fenestrae, the additional one is in the region of the postorbital; also the fossa nasalis is open in this skull but this appears due to damage. AM F:61110 has much smaller fenestrae that are clearly due to the extreme thinness of the bone in this region; in fact, both were nearly filled with very thin bone lost during preparation. Three specimens, MM F:13827, AM F:57984 (fig. 22) and AM F:61108 (fig. 31) have the temporal area preserved and have no fenestrae, thus the presence of fenestrae can hardly be considered characteristic of *Meiolania platycephs* and would appear to be another manifestation of the large amount of individual variation present in the species. Most importantly, however, the fenestrae of *Crossochelys* occur at sutural margins and are formed by the supraoccipital, squamosal, and parietal, whereas the fenestrae in the two skulls of *Meiolania platycephs* appear to be entirely within the parietal.

The processus inferior parietalis (figs. 46, 47) can be seen in MM F:13825a, AM F:61108 (fig. 31), AM F:57984, AM F:1209, AM F:43183, and AM F:61110. AM F:61108, the free left parietal, lacks the anteromedial portion of the processus but the remaining section is intact and, although slightly worn, seems to retain its original limits. AM F:61110 has all the bone of this area preserved and the prootic-parietal sutures are clear on both sides. In MM F:13825a some of

the sutures are visible but both sides have been damaged to some extent and differentiating cracks from sutures is difficult. In AM F:43183 the area is almost entirely preserved but no sutures are visible, whereas in AM F:1209 and MM F:13827 the region is damaged and no sutures are visible. The processus inferior parietalis is relatively low when compared with other turtles (see Gaffney, 1979b, figs. 66–80). In *Meiolania platycephs* the processus barely enters the foramen interorbitale, whereas in most other turtles (*Dermochelys* is an exception) the parietal is a major constituent of the foramen. The large epipterygoid (figs. 53, 55) occupies nearly all the side wall of the braincase between the foramen nervi trigemini and the foramen interorbitalis and reaches the processus inferior parietalis at its dorsal limit. Posterior to this, the parietal contacts the prootic and may have a narrow ventral projection covering part of the prootic medially (AM F:57984), whereas a dorsal process of the prootic may cover a portion of the parietal laterally (AM F:57984, AM F:61110). The sagittal view (fig. 46) shows the relatively small area of parietal exposed in the cavum cranii. The cast also shows the concavities, one in the midline and paired ones laterally, formed by the parietal. This region was probably filled with the cartilaginous remnants of the tectum synoticum (the cartilaginous precursor of the supraoccipital) during life. This feature is found in nearly all other turtles (see Gaffney, 1979b, p. 107), but in *Meiolania platycephs* it would appear that the cartilage lines the posterior half of the parietal in the cavum cranii.

Posteriorly, the parietal has the usual squamous articulation with the supraoccipital, based on the contact area in AM F:61108 (fig. 31). The other specimens lack sutures in this area.

## JUGAL

Figures 21, 28, 45

The jugal is preserved in AM F:43183, AM F:61110, AM F:18668 and MM F:13825a. Although MM F:13825a does have some of the jugal sutures visible on the right side, it is primarily AM F:18668 (fig. 44) that supplies the best information. The jugal in *Meiolania platycephs* has an anterior dorsally overlap-



ping articulation with the maxilla that floors a portion of the fossa orbitalis. The jugal sends a process medially along the maxillary articulation that appears to reach the pterygoid at its tip. The pterygoid is entirely absent in AM F:18668 and sutures are not present in this area on MM F:13825a, but AM F:57984 has the left maxilla and portions of the left palatine and pterygoid preserved that show the jugal suture area (even though the jugal itself is absent) and indicates a pterygoid-jugal contact. The jugal-maxilla suture forms the posterolateral limits of the triturating surface in ventral view.

The vertical portion of the jugal extends posteroventrally to form a portion of the ventral margin of the skull. Posteriorly it contacts the quadratojugal, and posterodorsally it contacts the postorbital; both sutures being visible in AM F:18668.

#### QUADRATOJUGAL

Figures 21, 46

The quadratojugal is present in AM F:61110, AM F:43183, AM F:18668, MM F:13827, and MM F:13825a, although its complete limits are not visible in any specimen. The only specimen showing any quadratojugal sutures is AM F:18668 (fig. 44) which has the anterior limits indicated. The jugal has the anteriormost contact with the maxilla but the portion of both bones that actually forms the ventral margin of the cheek is broken off and it is possible that either the jugal or quadratojugal was more extensive here. Dorsally the quadratojugal has a suture with the postorbital ending at the dorsal margin of the tympanic ring. In most turtles the quadratojugal is more extensive dorsally so that its limits are above the quadrate. On the left side of AM F:57984 (fig. 22), there seems to be a suture between the quadrate and the squamosal very near the position where the quadratojugal suture on AM F:18668 ends on the tympanic ring. The right side of AM F:57984 (fig. 22) has a fragment of the squamosal preserved below the cavum tympani that has a sutural surface as its anterior margin. This is the appropriate place for the squamosal-quadratojugal contact and, in the absence of contrary information, I am identifying it as such.

#### SQUAMOSAL

Figures 21, 22, 24, 25

The presumed region of the squamosal is preserved in AM F:61110, AM F:43183, AM F:57984, AM F:1209, AM F:18668, MM F:13827, MM F:13825a, BMNH R675, plus more than 50 Australian Museum, Mining Museum, and British Museum B horn cores.

The limits of the squamosal in *Meiolania platyceps* are poorly known and much of our understanding of the attachments of this element relies on extrapolation between *Meiolania platyceps* and *Crossochelys*. The only squamosal sutures known for *Meiolania platyceps* are seen in AM F:57984 (figs. 21, 22) and a skull as yet unprepared collected in 1980 (AM F:64471). One suture in AM F:57984 is on the right side, ventral to the cavum tympani, and it appears to be on the anterior margin of the squamosal, which, if correct, would make up all the bone of the skull roof behind the quadrate. This squamosal suture is presumed to articulate anteriorly with the quadratojugal. Another probable squamosal suture can be seen on the left side of this specimen (although a small fragment of it is also visible on the right) on the dorsal surface of the skull, anteromedial to the horn in the C-scuta area. This suture I interpret as the squamosal-postorbital contact. The medial limits of the squamosal on the skull roof are probably preserved in AM F:61108 (fig. 31), a disarticulated parietal, but it is not possible to be sure about the relative position of the parietal-squamosal junction, nor the relative size of AM F:61108 in comparison to AM F:57984. The new specimen shows most of the supraoccipital-squamosal contact and this is added to fig. 21. The suture tends posteromedially from the parietal to the back of the skull. The squamosal lies beneath most of the area covered by scutes A, B, C, K and some of D (fig. 23).

The squamosal forms the dorsolateral part of the cavum tympani; some of its medial limits can be seen in AM F:57984, but in the other specimens the sutures are fused. In AM F:57984 the squamosal reaches the posterolateral edge of the opisthotic and the suture extends anteriorly and slightly medially to a point about halfway along the otic chamber where the squamosal abuts against the quad-

rate. Other limits and contacts of the squamosal are unknown.

### POSTORBITAL

Figures 21, 27–29

Although the postorbital is preserved in BMNH R675, MM F:13825a, AM F:43183, and AM F:61110, it is only in AM F:57984, AM F:18668, and BMNH R9610 that sutures delimiting the bone are visible. In AM F:57984 and BMNH R9610 only the anterior section of the postorbital is present so that it is only on the left side of AM F:18668 that most of the bone is preserved and delimited by sutures.

The postorbital of *Meiolania* is of moderate size in comparison to other eucryptodires, such as chelydrids and cheloniods, that have well-developed temporal roofs. The postorbital of those forms makes up a significant part of the roof, whereas in *Meiolania* the squamosal occupies comparatively more of the roof.

The structure of the postorbital in *Meiolania* is similar to that in other turtles: a curved plate with a low ridge behind the orbit. This ridge separates the fossa orbitalis from the fossa temporalis and is best seen in figures 28 and 29. The contacts of the postorbital in *Meiolania* are with the prefrontal anteriorly, the frontal medially, the parietal postero-medially, the squamosal posteriorly, the quadratojugal posteroventrally, and the jugal anteroventrally.

### PREMAXILLA

Figures 21, 27, 29, 30, 45, 46, 47

The premaxilla is preserved in the following specimens: AM F:18669, AM F:16860, AM F:61110, AM F:43183, AM F:398, MM F:13825a, BMNH R675, BMNH R677, BMNH R677a, and BMNH R677b. Sutures can be seen in AM F:18668, AM F:57984, and AM F:61110.

The premaxilla of *Meiolania platyceps* has a long sagittal suture with the other premaxilla medially, its lateral margin meets the maxilla, and posteriorly it contacts the vomer. The dorsal surface of the vomer forms the ventral part of the apertura narium externa and the fossa nasalis, both of which are

highly modified in *Meiolania platyceps*. The premaxillary part of the apertura bears a dorsal process in the midline (each premaxilla forms half of it) which usually reaches the ventral process of the nasal (figs. 45, 46) to divide the apertura narium externa into two choanae but in some specimens (e.g., AM F:18668, fig. 44) the two processes may not meet (see also Nasal). The area of the premaxilla that forms the floor of the apertura is higher than the section forming the floor of the fossa nasalis and may be a flat area longer than wide (AM F:57984) or it may be shorter (AM F:18668), although it usually is extensive enough to produce the distinctively recessed apertura narium externa that is characteristic of *Meiolania platyceps*.

The portion of the premaxilla in the fossa nasalis begins anteriorly in a deep median pit that extends anteriorly under the part of the premaxilla forming the apertura narium externa, so that a shelf is formed by the premaxilla (fig. 46). Posterior to this pit, the paired premaxillae form a dorsally convex surface that is continuous with the dorsal surface of the vomer. Laterally, the premaxilla slopes ventrally to meet the maxilla with which it forms part of the lateral choanal channel. Between the maxillary contact and the vomerine contact, the premaxilla has a free lateral edge that forms a small section of the margin of the apertura narium interna which prevents the maxilla and vomer from meeting (visible only in AM F:57984, figs. 27, 45).

The foramen praepalatium of *Meiolania platyceps* lies entirely within the premaxilla rather than in the vomer-premaxilla suture (the latter is often the case in other turtles). The foramen is a canal that is nearly horizontal and extends anterodorsally from a small pocket formed just adjacent to the maxilla to the dorsal surface of the premaxilla.

The anterior surface of the premaxilla (figs. 21, 22) is nearly vertical and has a lateral suture with the maxilla that begins dorsally in the ventral margin of the apertura narium externa, near the lateral margin of the apertura and extends ventrally (and slightly laterally at first). The premaxilla in *Meiolania platyceps* is relatively broad when compared with other turtles and it bears a prominent portion of the triturating area (figs. 21, 22,

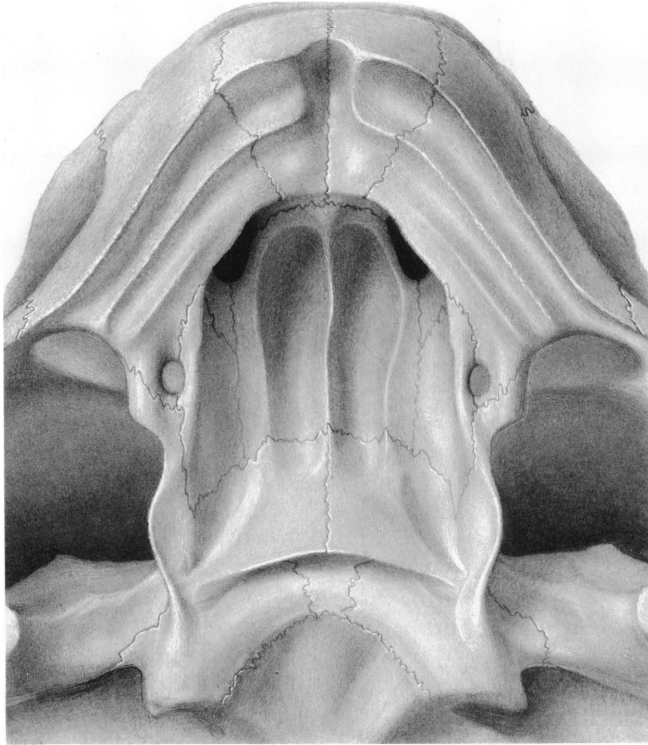


FIG. 32. *Meiolania platyceps*, MM F:13825a. Ventral view of palate, partially restored by transposing right to left. Sutures added from AM F:57984, see figure 21 for bone identifications.

32). The anterior surface of the premaxilla ends ventrally in a sharp ridge, the labial ridge, which is usually undulating so that the ridge has a pronounced median notch with a low, rounded cusp lateral to it but still formed entirely by the premaxilla. The premaxilla-maxilla suture is marked in AM F:57984 (figs. 21, 22) by another low undulation that reduces the height of the labial ridge at that point. It is only in AM F:57984 that the labial ridge appears to be perfectly preserved, although AM F:61110, AM F:18668, and AM F:16860 only lack the thin edges. The median notch is visible on all of these but the cusp is less pronounced.

The triturating surface of *Meiolania platyceps* (figs. 32, 38, 40, 42) bears three parallel ridges, the most exterior being the labial, followed by an intermediate or accessory ridge, with the lingual ridge being the most interior one. The cusp on the labial ridge has a low parasagittal ridge (best seen in AM F:18668,

fig. 44) that connects the labial and intermediate ridges and is lateral to a deep concavity that extends dorsally and posteriorly from the median notch on the labial ridge. A low, toothlike cusp is formed at the junction of this parasagittal ridge and the intermediate ridge. In most of the specimens the labial ridge is much higher and better developed than the intermediate ridge, but in AM F:61110 the labial ridge is relatively lower and the intermediate ridge higher, so that the latter is nearly the same height as the labial ridge. The median concavity is also distinctly deeper and better formed than in the other specimens. The lingual ridge is virtually absent in *Meiolania platyceps* and might be more appropriately termed the lingual ridge margin of the triturating surface. In any case, the premaxilla bears little of it because the bone narrows posteriorly as it approaches the vomer so that only a small part of the ridge lies on the premaxilla. Posterior to the ridge

(or margin) the premaxilla makes a sharp rise into the palatal trough area between the apertura narium interna before it reaches the vomer.

In "*Meiolania*" *oweni* there are two intermediate ridges, the more internal of them being lower than the more external. In *Meiolania platyceps* this second intermediate ridge is barely expressed posterolaterally on the maxilla, and only a slight rugosity can be seen which might represent it on the premaxilla. No premaxillary sutures can be seen in "*Meiolania*" *oweni*. The median notch and parasagittal ridge are clearly developed in "*Meiolania*" *oweni* and are about the same as in *Meiolania platyceps*. The dorsal surface of the premaxilla, to the extent it is preserved in "*Meiolania*" *oweni*, is also quite similar to *Meiolania platyceps*; there is a median dorsal process that nearly reaches the ventral process of the nasal. The apertura narium externa is recessed from the external surface of the skull and behind the apertura is a ventral step to the floor of the fossa nasalis.

Although Simpson (1938) did not describe a disarticulated premaxilla as belonging to *Crossochelys*, he did note the presence of one as associated with the other elements but thought it might belong to another kind of turtle (the presence of which he deduced from other undescribed fragments). It seems to me that this premaxilla does belong to *Crossochelys*. The bone is a right premaxilla that seems to have had a median dorsal process, now broken off, and in contrast to *Meiolania platyceps*, a relatively shallow apertura narium externa. Most of the dorsal surface is a slightly convex plate with the foramen prae-palatium near its posterior edge. The ventral surface shows a low labial ridge and a low, rounded lingual ridge with no median concavity. Although these features differ from *Meiolania platyceps*, they do occur on the cast and figures (Woodward, 1901) of *Nio-lamia* and should be considered characteristic of the South American forms.

#### MAXILLA

Figures 21, 28, 29, 32, 45

The specimens in which the maxilla is preserved are as follows: AM F:18668, AM F:16868, AM F:57984, AM F:61110, AM

F:43183, AM F:398, MM F:13825a, BMNH R677, BMNH R677a, BMNH R677b, BMNH R9620, and BMNH R675.

Anteromedially the maxilla contacts the premaxilla; above this contact the maxilla forms the posterolateral margin of the apertura narium externa and the anterolateral wall of the fossa nasalis. Within the apertura, which in *Meiolania platyceps* extends posteriorly as a tubelike structure, the maxilla forms the ventral half of the naso-maxillary sinus (figs. 27, 28, 45), a posterolateral pocket branching off the apertura. The dorsal half of the sinus is formed by the nasal (see Nasal). The maxillary portion of the fossa nasalis is a concave chamber that opens dorsomedially into the main section of the fossa nasalis and posteriorly into the apertura narium interna. Posterodorsally the maxilla meets the prefrontal in a ventrally trending suture, visible internally and externally in AM F:57984. Within the fossa nasalis this suture extends ventrally to the region of the apertura narium interna, where the suture in AM F:57984 is lost due to breakage. On the external surface of the skull the maxilla-prefrontal contact travels posteroventrally from the maxilla-nasal contact to the anterior margin of the orbit. Within the fossa orbitalis, the maxilla-prefrontal suture trends medially (best seen in AM F:18668) to the foramen orbito-nasale, the lateral part of which is formed by the maxilla. The maxilla margin then turns posteriorly as it runs onto the floor of the fossa orbitalis and meets the palatine laterally. The posterior margin of the maxilla in the floor of the orbit is sutured to the medial process of the jugal.

The dorsal surface of the maxilla has a vertical ridge, nearly parasagittal in orientation (figs. 27, 45), that forms the ventral part of the wall between the fossa orbitalis and the choanal groove or chamber of the fossa nasalis. The ridge is higher anteriorly where it meets the prefrontal than posteriorly where it is lateral to the palatine.

The triturating surface of the maxilla (figs. 30, 32, 38, 40, 42) continues the structures seen on the premaxilla. There is a high and well-developed labial ridge, becoming relatively low beneath the orbit where the maxilla is thinner. There are undulations in this ridge in AM F:57984 (fig. 22) but not in AM

F:61110 (fig. 40), which has the ridge straight. The intermediate ridge is generally lower than the labial ridge. The maxilla of "*Meiolania*" *oweni* differs from *Meiolania platyceps* primarily in the possession of a second intermediate ridge, internal to the one described above. In most specimens of *Meiolania platyceps* that have the posterior part of the maxilla sufficiently well preserved (AM F:57984, AM F:18669, AM F:16860) there is a trace of this second intermediate ridge. The ridge is lacking anteriorly, except for some vague rugosities, but becomes more distinct posterolaterally; however, it is never developed to the extent seen in "*Meiolania*" *oweni*.

The lingual "ridge" is really not present in *Meiolania platyceps*; the internal margin of the maxilla simply ends. There are only two specimens that preserve the inner margin of the triturating surface, because it becomes quite thin along the apertura narium interna and is commonly broken. Where intact the margin almost exactly parallels the labial ridge so that *Meiolania platyceps* can be described as having a triturating surface margin which is expanded equally in a medial direction, causing a shelf or fold in the premaxilla and a partial obscuring of the apertura narium interna in ventral view.

#### VOMER

Figures 21, 27, 28, 29, 32, 45, 46

A complete vomer is not present in any available *Meiolania platyceps* specimens; this description relies primarily on MM F:13825a and AM F:57984, both of which retain more than half of the bone and have some sutures visible. In AM F:16860, AM F:18668, AM F:61110 and AM F:43183 the anterior end of the vomer is preserved but there are few sutures. The best vomer is in MM F:13825a (fig. 42) where it lacks only the section underlying the center of the fossa nasalis, an area that is not preserved in any *Meiolania platyceps* and is particularly susceptible to damage because it is so thin. All the posterior suture are ambiguous in MM F:13825a, but AM F:57984 provides better information on contacts.

Anteriorly, the unpaired vomer meets the two premaxillae in a broad suture visible in AM F:57984 (figs. 21, 22, 27) and other specimens. This suture ends in the apertura

narium interna, the posteromedial margin of which is formed by the vomer. In AM F:57984 a portion of the vomer-palatine suture can be seen on both sides while in MM F:13825a two possible vomer-palatine sutures can be made out on the left side, presumably only one of which is correct. The palate of *Meiolania platyceps* consists of a broad arch with paired troughs, concave ventrally, in its center divided by a median ridge (fig. 32). The vomer forms the ridge and most if not all of the troughs. In AM F:57984 the vomer-palatine suture on the right runs just lateral to the lateral margin of the trough but on the left side the suture runs much farther laterally, presumably coincidental with an asymmetry of the troughs (see below). The part of the vomer-palatine suture preserved in AM F:57984 (on both sides) is the section anterior to the pterygoid-vomer contact but posterior to the apertura narium interna. In AM F:13825a there is a possible vomer-palatine suture on the left side but it is poorly preserved and may be a crack. It extends anteriorly from the pterygoid nearly in the center of the trough, more medial than either vomer-palatine suture of AM F:57984. Posteriorly the vomer has a roughly transverse contact with the pterygoids visible in both MM F:13825a and AM F:57984.

On the dorsal surface of the vomer there is a contact with the premaxillae that is the same as the contact on the ventral surface, and can be seen in AM F:57984. Also visible on this specimen is the dorsolateral contact with the descending process of the prefrontal. In the left orbit of MM F:13825a is a portion of this contact and a short section of what appears to be the vomer.

The vomer of *Meiolania platyceps* has a pair of troughs on the palatal surface separated by a midline ridge; however, the two skulls (MM F:13825a, figs. 32, 42; and AM F:57984, fig. 22) which best show these troughs have some differences between them. In both skulls the troughs begin anteriorly just posterior to the vomer-premaxilla suture. In MM F:13825a the anterior end of the trough is deeper and better defined than the posterior portion and the bone forming the anterior end is nearly vertical in the anterior wall of the trough, whereas in AM F:57984 the anterior part of the trough is not quite so well developed although it is still differen-

tiated from the rest of the trough. The lateral margin of the trough is a low, but well defined, ridge in MM F:13825a but in AM F:57984 this lateral ridge is distinctly higher and developed to the extent that a second set of troughs are defined lateral to the median pair. In MM F:13825a the median troughs are slightly asymmetric; generally wider anteriorly and narrower posteriorly. In AM F:57984 the troughs are generally the same but the left one has a distinct lateral bulge anteriorly. The posterior limits of the troughs are much less well defined than any of the other trough limits but can still be readily determined. This posterior limit is coincident with the vomer-ptyergoid suture in AM F:57984 but distinctly posterior to this suture in MM F:13825a.

The dorsal surface of the vomer parallels the ventral in the broad arching of the palate (fig. 46). The anterior half of the vomer floors the posterior portion of the fossa nasalis and bears a pair of anterodorsolaterally directed processes that attach to the descending processes of the prefrontals. The vomer forms the ventral portion of the fissura ethmoidalis (see Prefrontal) and has along its entire dorsal surface (fig. 45) the sulcus vomeri a dorsally open, median trough that in *Meiolania platyceps* is delimited by relatively broad but low ridges.

The sulcus in *Meiolania platyceps* differs from that in testudinids in being broad rather than narrow and distinctly defined by sharp ridges; otherwise the structure of the vomer in *Meiolania platyceps* is very similar to the vomer in testudinids. Both have an elongate vomer, separating the internal nares, extending posteriorly to separate the palatines and reach the pterygoids, and have paired choanal troughs on the palatal surface separated by a sharp ridge. Although I have not found significant differences between palatal surfaces of the vomers in *Meiolania platyceps* and testudinids, I conclude, on the basis of other characters, that these features have arisen independently.

#### PALATINE

Figures 21, 32, 45

The palatine is preserved best in MM F:13825a (fig. 32) and AM F:57984; small portions of the palatine lying just medial to

the pterygoid articulation are also preserved in AM F:43183 (fig. 38). Although it is nearly complete on the left side of MM F:13825a the sutures on this specimen are dubious and complete information on this bone is not available even by combining the two skulls. A small portion of the palatine is preserved in AM F:16860 and AM F:18668.

The palatine is a thin, platelike element that forms a significant portion of the palate. The specimen that has the best preserved vomer is MM F:13825a but sutures between the vomer and the palatine are not visible everywhere and some areas on the dorsal surface are obscured by matrix retained to hold the bone together. AM F:57984 has some sutures but a significant portion of the bone is missing; the sutures on the right side are clearest (fig. 27). There is a parasagittal suture running just lateral to the ridge marking the lateral limit of the palatal trough; this suture seems to be between the vomer medially and the prefrontal laterally. This lateral element can be traced around to the dorsal surface through the apertura narium interna, substantiating its identification as the prefrontal. Furthermore, lateral to the prefrontal is a suture with the palatine which is present on both sides of the skull. The vomer-prefrontal suture, however, appears to be fused on the left side because the vomer-prefrontal suture can be followed from the dorsal surface around the margin of the apertura narium interna where it disappears. It should be emphasized, however, that this interpretation of palatine-prefrontal-vomer morphology requires confirmation. In many cryptodire skulls the prefrontal-vomer suture is visible on the ventral surface as in *Meiolania platyceps*.

Medially, the palatine has a presumed long contact with the vomer, the position of which is questionable in MM F:13825a (see Vomer) and cannot be followed very far posteriorly in AM F:57984. In MM F:13825a this vomer-palatine suture appears to lie in the trough formed by both bones but in AM F:57984 it is just lateral to the ridge defining the lateral limits of the trough. Anterolaterally, the palatine reaches the maxilla, a contact that can be seen on the left side of AM F:57984 where it is exposed in a broken area around the apertura narium interna, and in the floor of both orbits of MM F:13825a. Just



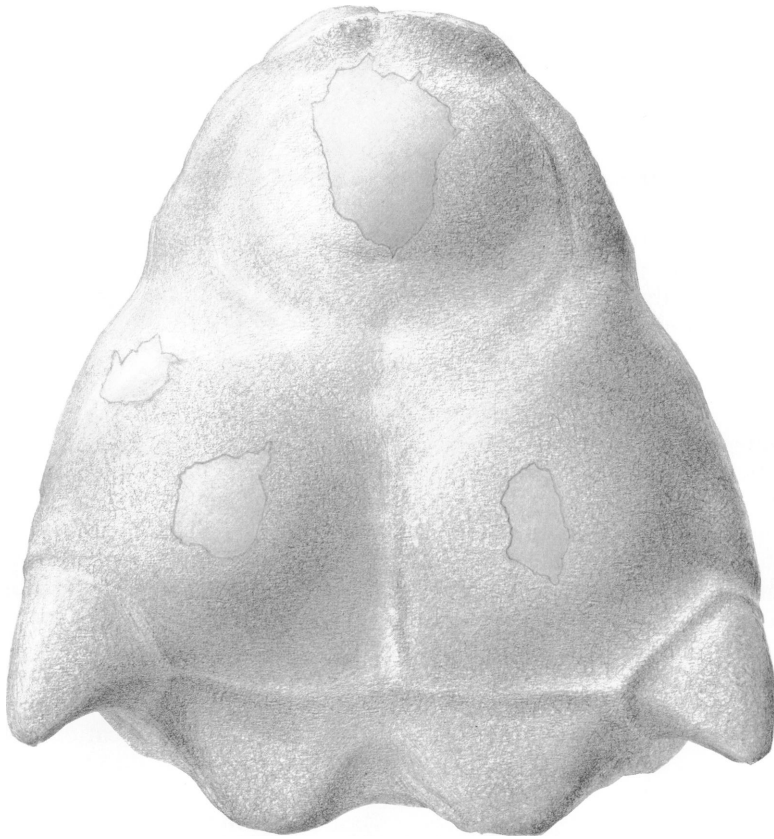


FIG. 33. *Meiolania platyceps*, AM F:43183, dorsal view. Missing areas are smoothly shaded.

posterior to this contact, the palatine reaches the jugal posterolaterally. The palatine in the orbital floor overlies much of the maxilla, as can be seen in the left side of AM F:57984, so that on the ventral surface the maxilla is broadly exposed on the triturating surface rather than narrowly exposed as in the orbit. On its dorsal surface (AM F:57984) the palatine forms nearly all of the foramen palatinum posterius (possibly it does form all, one section is missing), whereas on the ventral surface the maxilla forms a significant portion and the palatine is limited to the medial half of the foramen. The foramen palatinum posterius on the left side of MM F:13825a is divided into two foramina, a common variation in turtles.

Posterior to the foramen palatinum posterius, the palatine and the pterygoid have a long parasagittal suture. This suture changes

direction more posteriorly and extends anteromedially toward the vomer, to form the posterior limits of the palatine. On the dorsal surface of the palatine in AM F:43183 (to the slight extent preserved) and in MM F:13825a there is an anterolaterally directed ridge between the processus pterygoideus externus and the epipterygoid.

The palate of *Meiolania platyceps* (fig. 32) is distinctive in having a pair of troughs on either side of the midline on a broad dome concave ventrally. The palate is arched in a sagittal plane, that is, the vomer is flexed anteroposteriorly as well as transversely. The palatine bone forms the region just lateral to the median troughs and extends laterally to form a recurved ridge just medial to the palatine-ptyergoid suture. The morphology of the palatine in *Meiolania platyceps* is very similar to that in testudinids. The broad

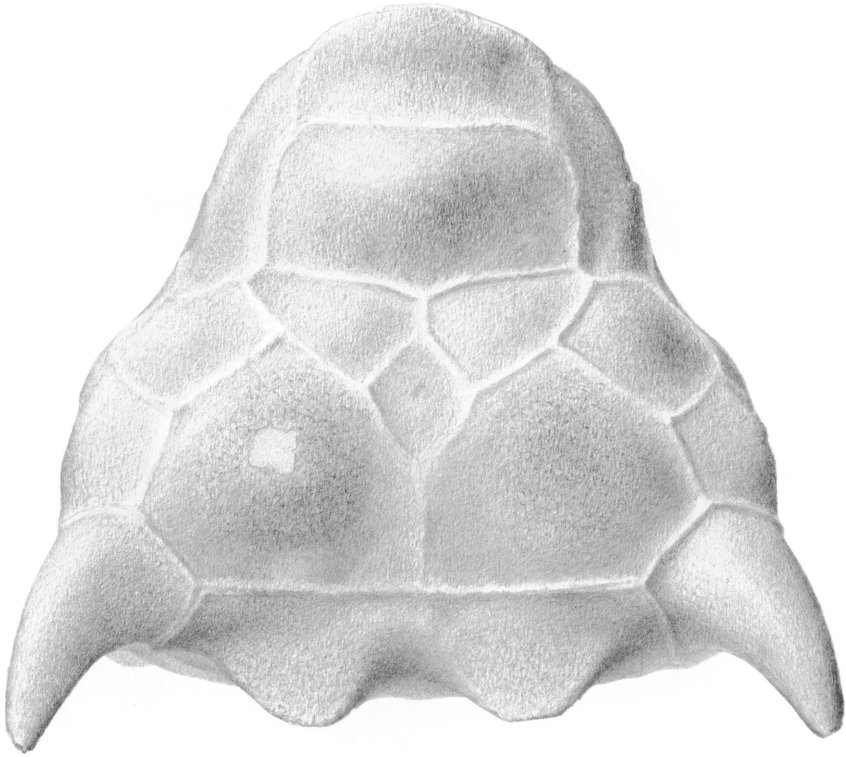


FIG. 34. *Meiolania platyceps*, AM F:61110, dorsal view.

doming of the palate and the long pterygoid-palatine suture are particularly distinctive similarities.

#### QUADRATE

Figures 21, 35, 37, 45

The quadrate is preserved in BMNH R675, BMNH R682, AM F:57984, AM F:61110, AM F:43183, AM F:18668, AM F:208b, AM F:18671, MM F:13825a, MM F:13827, AM F:1209, BMNH R9626, and BMNH R9629-R9635.

One of the prominent features of the meiolaniid skull is the complete enclosure of the cavum tympani and incisura columellae auris by the dermal skull roof. Some cryptodires and pleurodires have closed the incisura columellae auris, however, the extent of bone involved is never so great as in meiolaniids. The resulting expression of the ear on the surface of the skull is a D-shaped opening (facing anteriorly) that has a slightly recessed

margin, presumably for the tympanic membrane (fig. 35). In *Meiolania platyceps* there is limited information about the identity of the bones surrounding the tympanic margin because sutures are absent on nearly all available specimens. Nonetheless, it seems likely that the quadrate itself does not extend onto the cheek but simply abuts laterally against the cheek elements. The anterior edge of the tympanic margin is formed by the quadratojugal; the dorsal limits can be seen in AM F:18668. The quadrate-quadratojugal suture is visible for a short distance ventral to the dorsal limits of the quadratojugal, presumably continuing ventrally along the tympanic margin. In *Crossochelys* the right disarticulated quadrate shows a sutural edge along the lateral margin of the cavum tympani and extending down to the processus articularis, which agrees closely with the presumed quadrate-quadratojugal contact in *Meiolania platyceps*. In AM F:57984 (fig. 22) there is a portion of the squamosal preserved on the

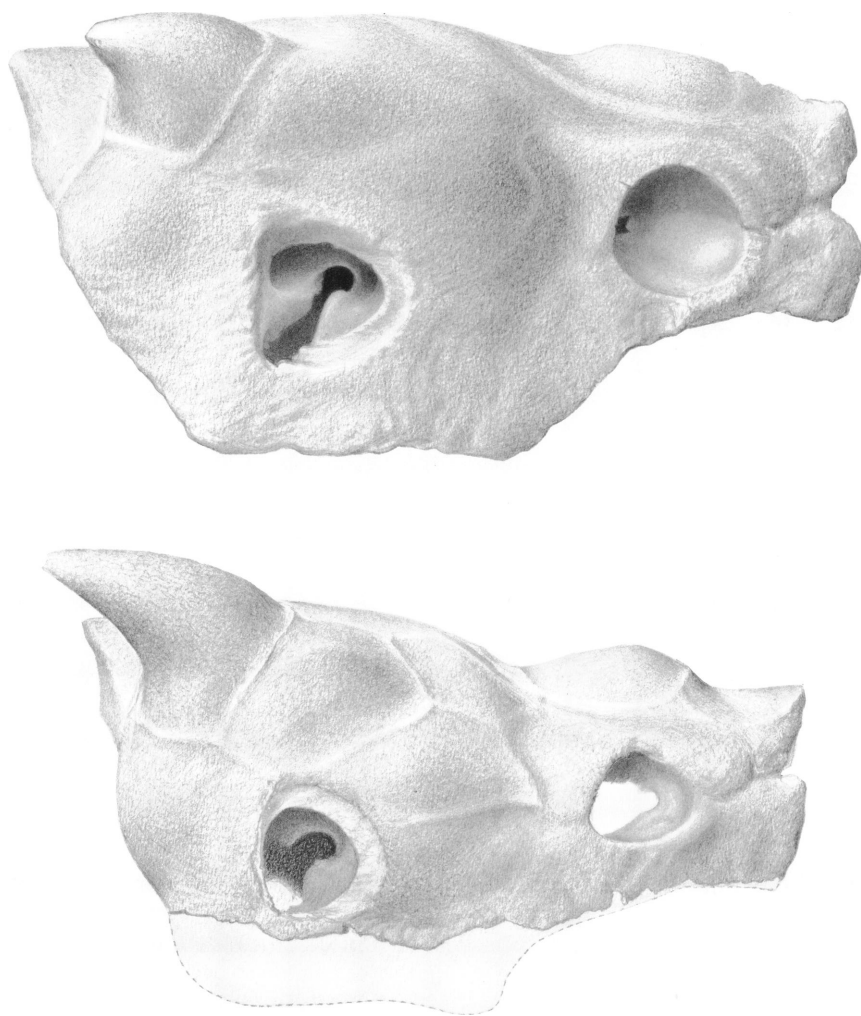


FIG. 35. *Meiolania platyceps*, lateral views. Upper, AM F:43183; lower, AM F:61110. Line marking ventral edge in AM F:61110 is conjectural and based on other specimens.

right side that bears a sutural surface, probably the squamosal-quadratojugal contact, facing anteriorly just below the cavum tympani. The entire posterior portion of the tympanic margin appears to be formed by the squamosal which also extends dorsally and, as can be seen on the left side of AM F:57984, internally. This internal portion of the squamosal forms part of the cavum tympani, again as seen in AM F:57984.

The cavum tympani in *Meiolania platyceps* is quite large in comparison with that in most turtles, but roughly comparable in size

to that seen in some testudinids. The region inside the cavum tympani in most turtles is partially divided into a posterodorsal pocket, the antrum postoticum, and precolumellar fossa (see Gaffney, 1979b, fig. 140). In testudinids both of these areas are quite large and divided by the foramen-like incisura columellae auris and a ridge extending postero-ventrally. In *Meiolania platyceps* the cavum tympani is not divided up in this way and the space shows no particular subdivision but is an irregular, oblong spheroid. Only AM F:43183 has a virtually complete cavum tym-

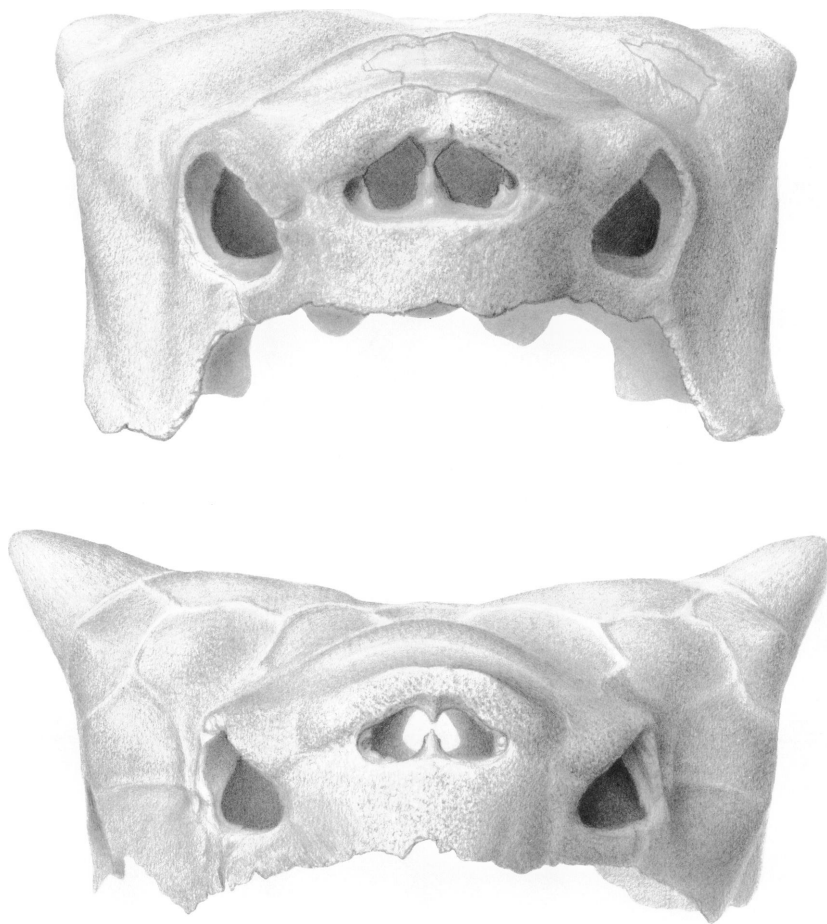


FIG. 36. *Meiolania platycephala*, anterior views. Upper, AM F:43183; lower, AM F:61110. Missing areas are smoothly shaded.

pani, but AM F:61110 and MM F:13825a are partially complete and provide useful views into the cavum tympani. The elongate incisura columellae auris lies along the more ventral portion of the cavum with the greater part of the cavum extending above it. The cavum extends deeply into the skull medially (fig. 45) and is barely separated from the canalis stapedio-temporalis (see right side of MM F:13825a). The dorsal section of the cavum is more or less circular and completely continuous with the region that could be identified as the antrum postoticum. There is no such development of a posterior chamber for the antrum postoticum, as seen in testudinids and many other turtles.

The columellae auris is preserved on both sides in MM F:13825a (figs. 42, 43). On the right side it can be seen in its natural position in the incisura columellae auris. The incisura has an elongate shape which is roughly separated into two oval lobes, a more medial one and a more lateral one. The whole incisura lies in a more horizontal plane rather than the vertical plane seen in most turtles, but it slopes ventrally as it extends laterally. As preserved, the columella lies on the anterior margin of the medial lobe and as it extends laterally it is enclosed ventrally by a blunt fold of bone that extends from the anterior margin of the incisura and curves dorsally behind the columella (fig. 45). This pro-

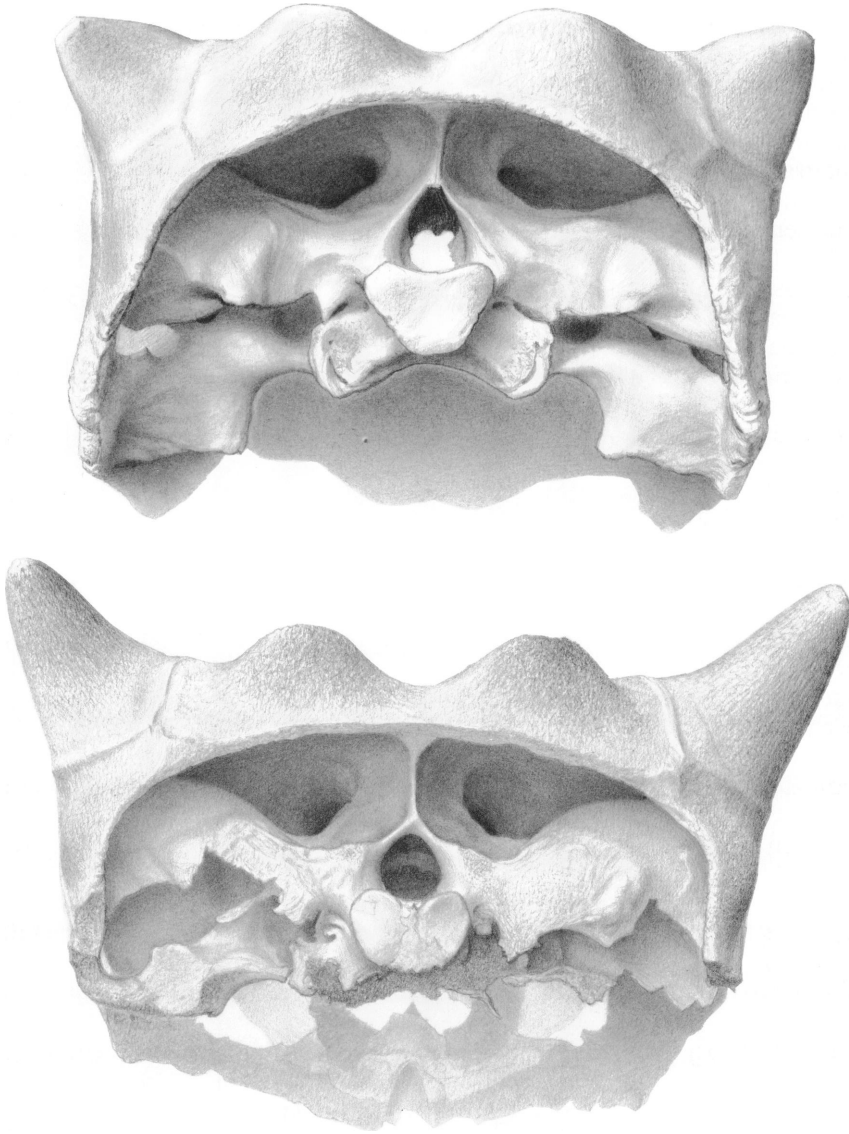


FIG. 37. *Meiolania platyceps*, occipital views. Upper, AM F:43183; lower, AM F:61110.

cess also separates the incisura into two emarginations, apparently the division into stapelial (dorsomedial) and eustachian (ventrolateral) portions. Although the medial emargination is more circular in shape, the lateral lobe is more elongate.

Most of the internal surface of the cavum tympani is formed by a thin sheet of quadrate. Posterodorsally this sheet ends and the

squamosal and a small area of the opisthotic form the antrum postoticum region. The actual limits of the squamosal here are not entirely clear because sutures are visible only in AM F:57984, which is partly broken.

The processus articularis of the quadrate in *Meiolania platyceps* is developed into a moderate extension that bears the condylus mandibularis ventrally. The condylus is near-

ly flat, with a shallow trough in the center as in most cryptodires.

The medial surface of the quadrate is complex because it is involved in the formation of the lateral wall of the cavum acustico-jugulare (see Cavum Acustico-Jugulare). Ventrally, the quadrate ramus of the pterygoid meets the quadrate but even in AM F:57984 the suture is not entirely clear. It can be seen on the right side of this specimen in the floor of the cavum acustico-jugulare but it is lost posteriorly as it reaches the edge of the bone. The suture can be picked up again on the ventral surface just lateral to the fossa cartilaginis epipterygoidei. The processus epipterygoidei (fig. 55) is a short, blunt process that forms the lateral margin of the fossa epipterygoidei, and fits into a trough on the pterygoid, which, in turn, forms the ventral margin of the fossa. In anteromedial view the end of the processus epipterygoideus is thicker ventrally, becomes thinner dorsally, and appears to have been finished in cartilage. At the dorsal margin of the processus epipterygoidei the quadrate-prootic suture begins and can be followed (only in AM F:57984) dorsally and posteriorly to the region of the foramen stapedio-temporalis. The quadrate, however, does not enter the superficial margin of this foramen, occluded by the contact of the prootic and opisthotic. The quadrate underlies the thin posterior flange of the prootic and extends to the opisthotic, so that the lateral wall of the canalis stapedio-temporalis itself is formed by the quadrate. A large dorsomedial area of the quadrate is covered by the lateral projection of the opisthotic, which, together with the squamosal, prevents extensive exposure of the quadrate in the fossa temporalis.

The quadrate-prootic suture can readily be seen within the canalis stapedio-temporalis and the cavum acustico-jugulare in AM F:57984. This suture extends ventrally to the lateral wall of the canalis cavernosus where it enters the cavum acustico-jugulare and then meets the quadrate-ptyergoid suture in the floor of the cavum.

The processus trochlearis oticum (fig. 45) is formed by the prootic and quadrate in *Meiolania platyceps* as it is in most other cryptodires. The processus is weakly devel-

oped in *Meiolania platyceps* with no distinct anterior projection on the otic chamber; nonetheless the processus is larger than in cheloniids and has a morphology very similar to that in some baenids, such as *Plesiobaena*. The quadrate forms a slight anterior overhang when seen in side view with a low convexity on the anterior surface.

The quadrate of *Crossochelys* is very similar to *Meiolania platyceps*. The cavum tympani is the same shape, the medial structures appear the same and the incisura columellae auris is the same to the extent it is preserved. Information on the closure of the incisura posteriorly is lacking due to breakage but the ridge in the lateral part of the incisura is very similar to *Meiolania platyceps*.

#### EPIPTERYGOID

Figures 45, 47, 53, 55

The epipterygoid is preserved in: MM F:13825a, AM F:1209, AM F:18668, AM F:43183, BMNH R682, AM F:18671, AM F:401 and AM F:61110, with sutures visible in AM F:57984, AM F:18668 and AM F:18671. The epipterygoid in *Meiolania platyceps* is a large element forming the dominant portion of the posterior margin of the foramen interorbitale and of all the anterior margin of the foramen nervi trigemini (fig. 47). Dorsally, the epipterygoid reaches the relatively small processus parietalis inferior and extends ventrally to the pterygoid, resulting in an epipterygoid of unusual size. I am not aware of any other turtle (with the possible exception of *Proganochelys*) with an epipterygoid that extends this high dorsally and occupies all of the area between the foramen nervi trigemini and the foramen interorbitale. The posterior margin of the epipterygoid has a short vertical suture with the prootic between the parietal and dorsal margin of the foramen nervi trigemini. The epipterygoid-parietal and epipterygoid-prootic sutures are clearly visible only on the left side of AM F:57984. A well-developed ridge is formed on the lateral surface of the epipterygoid extending the length of the bone from parietal contact to the base of the foramen nervi trigemini.

The ventral portion of the epipterygoid



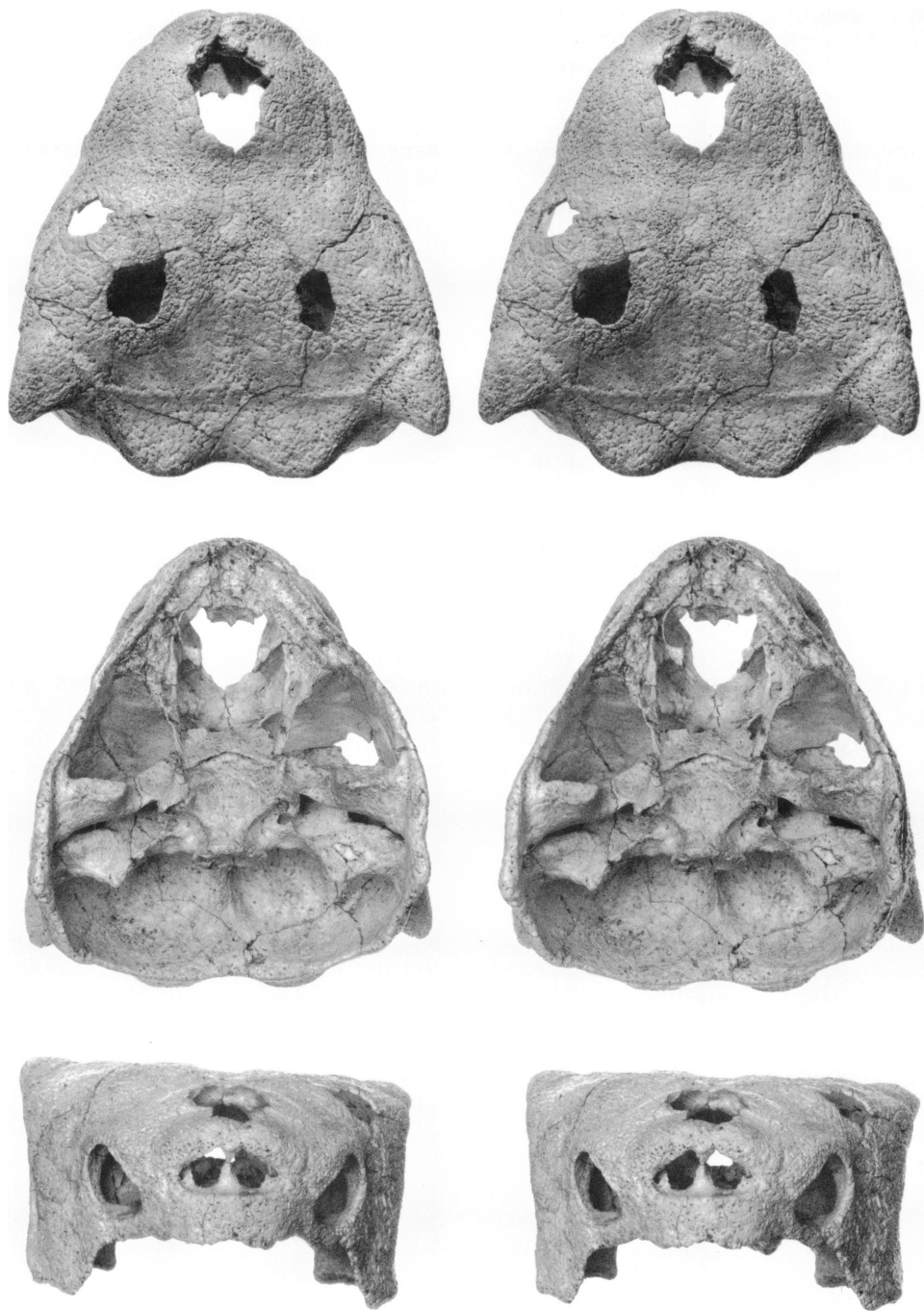


FIG. 38. *Meiolania platyceps*, AM F:43183, stereophotographs.

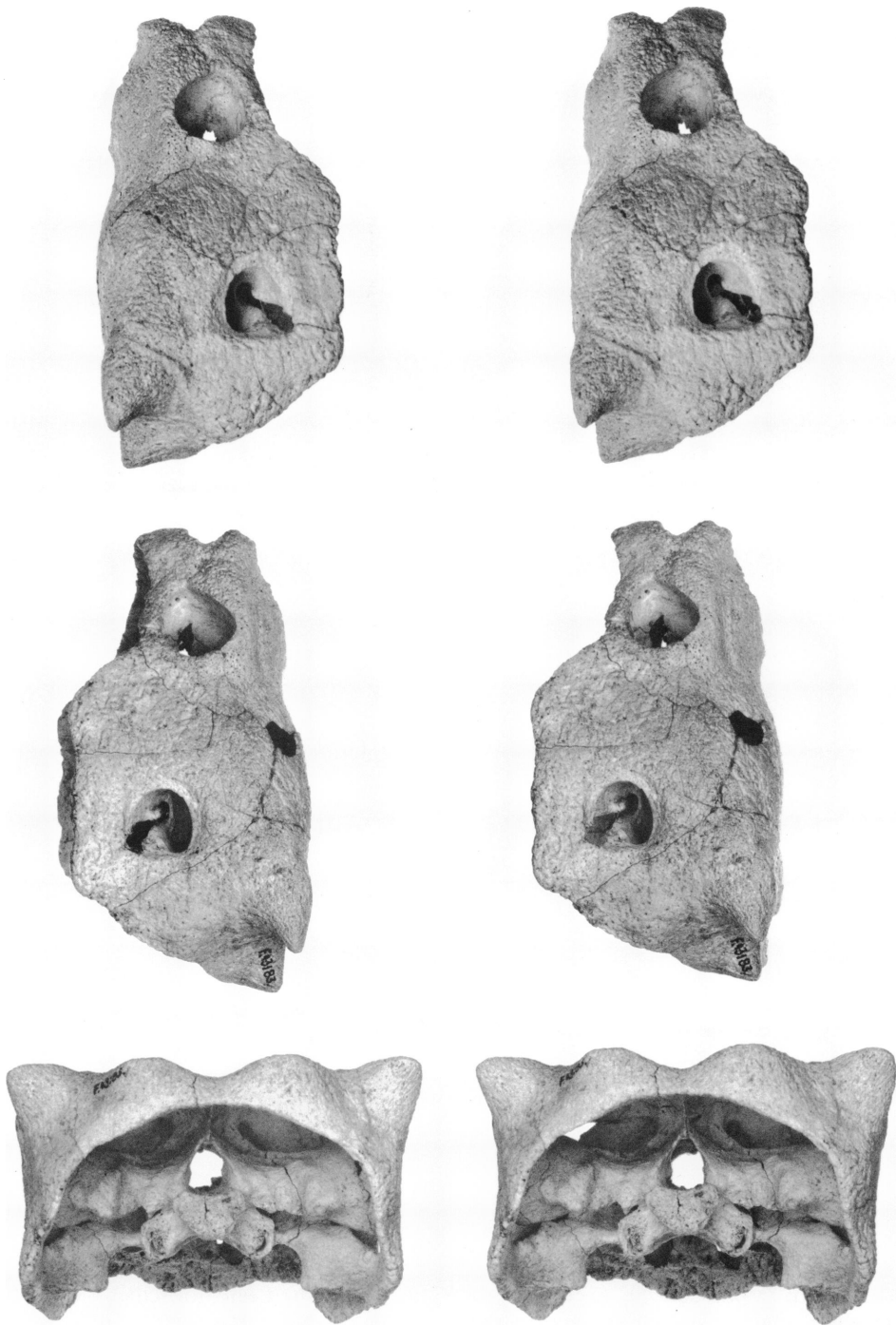


FIG. 39. *Meiolania platyceps*, AM F:43183, stereophotographs.

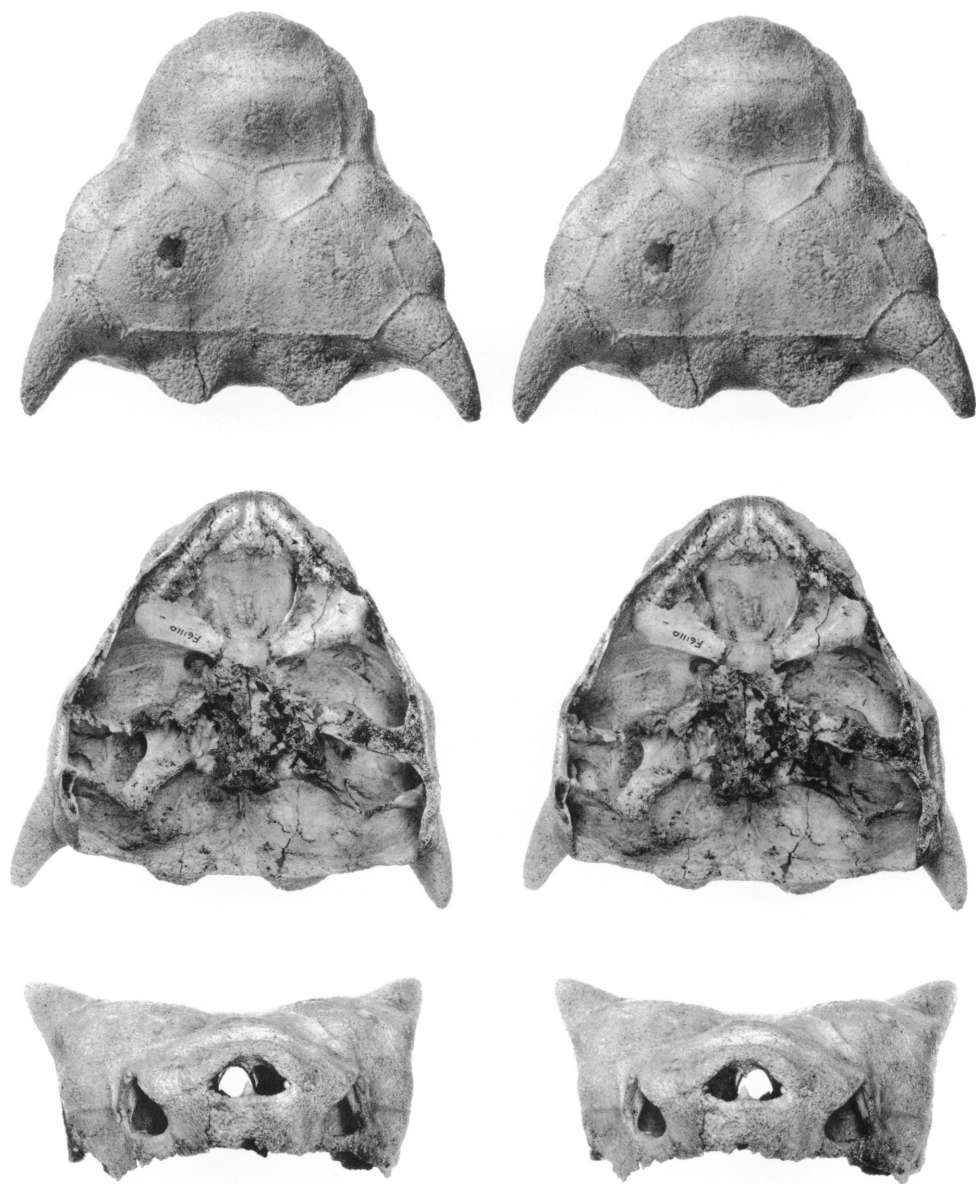


FIG. 40. *Meiolania platyceps*, AM F:61110, stereophotographs.

widens into two processes, an anterior one that extends along the dorsal surface of the palatine (right side of MM F:13825a, and left side of AM F:57984) and a posterior one forming a margin of the fossa cartilaginis epipterygoidei. Both processes usually have

an unfinished end indicating that they were continued in cartilage, as in Recent cryptodires. The anterior process is quite thin, and may be relatively short and blunt, as in AM F:57984 or longer with a widened distal end, as in MM F:13825a. The posterior process

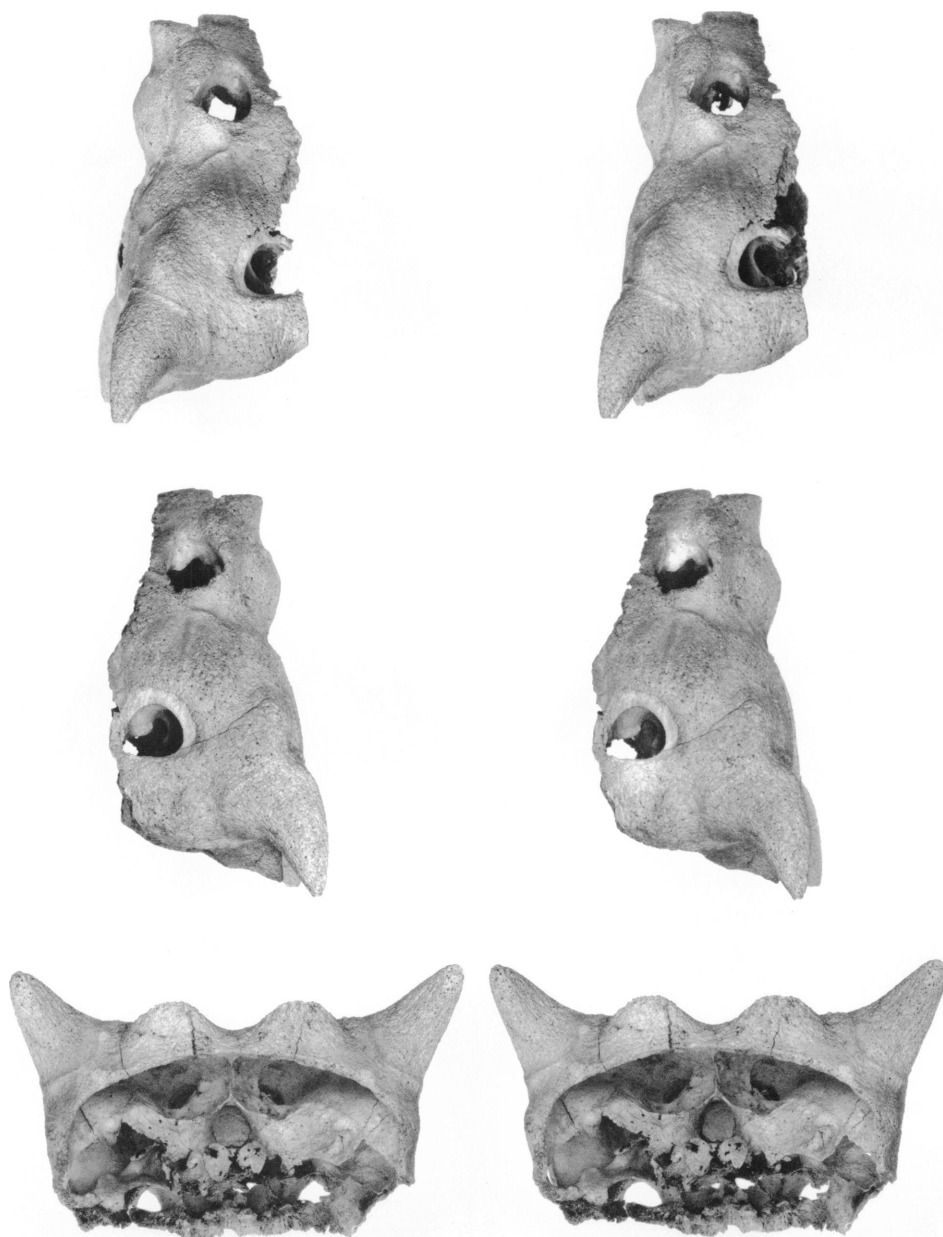


FIG. 41. *Meiolania platyceps*, AM F:61110, stereophotographs.

has thicker bone and lies lateral to the crista pterygoidea, which forms the medial wall of the fossa cartilaginis epipterygoidei. The fossa is best seen in AM F:57984, but it is pres-

ent and developed to about the same extent in AM F:43183, AM F:1209, and MM F:13827. On the left side of MM F:13825a (the right side is damaged and covered by

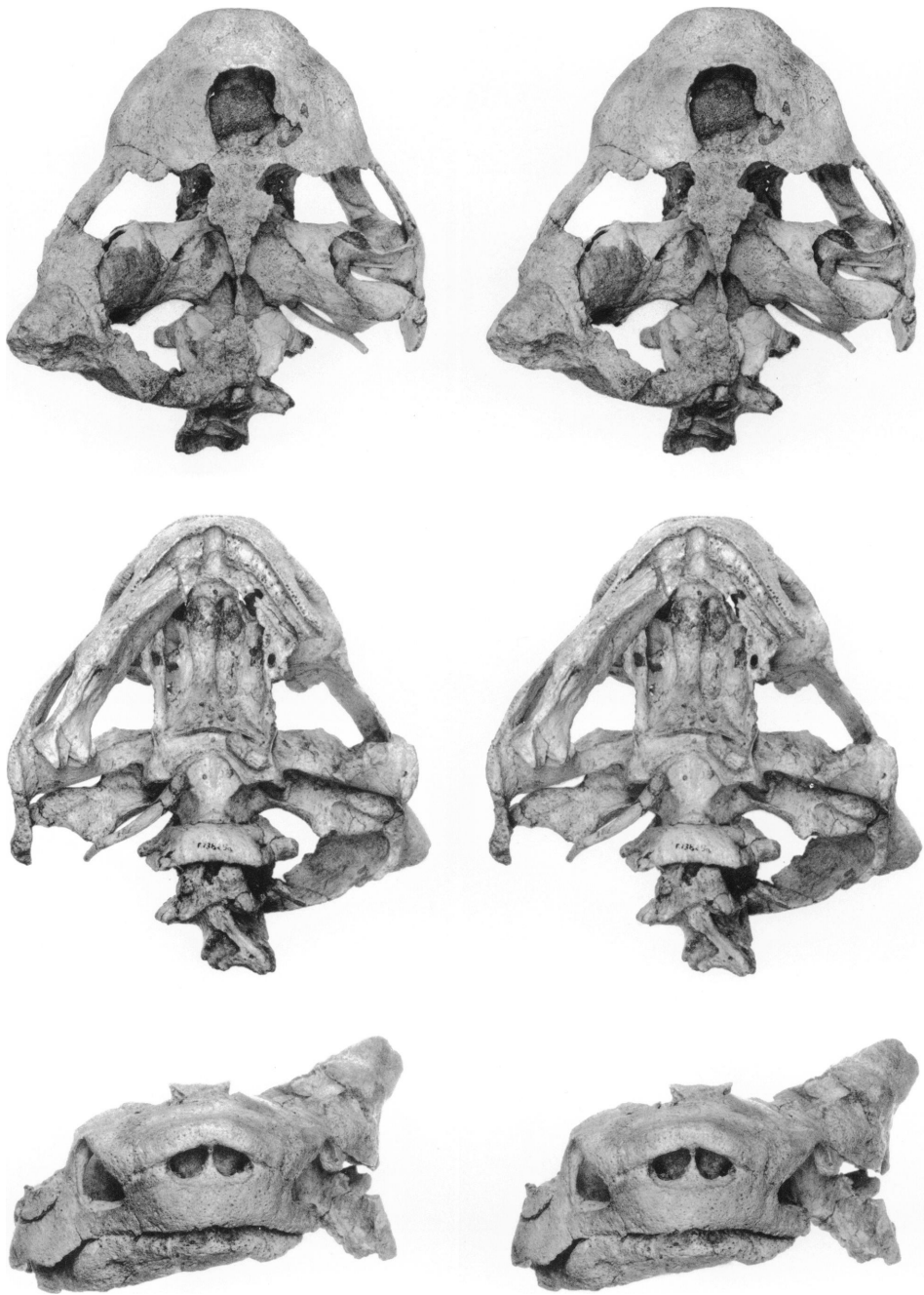


FIG. 42. *Meiolania platyceps*, MM F:13825a, stereophotographs.

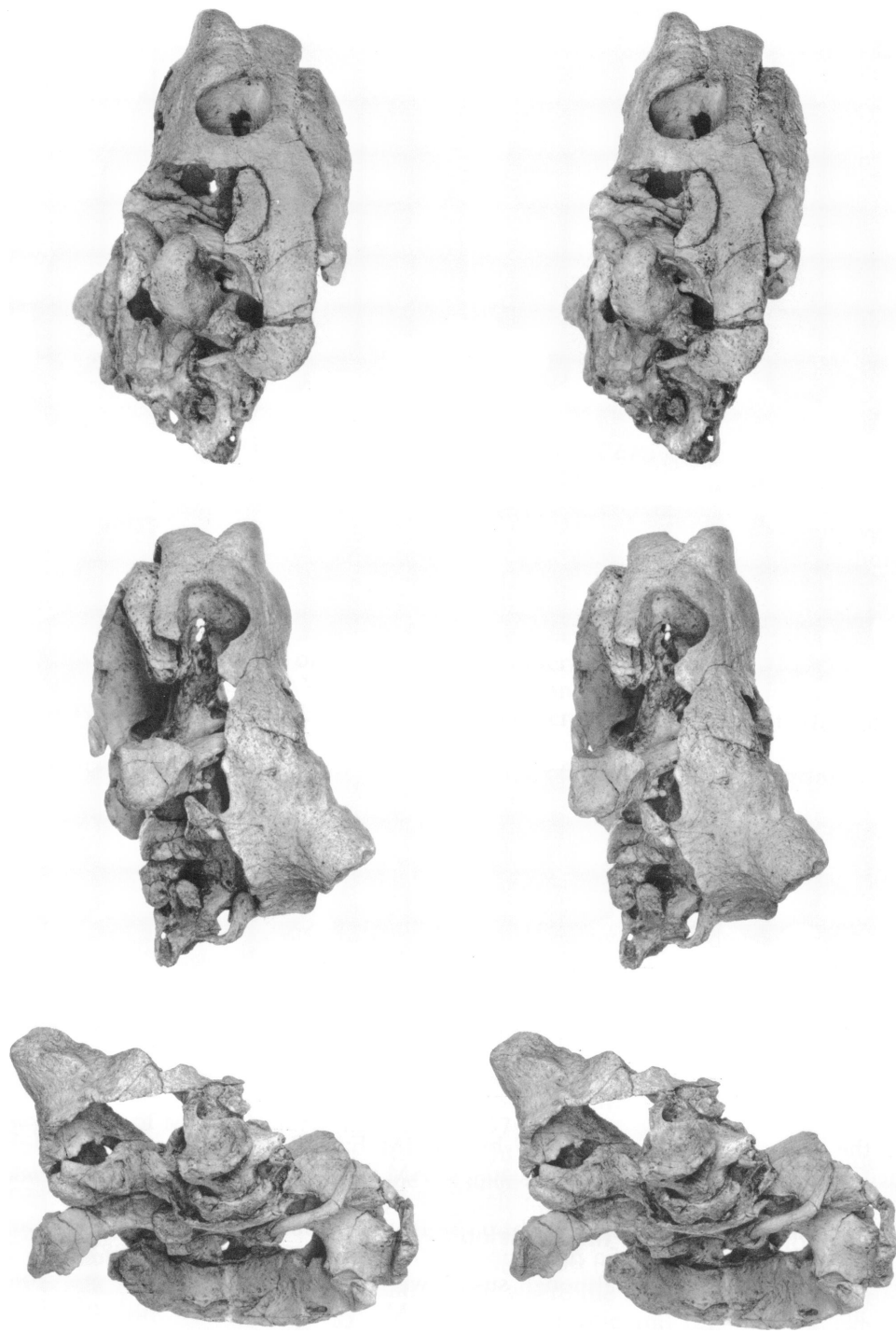


FIG. 43. *Meiolania platyceps*, MM F:13825a, stereophotographs.



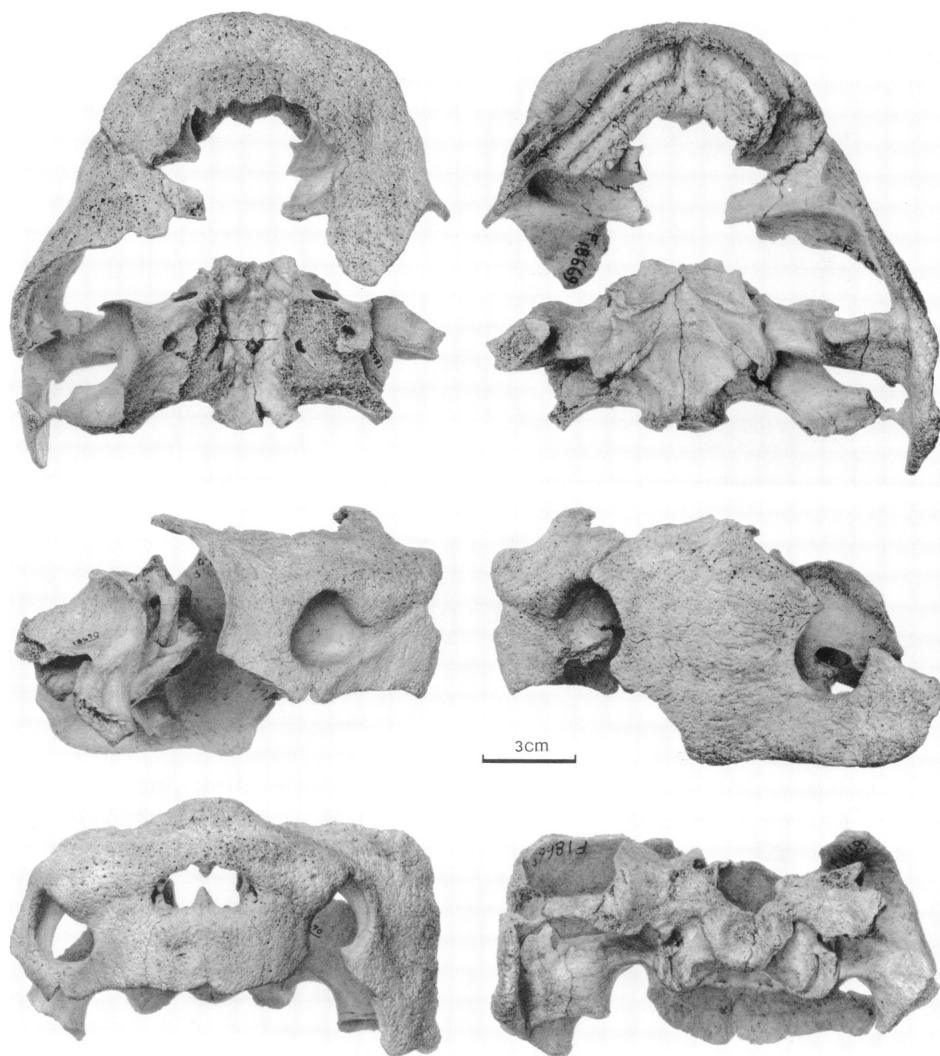


FIG. 44. *Meiolania platyceps*, AM F:18668. Top row, dorsal (left) and ventral (right). Center row, right lateral (left) and left lateral (right). Bottom row, anterior (left) and occipital (right).

matrix), the fossa is entirely obliterated by presumed fusion of epipterygoid and quadrate, the two bones that ossify in the palatoquadrate cartilage (see Gaffney, 1979b, p. 97). This is the only instance of a presumed epipterygoid-quadrate contact, although sutures are absent.

#### PTERYGOID

Figures 21, 32, 45, 58

The pterygoid, or significant portions of it, is preserved in AM F:43183, AM F:1209,

MM F:13825a, AM F:61110, AM F:208a, AM F:208b, AM F:401, AM F:18364, BMNH R675, BMNH R9605, BMNH R9606, and BMNH R682, but the most useful information comes from AM F:57984 (figs. 21, 22) which has the most complete pterygoids, and AM F:18671 (fig. 58), both of which have sutures.

The pterygoid of *Meiolania platyceps* has an anterior process, bearing the processus pterygoideus externus, that extends parasagittally along the lateral margin of the palatine

to the foramen palatinum posterius. In AM F:43183, MM F:13825a, and AM F:57984 the pterygoid forms the posterior portion of the foramen and also extends anterior to it on the lateral side to reach or nearly reach the jugal. Unfortunately the area of the jugal-ptyergoid contact is missing in AM F:57984 and in MM F:13825a and AM F:43183 the sutures are indeterminate, and so the presence or absence of this contact is unknown. On the dorsal surface of the palate in AM F:57984 the palatine overlies enough of the pterygoid to prevent its exposure in the margin of the foramen palatinum posterius. This development of an anterior process of the pterygoid that bears the processus pterygoideus externus is presumably related to the anteroposterior shortening of the main body of the pterygoid. These same features are seen in testudinids and, as in *Meiolania platycephs*, seem to be coincident with the domed palate present in both.

On the left side of MM F:13825a (fig. 32) the lateral margin of the pterygoid is preserved and it has a shallow convex outline with a low, ventrally directed ridge on the margin.

The processus pterygoideus externus is preserved in AM F:43183, AM F:57984, and MM F:13825a and has a morphology very similar to that of testudinids. The vertical plate on the lateral margin of the processus in most cryptodires is absent in *Meiolania platycephs* and testudinids but a distinct swelling of the pterygoid marks the position of the processus (figs. 45, 47). On the dorsal surface of the palate AM F:43183 and MM F:13825a there is an anterolaterally directed ridge beginning on the palatine medially and ending at the processus pterygoideus externus, which appears to be related to a continuation of the epipterygoid onto the palatine (right side of MM F:13825a). A similar feature is seen in other cryptodires, particularly testudinids. On the posterior surface of this ridge, where it lies on the dorsal surface of the processus pterygoideus externus, is a posteriorly facing concavity best seen in AM F:43183 but also preserved in MM F:13825a. This structure is lacking in AM F:57984 although the region where it should occur is preserved on the left side.

The dorsal surface of the main body of the pterygoid is a complex region that, in the

absence of a disarticulated pterygoid for *Meiolania platycephs*, cannot be thoroughly described. The canalis caroticus internus and its associated structures are described elsewhere but the contacts and other structures are described here (see Canalis Caroticus Internus and Associated Structures).

The crista pterygoidea of *Meiolania platycephs* is well developed and generally similar to that of other turtles. It rises dorsally on the medial surface of the epipterygoid to a point just below the ventral margin of the foramen nervi trigemini. In most turtles the crista forms part of the foramen nervi trigemini but in *Meiolania platycephs* the prootic and epipterygoid have a well-developed contact that excludes the pterygoid from the foramen. The fossa cartilaginis epipterygoidei (figs. 53, 55) is formed on the external surface of the pterygoid between the epipterygoid and the processus epipterygoideus of the quadrate. The fossa is narrow dorsoventrally in AM F:57984.

Just medial to the crista pterygoidea is the sulcus cavernosus (fig. 45) which contained the vena capitis lateralis. The sulcus is open dorsally until it reaches the foramen cavernosum, just behind the foramen nervi trigemini, where the sulcus is roofed over dorsally by the prootic and becomes the canalis cavernosus (fig. 50). The foramen cavernosum is oblong and pinched at its center by ridges on the epipterygoid and prootic so that it is incompletely divided into dorsal and ventral portions. The canalis cavernosus itself retains the prootic ridge but does not have an opposing one on the quadrate (which forms the canalis posterior to the foramen cavernosum).

Medially, the anterior half of the pterygoid contacts the basisphenoid and the posterior half meets the basioccipital (fig. 48). The basisphenoid contact begins anteriorly at the dorsal margin of the intrapterygoid slit and can be followed dorsally to the medial wall of the sulcus cavernosus where the prootic-ptyerygoid suture begins. Ventrally, the basisphenoid-ptyerygoid suture extends posteriorly parasagittally along the roof of the intrapterygoid slit to the basioccipital (fig. 21). In AM F:18671 the foramen caroticum basisphenoidale (see section on Canalis Caroticus Internus for discussion) is formed in this suture but in AM F:57984 the suture passes

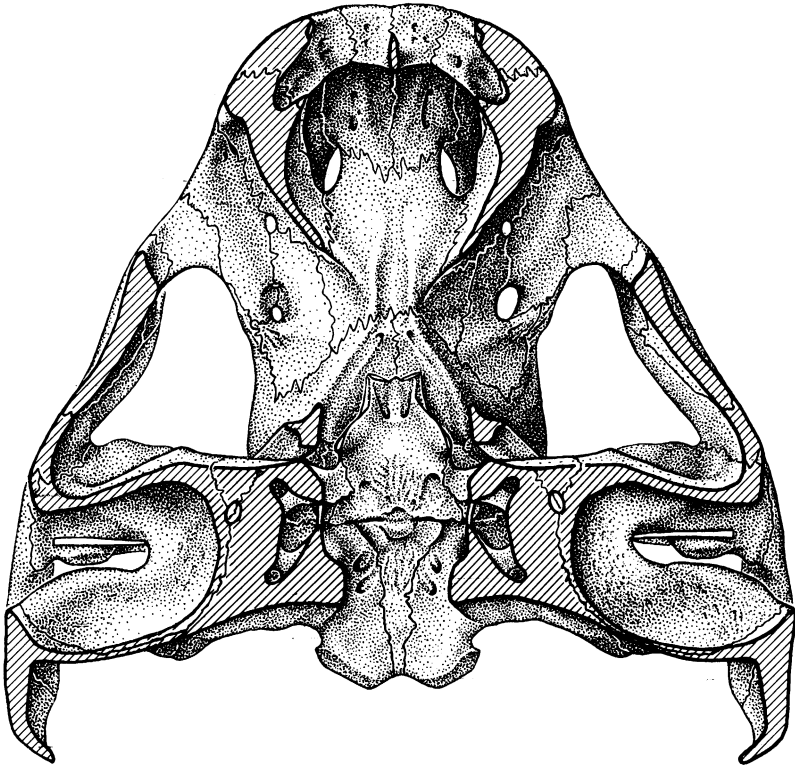


FIG. 45. Part 1. *Meiolania platyceps*, dorsal view of horizontally sectioned skull. Composite based on MM F:13825a, AM F:57984, and AM F:18668. See abbreviations.

lateral to this opening (which is formed entirely by the basisphenoid) and medial to the "small foramen" (formed by the pterygoid). Posterior to the foramen caroticum basisphenoidale the pterygoid-basisphenoid suture irregularly trends medially, more so in AM F:57984, where the pterygoids nearly meet in the midline, than in AM F:18671.

The basioccipital-ptyergoid suture is better known than the other pterygoid contacts because in AM F:18363 (fig. 48) the pterygoid has been disarticulated leaving the basioccipital and right exoccipital that show many of the sutural surfaces. In ventral view the pterygoid-basioccipital suture coincides with the margin of the deep embayment on the ventral surface of the basioccipital. The suture trends posterolaterally to bisect each tuberculum basioccipitale (figs. 21, 22, 37). Anteriorly, the pterygoid is thick; the sutural surface extends vertically between the basioccipital and pterygoid but the more posterior contact sur-

face becomes concave posteriorly so that the pterygoid extends around an anterolaterally facing convexity on the basioccipital. In most *Meiolania platyceps* specimens this curved contact area is a meniscus-shaped space, presumably representing the former presence of cartilage or ligament. The morphology of this space can be seen best in AM F:18364 where portions of the pterygoid are broken revealing the anterior limits of the meniscus-shaped area. In this specimen and in AM F:18671 the anterior portion of the space extends dorsally to open in the floor of the cavum acustico-jugulare. In AM F:18364, AM F:18671, AM F:57984, and AM F:43183 the space is relatively large, while in AM F:401, and AM F:208b the space is greatly reduced or entirely filled with bone.

Examination of AM F:18364 (fig. 48) suggests that the pterygoid met the exoccipital in the floor of the cavum acustico-jugulare just anterior to the foramen jugulare poste-

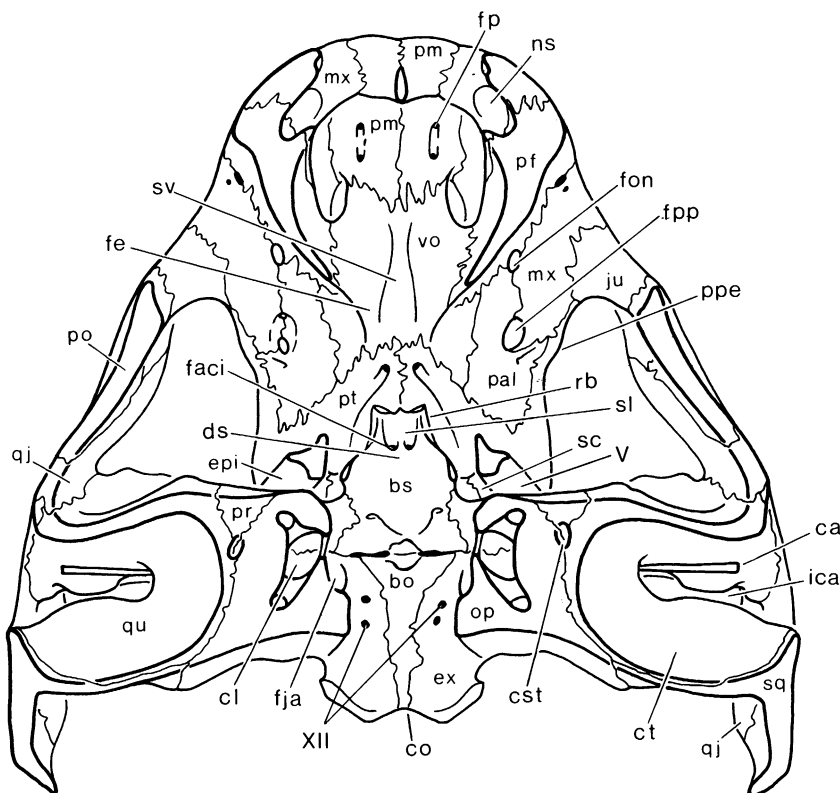


FIG. 45. Part 2.

rius. Unfortunately, neither AM F:18671 nor AM F:57984, both of which show sutures generally, have no sutures visible in this area.

The pterygoid-prootic contact area is best seen in AM F:18364 (fig. 52) and AM F:18671. The prootic, a cubelike element, sits on top of the medial portion of the pterygoid and the lateral portion of the basisphenoid. The pterygoid-prootic suture can be followed in AM F:18671 from the sulcus/canalis cavernosus posteromedially into the cavum acustico-jugulare where it turns anteromedially and ends at the pterygoid-basioccipital suture. The structures, such as the canalis caroticus internus and foramen nervi facialis that occur in this area are described elsewhere (see Canalis Caroticus Internus and Associated Structures).

The most unusual feature of the basicranium in meiolaniids is the thin sheet of bone formed by the pterygoids that enclose a space ventral to the basisphenoid (figs. 21, 22, 46). Owen, in his 1888 description of MM

F:13825a, identified this structure as the "inner or hinder nostril" (Owen, 1888, p. 182; h' in pl. 32) and used this feature as a further distinction from true turtles and as a characteristic of his new group "Ceratosauria." Anderson (1925) coined the term "intrapterygoid slit," which is adopted here, and recognized that it was a unique feature of meiolaniids.

The intrapterygoid slit of *Meiolania platyceps* (figs. 21, 22, 46) is almost completely preserved in AM F:57984 with AM F:18671 supplying significant supplementary data. As described by Anderson (1925) the slit is a space formed by the ventral union of paired pterygoid flanges or lamellae that arise from the lateral margin of the pterygoid and extend medially to join in the midline. This lamella is of a more or less uniform thickness anteriorly where it meets the vomer and palatine but posteriorly it becomes quite thin before it terminates. The lamella from each pterygoid meet in the midline to form a suture,

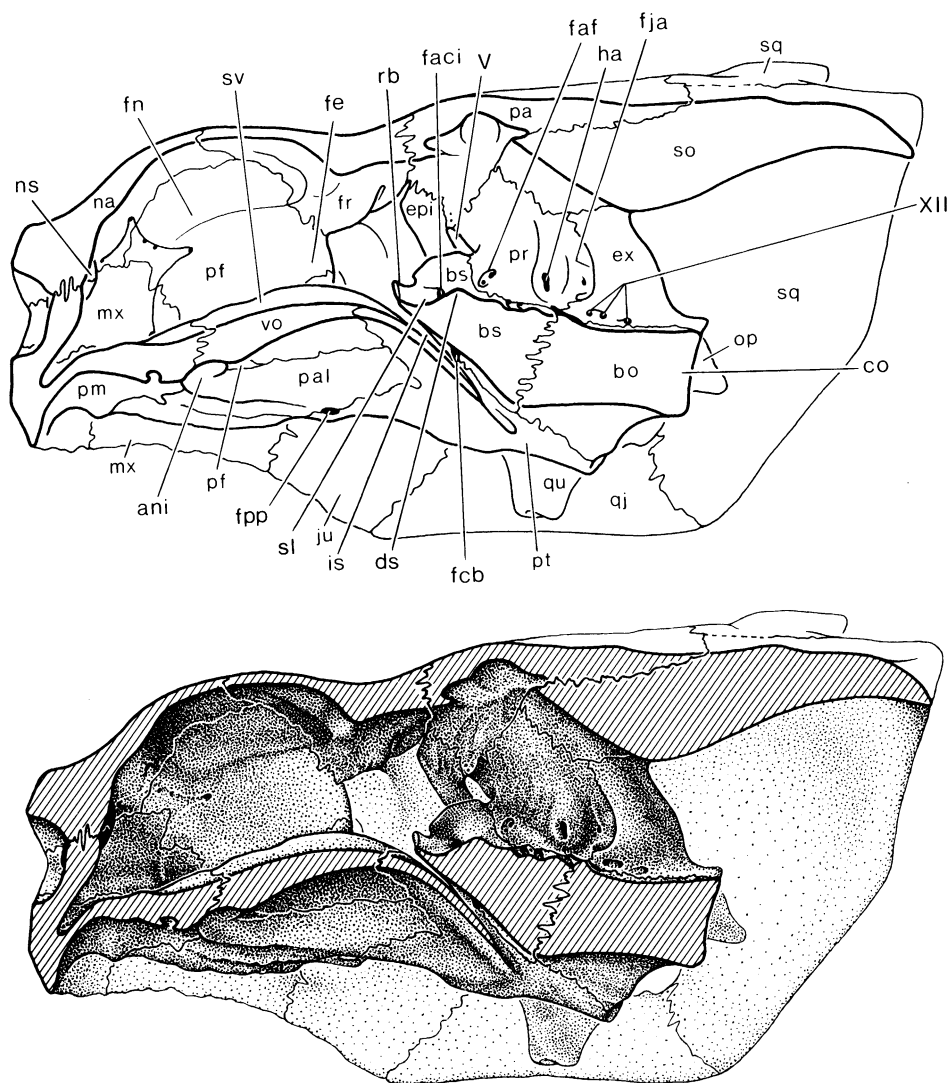


FIG. 46. *Meiolania platyceps*, sagittally sectioned skull. Composite based on MM F:13825a, AM F:57984, AM F:18668, and other specimens. See abbreviations.

visible in AM F:57984 (fig. 21). The dorsal surface of the pterygoid lamella in AM F:57984 has a short ridge that contacts a median ridge on the ventral surface of the basisphenoid to divide the intrapterygoid slit into two slits for a short distance about half-way along the median suture of the pterygoids. It is difficult to demonstrate the presence or absence of this division in any of the other specimens, but the basisphenoid of AM F:18671 (fig. 58) and AM F:18364 both have

a partial basisphenoid ridge (the pterygoids are broken away) indicating that the division was present. Anteriorly, the rostrum basisphenoidale lies very close to the pterygoid in AM F:57984 and appears to lie on it in AM F:61110 and MM F:13825a.

"*Meiolania*" *oweni* does not have the pterygoid preserved, *Niolamia* has both preserved but Woodward's figures (Woodward, 1901) and the cast convey a minimum of useful information; *Crossochelys*, however,

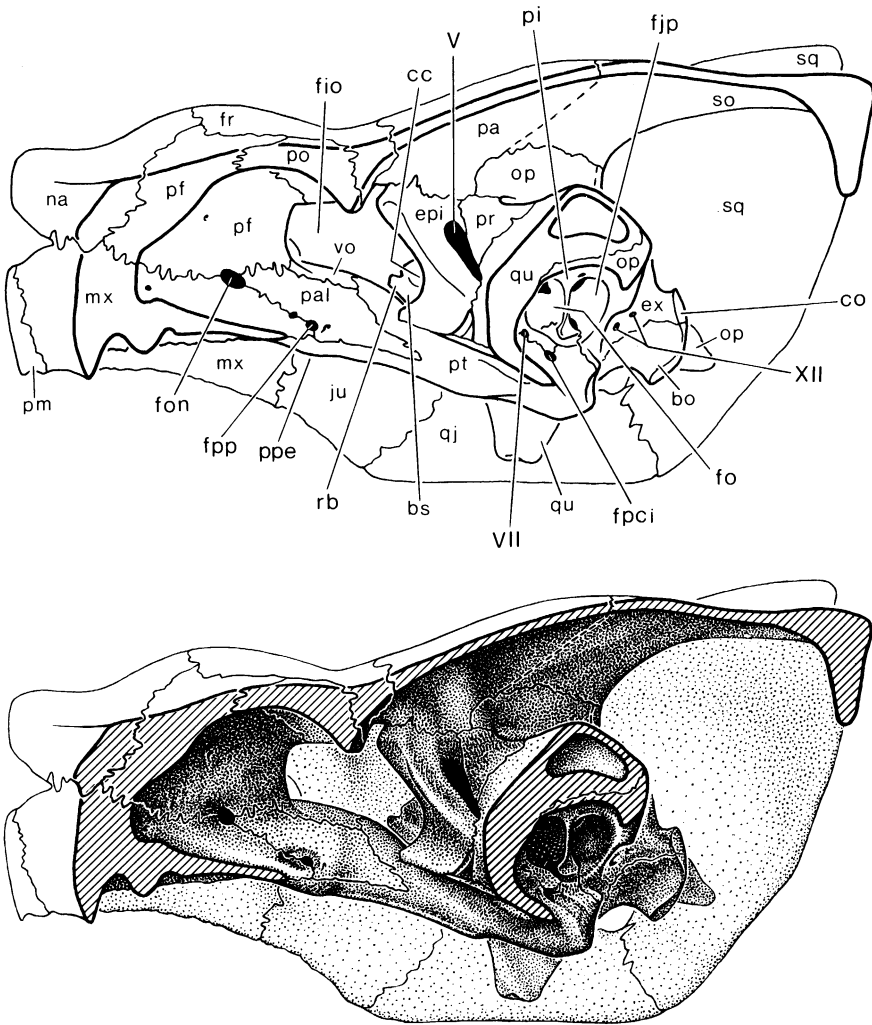


FIG. 47. *Meiolania platyceps*, parasagittally sectioned skull. Composite based on MM F:13825a, AM F:57984, AM F:18668 and other specimens. See abbreviations.

has a right disarticulated pterygoid that provides a number of useful comparisons with *Meiolania platyceps* (fig. 60). The processus pterygoideus externus is not preserved in *Crossochelys* and some of its limits are broken but for the most part the bone appears complete and is generally quite similar to *Meiolania platyceps*. There is a site for the articulation of an epipterygoid of about the same size, ventrally, as in *Meiolania platyceps*, and this is bordered ventrally by a ridge that continues posteriorly, which in *Meiolania platyceps* forms the ventral margin of

the fossa cartilaginis epipterygoidei. This ridge runs posteriorly into the sutural surface contacting the quadrate and forms the lateral margin of the canalis/sulcus cavernosus. The morphology of the pterygoid in this region is nearly identical in both *Meiolania platyceps* and *Crossochelys*, and suggests the presence in *Crossochelys* of a large epipterygoid like that in *Meiolania platyceps*.

The foramen posterior canalis carotici interni of *Crossochelys* lies at the posterior edge of the pterygoid, as in *Meiolania platyceps* and eucryptodires, and is formed by both



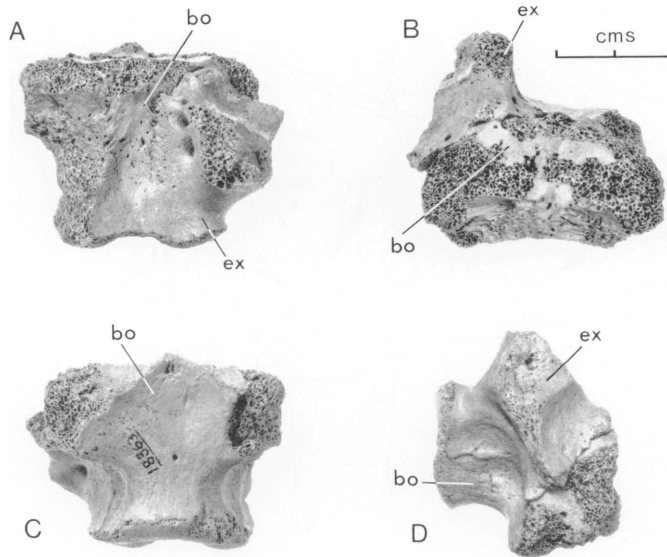


FIG. 48. *Meiolania platyceps*, AM F:18363, fragment consisting of basioccipital and portions of exoccipitals. A, dorsal; B, anterior; C, ventral; D, right lateral. In A and C anterior is toward top of page. See abbreviations.

pterygoid and, apparently, basisphenoid (the latter element is absent in the only specimen of *Crossochelys*) rather than entirely by the pterygoid as seems to be the case in *Meiolania platyceps*. In *Meiolania platyceps* the pterygoid continues posterior to the foramen posterius canalis carotici interni to form a significant portion of the tuberculum basioccipitale, however, in *Crossochelys* has no extension posterior to this foramen and a basioccipital contact would be absent or of limited extent in contrast to the extensive basioccipital-pterygoid contact in *Meiolania platyceps*. Following the canalis caroticus internus anteriorly, there is the dorsal opening into the foramen pro ramo nervi vidiani, as in *Meiolania platyceps*, and anterior to this, the ventral opening onto the surface of the pterygoid, the foramen caroticum basisphenoidale. As in *Meiolania platyceps* the position of the foramen caroticum basisphenoidale marks the change from pterygoid to basisphenoid in the formation of the lateral wall of the canalis caroticus internus. The "pit" (noted by Simpson, 1938, p. 232) in the ventral surface of the pterygoid in *Cros-*

*sochelys*, just anterior and lateral to the foramen caroticum basisphenoidale, does not have a match in *Meiolania platyceps*. However, it is possible that this pit is that described by Evans and Kemp (1975) in *Mesochelys* and Gaffney (1979a) in *Glyptops*, and which contained a lateral spur of the basisphenoid. If the hypothesis that the foramen caroticum basisphenoidale of meiolaniids is homologous to the foramen posterius canalis carotici interni of baenids is accepted, then the identification of the pit in *Crossochelys* with the pit in *Mesochelys* and *Glyptops* takes on some significance. A close examination of the pit in *Crossochelys*, however, suggests to me that the size and perhaps the presence of the pit may be due to postmortem breakage or over-preparation.

The medial lamella that forms the floor of the intrapterygoid slit is quite apparent in *Crossochelys* and has been described by Simpson (1938). Restoring the intrapterygoid slit in *Crossochelys* can be done by flipping the pterygoid over and around the most likely midline axis with very interesting results (fig. 60). In *Meiolania platyceps* the foramen ca-

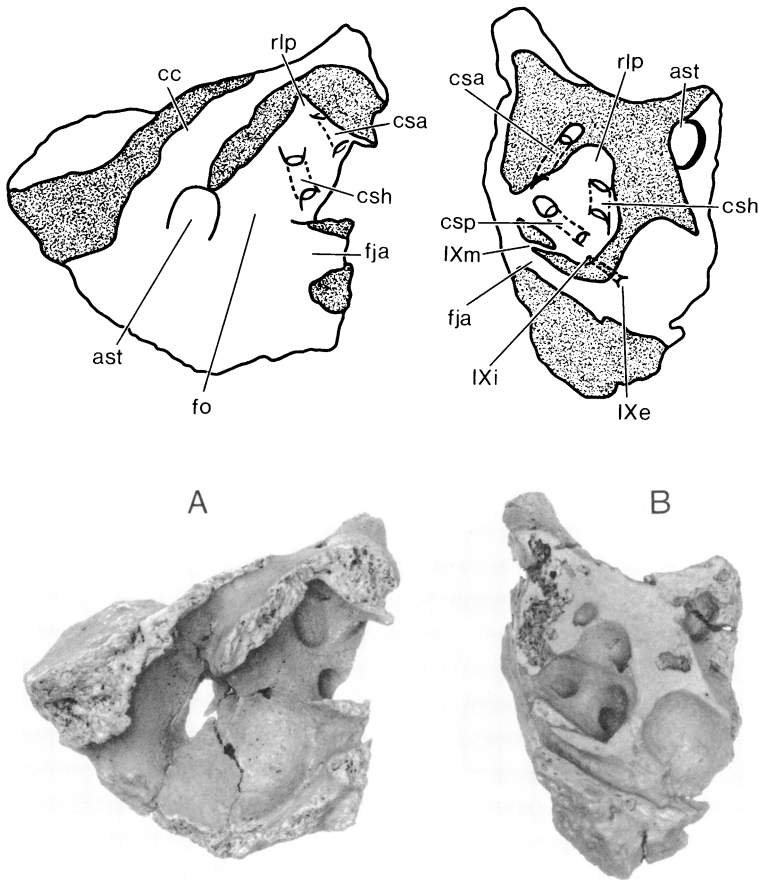
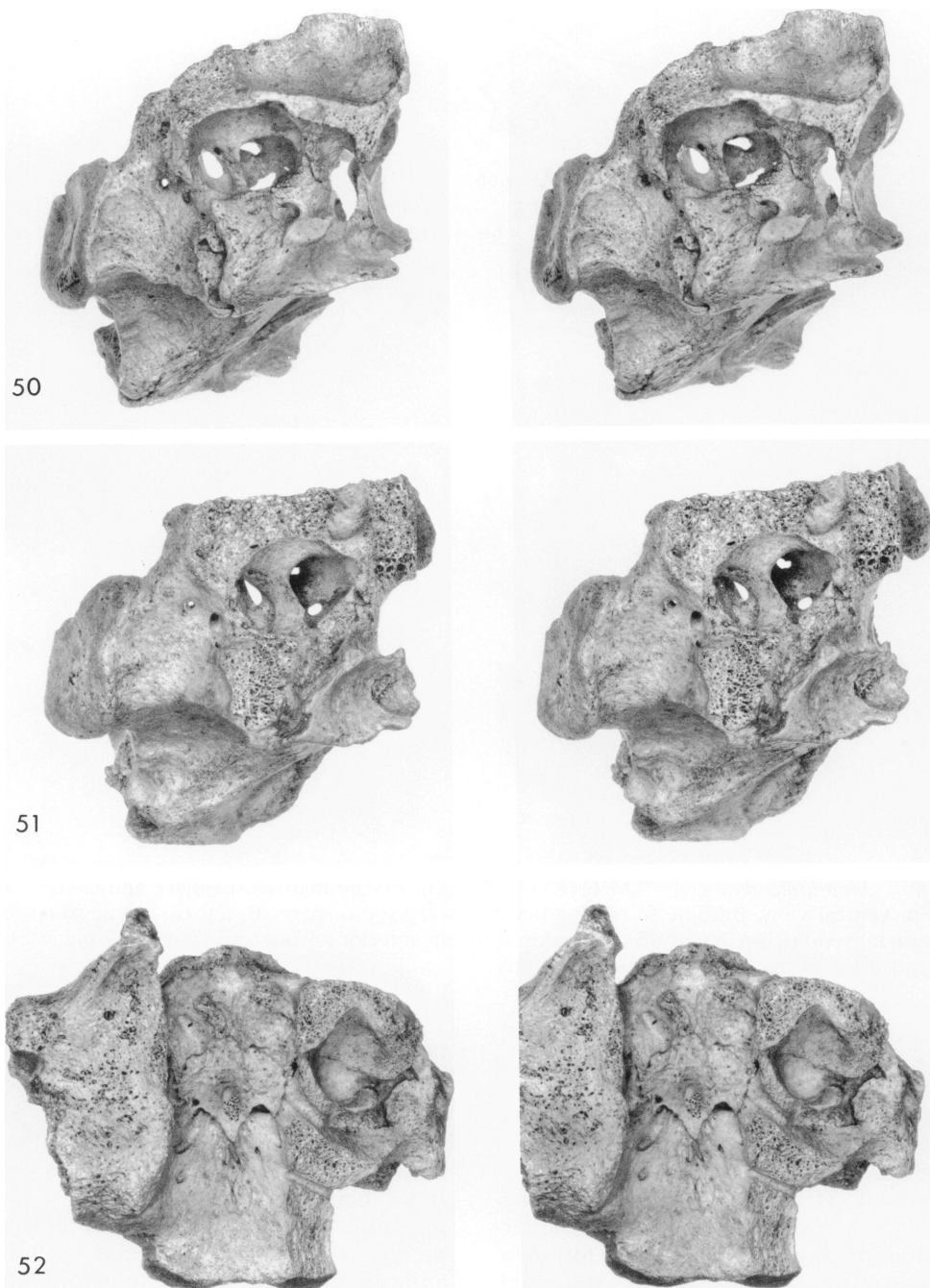


FIG. 49. *Meiolania platyceps*, AM F:18314. A, right, cavum acustico-jugulare and cavum labyrinthicum in ventral view, midline to right, anterior toward top of page; B, left cavum acustico-jugulare and cavum labyrinthicum in ventral view, midline to left, anterior toward top of page. The plane sectioned in B is more dorsal than in A. See abbreviations.

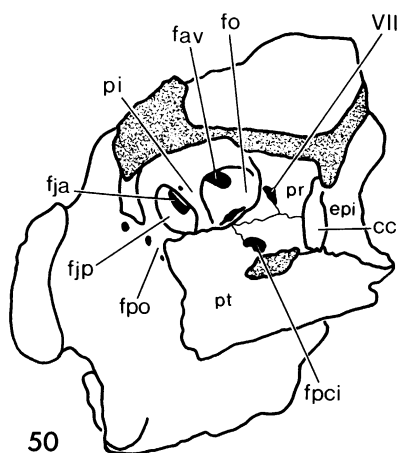
roticum basisphenoidale is completely concealed beneath the pterygoid lamella which extends posteriorly to cover much of the basisphenoid and forms the intrapterygoid slit. In *Crossochelys*, the foramen caroticum basisphenoidale is visible in ventral view because the posterior margin of the intrapterygoid slit is distinctly anterior to the foramen, thereby exposing most of the basisphenoid. I think that this difference in morphology is quite significant phylogenetically. The *Crossochelys* condition of the intrapterygoid slit is more like the primitive casichelydian condition and may be hypothesized as primitive with regard to the condition in *Meiolania*

*platyceps*. In other cryptodires and pleurodires (the Casichelydia of Gaffney, 1975), the two pterygoids usually lie on either side of the basisphenoid in such a way that the main body of the basisphenoid prevents the posterior half of the pterygoids from meeting medially, whereas the anterior half of the pterygoids meet medially and underlie the anterior portion of the basisphenoid. This anterior part of the pterygoid is a flange that is very similar to the ventral lamella of the pterygoid in meiolaniids in the following features:

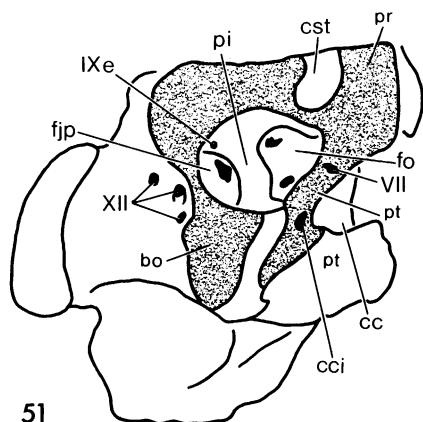
- (1) It is the anteromedial part of the pterygoid.



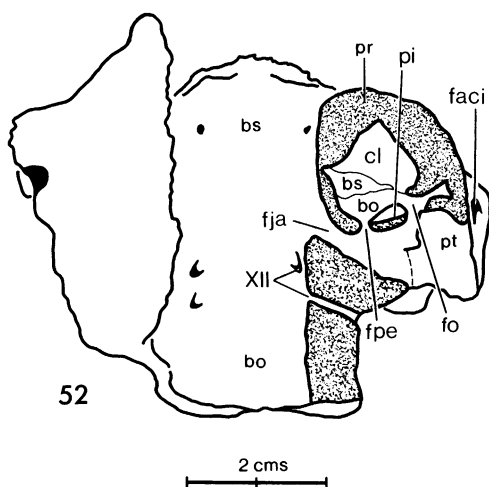
FIGS. 50–52. *Meiolania platyceps*: 50. AM F:18671, lateral oblique stereophoto of right otic region. 51. AM F:18364, lateral oblique stereophoto of left otic region (reversed to facilitate comparison with fig. 50). 52. AM F:18364, dorsal stereophoto of braincase with right otic chamber exposed. See abbreviations.



50



51



52

- (2) It has the shape of a flat sheet of bone projecting medially from a thicker section of the pterygoid.
- (3) It underlies the rostrum basisphenoidale.
- (4) It forms the ventral and lateral wall of the canalis caroticus lateralis and foramen caroticum laterale (hypothesized in meiolaniids).

In *Crossochelys* the lamella is in virtually the same position as in casichelydians, except that it is separated from the basisphenoid by a horizontal fissure, the intrapterygoid slit. In *Meiolania platyceps*, however, the lamella is telescoped or pushed posteriorly in relation to the rest of the pterygoid and the basisphenoid so that structures visible ventrally in *Crossochelys* (the foramen caroticum basisphenoidale and the main body of the basisphenoid) are mostly covered in *Meiolania platyceps*. Therefore, *Crossochelys* would appear to be more like the generalized casichelydian condition in this feature than *Meiolania platyceps*.

*Crossochelys* has what appears to be the canalis nervi vidiani with a posterior foramen at the anterolateral margin of the intrapterygoid slit and the anterior foramen at the anterior edge of the epipterygoid contact. The two foramina cannot be probed and their continuity is undemonstrated but this is the usual position for this structure.

#### SUPRAOCCIPITAL

Figures 21, 37, 46, 47

The region of the supraoccipital is preserved in AM F:43183, AM F:61110, AM F:57984, AM F:18364, AM F:18671, AM F:208a, AM F:208b, AM F:1209, MM F:13825a, MM F:13827, BMNH R606, BMNH R608, BMNH R9617, BMNH R9618, and AM F:64471.

Unfortunately, the supraoccipital is one of the elements in *Meiolania platyceps* for which there is still little information regarding sutures. The anterodorsal suture with the parietal can be seen on the parietal of AM F:57984 (fig. 22) and AM F:61108 (fig. 31) even though the supraoccipital lies in a V-shaped median fissure formed between the two parietals as in other turtles and ends an-

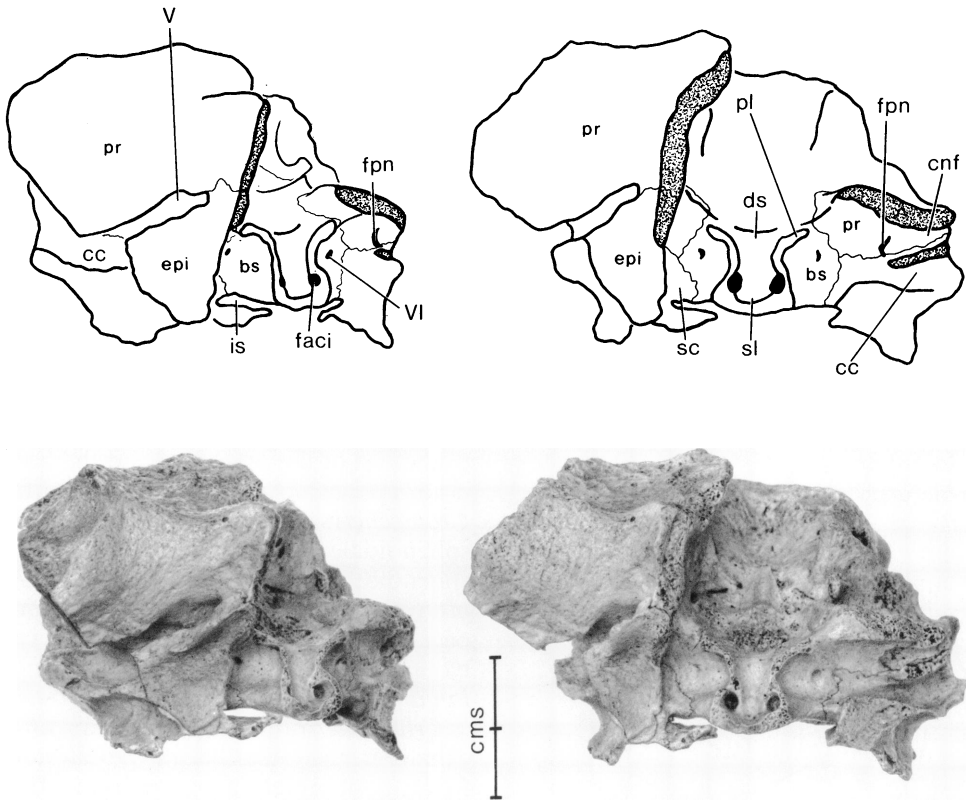


FIG. 53. *Meiolania platyceps*, AM F:18671, braincase. Left, anterolateral view of ethmoid region; right, anterior view. See abbreviations.

teriorly in a cartilaginous block, visible in the endocast. The anteroventrolateral limits of the supraoccipital, which presumably contacted the processus inferior parietalis, are not determinable.

The posteroventral part of the supraoccipital consists of the crista supraoccipitalis, a structure which is usually extensive in other turtles, but not well developed in *Meiolania platyceps*. The crista is nearly complete in AM F:61110 and AM F:43182. The crista is attached to the skull roof from the anterior-most position of the supraoccipital to the posterior limits of the crista where it broadens dorsally in its contact with the skull roof. The crista is deepest over the foramen magnum and becomes shallower in front and behind it.

In most turtles the supraoccipital has little

if any part in the skull roof formation but in *Crossochelys* and *Meiolania*, this bone has a prominent position in the skull roof. The supraoccipital of *Crossochelys* has a considerable expansion of bone on the dorsal and posterior part of the crista supraoccipitalis that forms the medial part of the large horizontal crest characteristic of the South American meiolaniids. The squamosal in *Crossochelys* forms all the A-horn, whereas the large supraoccipital fits between the squamosals so that there is a considerable distance between the A-horns of each side. In *Meiolania platyceps*, however, the A-horn scale areas are relatively close together, the median area of the "frill" is small, and there is little room for a posterior expansion of the supraoccipital such as seen in *Crossochelys*. The supraoccipital in *Meiolania platyceps* is

wide anteriorly and becomes narrow posteriorly.

The ventral part of the supraoccipital forms the dorsal third of the cavum labyrinthicum (described under Cavum Labyrinthicum).

### EXOCCIPITAL

Figures 21, 37, 45, 46, 48

The exoccipital is preserved in the following specimens: AM F:57984, AM F:61110, AM F:43183, AM F:401, AM F:18671, AM F:18364, AM F:208a, AM F:208b, AM F:18314, AM F:18668, MM F:13825a, BMNH R9605, BMNH R9606, and BMNH R682.

The dorsolateral portion of the exoccipital has no determinable sutures in any of the *Meiolania platycephs* specimens, although it presumably contacts the opisthotic and supraoccipital as in other turtles. This dorsolateral part of the exoccipital forms most of the foramen magnum, which in *Meiolania platycephs* is inclined so that the dorsal margin is farther anterior than the ventral margin, an unusual situation in turtles (figs. 37, 46). The margin of the foramen magnum varies in *Meiolania platycephs* from relatively thick in AM F:57984 to quite thin in AM F:61110.

Ventromedially, the exoccipital has a broad articulation with the basioccipital, with the exoccipitals meeting or nearly meeting in the midline (figs. 45, 48). Presumably, as in other turtles, the exoccipital forms the posterior margin of the foramen jugulare anterius. Just posterior to the foramen jugulare anterius are the foramina nervi hypoglossi which in *Meiolania platycephs* consist of two prominent foramina with a third much smaller one between the most anterior foramen nervi hypoglossi and the foramen jugulare anterius in some specimens (AM F:18363, AM F:208a). The contact of the exoccipital with the basioccipital is best seen in AM F:18363, the only specimen in which these sutures are preserved.

The exoccipital forms the posterior wall of the recessus scalae tympani as in other turtles and, apparently all of the foramen jugulare posterius (figs. 50–52). The foramen jugulare posterius is a variable structure in *Meiolania platycephs*. In AM F:57984, AM F:18671, and

AM F:43183 it is open laterally and continues with the fenestra postotica, whereas in BMNH R9605 and AM F:208b it is surrounded by bone. Just anterolateral to the foramen jugulare posterius in the floor of the cavum acustico-jugulare is a presumed contact of the exoccipital with the pterygoid.

### BASIOCCIPITAL

Figures 21, 37, 45, 46, 48, 58

The following specimens preserve the basioccipital: AM F:57984, AM F:61110, AM F:43183, AM F:401, AM F:18671, AM F:18364, AM F:208a, AM F:208b, AM F:18314, AM F:18668, MM F:13825a, MM F:13827, BMNH R682, BMNH R9605, BMNH R9606, and BMNH R675. The presence of a disarticulated basioccipital plus right exoccipital (AM F:18363, fig. 48; also figured in Anderson, 1925, pl. 33, fig. 1) considerably aids study of these elements and much of this description relies on this specimen.

The anterior surface of the basioccipital articulates with two elements, dorsally with the basisphenoid in a deep transverse suture and ventrally with the pterygoids in a shallower, posterolaterally trending suture that curves dorsally at the posterior margin of both elements to form a more vertical contact area within the tubercula basioccipitale (see Pterygoid for description). This contact area on the basioccipital is in the shape of anterolaterally directed protuberances that fit into each pterygoid. Much of the sutural surface was formed in cartilage because C-shaped cavities remain in all *Meiolania platycephs* specimens (figs. 37, 44) but a few, and are visible posteriorly and in some cases in the floor of the cavum acustico-jugulare (fig. 52).

The dorsal surface of the basioccipital (fig. 45) is largely covered by the exoccipitals but a variably exposed area is present on the midline. In AM F:18363 (fig. 48) the exoccipitals do not meet in the midline until the condylus occipitalis is reached, whereas in AM F:18671 the exoccipitals meet at the level of the foramen jugulare anterius leaving only a small triangular area of the basioccipital exposed near the basisphenoid suture. Laterally the basioccipital forms part of the floor of the cavum labyrinthicum and the cavum acus-

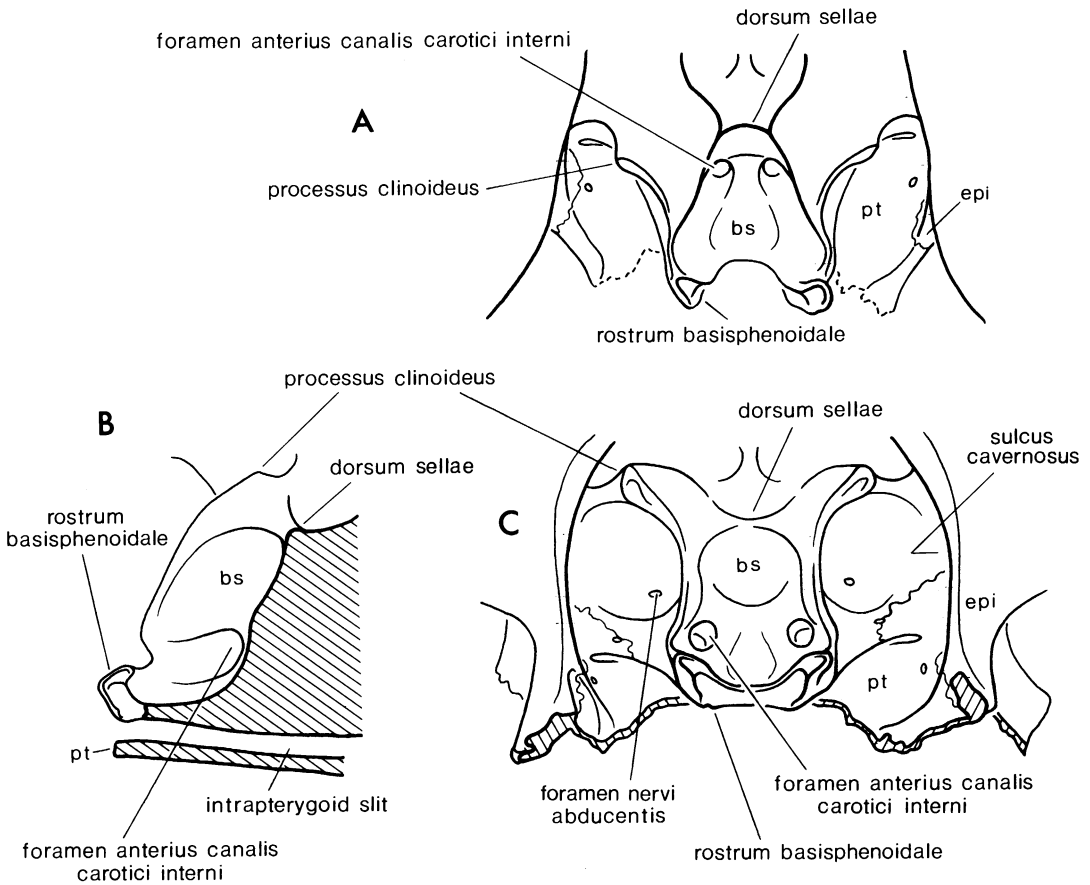


FIG. 54. *Meiolania platyceps*, AM F:61110, region around basisphenoid. A, dorsal view; B, sagittal section; C, anterior view. Facing page stereophotographs; upper, dorsal view; lower, anterior view. Photographs and line drawings are reversed, left to right, because they were made using a mirror. See abbreviations.

tico-jugulare (fig. 52). A small portion of the prootic seems to contact the basioccipital where they form part of the ventral rim of the fenestra ovalis. More posteriorly the ventral end of the processus interfenestralis of the opisthotic articulates with the basioccipital.

The basioccipital may or may not be exposed in the foramen magnum; sutures are difficult to determine and both conditions can be seen. The condylus occipitalis is solid in all specimens but a trace of sutures can be seen in AM F:18363 and AM F:61110. In AM F:18363 (fig. 48) the basioccipital-exoccipital suture can be followed along the lateral side of the condylus where it indicates

the exoccipital as forming the upper half and the basioccipital the lower half. As the suture turns medially onto the articular surface of the condylus it extends dorsomedially so that the exoccipitals form the dorsolateral corners of the condylus. In AM F:61110 (figs. 37, 41) the portion of the basioccipital intervening between the dorsally converging exoccipitals is recessed slightly showing its position and that in this specimen, which may be a juvenile, the exoccipitals do not meet in the midline.

The articular surface of the condylus occipitalis (fig. 37) is quite similar to other turtles: there is a median concavity surrounded by a low rounded ridge. On the outside of the



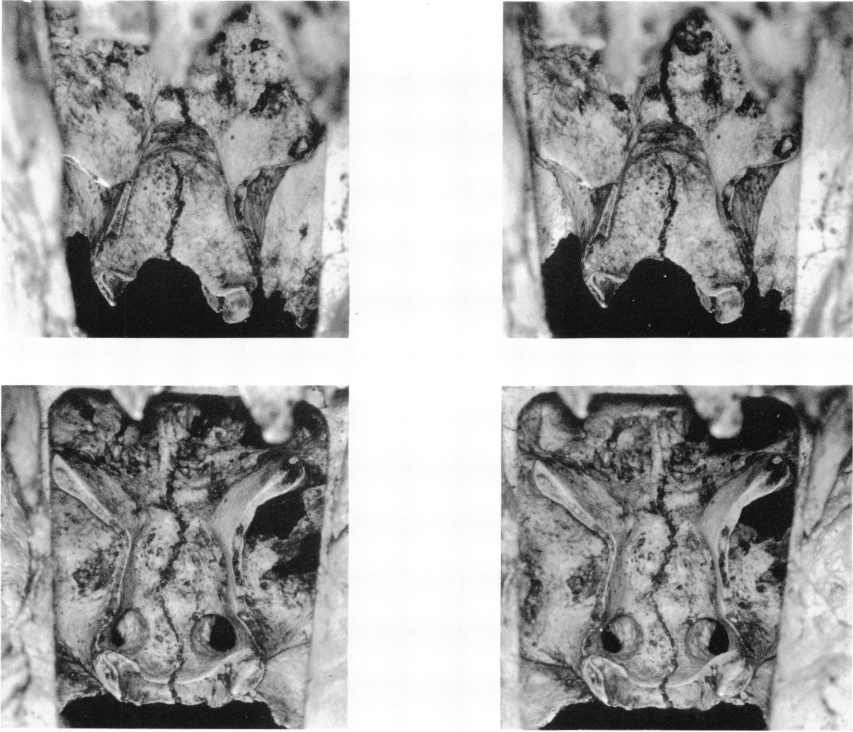


FIG. 54. Continued.

ridge three articular areas can be roughly demarcated: a ventral one and two dorsal ones (borne primarily by the exoccipitals).

### PROOTIC

Figures 21, 45–47, 50–52

The prootic is preserved in: AM F:208a, AM F:208b, AM F:401, AM F:18364, AM F:57984, AM F:61110, AM F:43183, BMNH R9605, BMNH R9603, BMNH R682, and MM F:13825a.

Anterodorsally, the prootic has a short anterior process that articulates with the unusually high epipterygoid in an interdigitating suture visible in AM F:57984 (fig. 55). The ventral edge of this process forms the anterodorsal margin of the foramen nervi trigemini, whereas the entire dorsal margin of the foramen is formed by the main body of the prootic. The epipterygoid forms the remainder of the foramen nervi trigemini. Ventromedially, the prootic contacts the basisphenoid and ventrolaterally the pterygoid. The prootic forms the roof and, together with the

pterygoid, the medial wall of the sulcus/canalis cavernosus and the foramen cavernosum (see Pterygoid for further description).

Dorsolaterally, the prootic contacts the quadrate and, together with the opisthotic, they form the canalis stapedio-temporalis. The way in which these three bones make up the canal is complex and different from other turtles, which generally lack an opisthotic contribution to this canal. Laterally, the quadrate makes up part of the aditus canalis stapedio-temporalis and the lower two-thirds of the canalis stapedio-temporalis. The opisthotic curves anteriorly and the prootic posteriorly to meet above the quadrate to form the upper third of the canal so that the foramen stapedio-temporale does not have a quadrate contribution. Medially, the prootic forms most of the canalis stapedio-temporalis and the opisthotic forms part of the canal dorsally and ventrally, the intervening sutures being unclear. It is only in AM F:57984 that any sutures in this area are visible and the prootic-opisthotic suture is often fused. It is even possible that the supraoccipital may

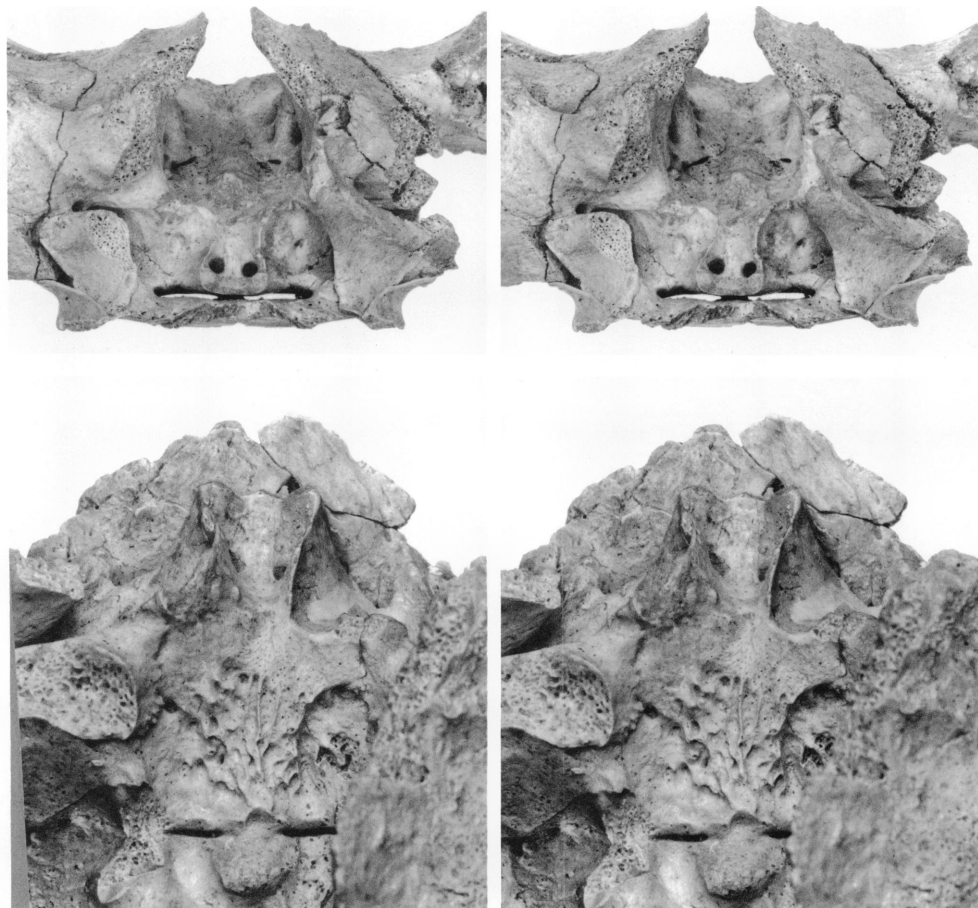


FIG. 55. *Meiolania platyceps*, AM F:57984, stereophotographs of braincase. Upper, anterior view; lower, dorsal view (magnified 2 $\times$  in comparison to upper view). See figures 53, 54 for identification of structures.

enter the margin of the foramen stapediotemporale because there are no sutures known between that element and the prootic or opisthotic.

The ventral limits of the prootic (figs. 45, 35) can be seen in AM F:57984 and AM F:18671, although some of the sutures are ambiguous. The prootic lies on top of the pterygoid laterally and the basisphenoid medially so that the dorsal suture between these two bones is entirely obscured. In AM F:18671 the prootic-basisphenoid suture can be followed from the fossa acustico-facialis laterally into the floor of the cavum labyrinthicum. About halfway across the cavum

labyrinthicum the prootic, trending postero-laterally, crosses the basisphenoid-basioccipital suture and continues to the margin of the fenestra ovalis. Lateral to the fenestra ovalis the prootic crosses the basioccipital-ptyergoid suture and lies on the latter bone. The prootic forms an irregular wall above its contact with the pterygoid between the canalis cavernosus laterally and the main portion of the cavum labyrinthicum medially. At the posterior margin of this wall (figs. 50, 51) is a foramen for a branch of the VII nerve (see below and Canalis Caroticus Internus and Associated Structures). The prootic does not appear to contribute to the formation of the

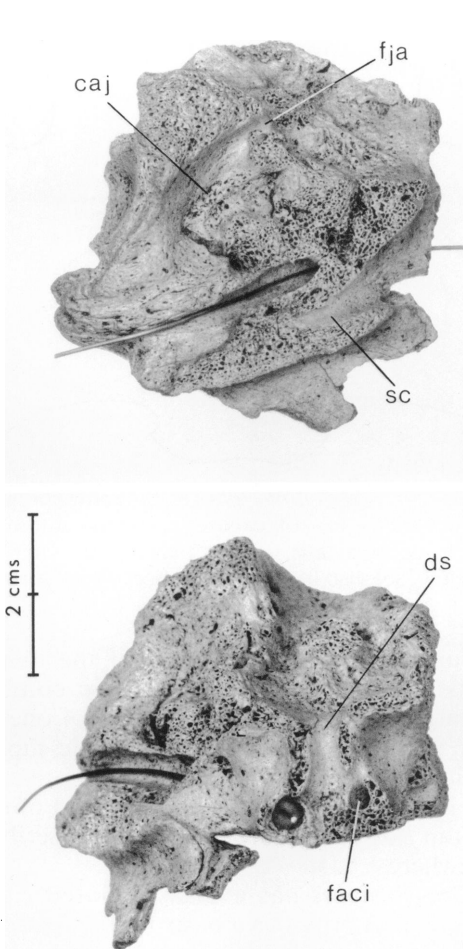


FIG. 56. *Meiolania platyceps*, AM F:401, basicranial fragment showing path of canalis caroticus internus (wire) in lateral (upper) and anterior (lower) views. See also figures 57, 58. See abbreviations.

foramen posterius canalis carotici interni nor to the canalis caroticus internus.

The medial surface of the prootic forms part of the lateral wall of the cavum cranii (fig. 46). The most anterior structure of this surface is the fossa acustico-facialis, which is relatively deep and contains (as in most turtles) three foramina, one for the facial nerve, and two for parts of the acoustic nerve. Within the fossa, the foramen nervi facialis is the

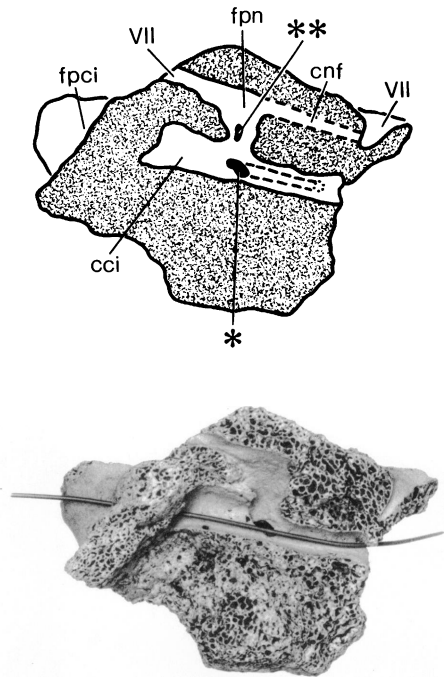


FIG. 57. *Meiolania platyceps*, BMNH R9606, medial view of eroded left prootic and pterygoid showing canalis caroticus internus (wire). Single asterisk is a foramen leading into a small canal (here exaggerated in size for clarity) of unknown function. Double asterisk is a foramen leading from the foramen pro ramo nervi vidiani into the canalis cavernosus. See also figures 56, 58. See abbreviations.

most anterior with one of the foramina nervi acustici very close to it. The more posterior foramen nervi acustici is somewhat variable in the available specimens; in AM F:18364, AM F:208a and AM F:208b it is fully formed in bone but in AM F:57984 and AM F:18671 this foramen is irregular and continuous with a ventral unossified part of the hiatus acusticus. The hiatus acusticus is usually fully ossified in *Meiolania platyceps*, however, this small region around the prootic-basisphenoid suture may remain cartilaginous. Posterodorsal to the fossa acustico-facialis is another foramen, the foramen aquaducti vestibuli. This foramen lies in an area that seems to be one of the last parts of the hiatus acusticus to ossify so that it may be quite large

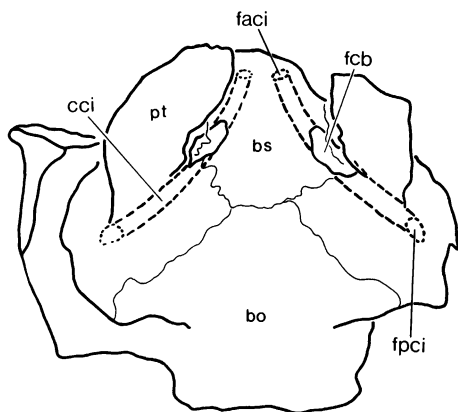


FIG. 58. *Meiolania platyceps*, AM F:18671, braincase in ventral view showing canalis caroticus internus and related structures. See also figures 56, 57. See abbreviations.

(cf. AM F:57984) and irregular in some specimens that had portions of the cartilage remaining. The foramen aqueducti vestibuli and the foramina nervi acustici penetrate the relatively thin medial wall of the cavum labyrinthicum but the foramen nervi facialis travels posterolaterally as a canal and exits in the cavum acustico-jugulare (figs. 50, 51). About midway along this canal lies the foramen pro ramo nervi vidiani, a short ventral connection with the canalis caroticus internus. At about this same position another foramen in the lateral wall communicates with the canalis cavernosus (see Canalis Caroticus Internus and Associated Structures for further description).

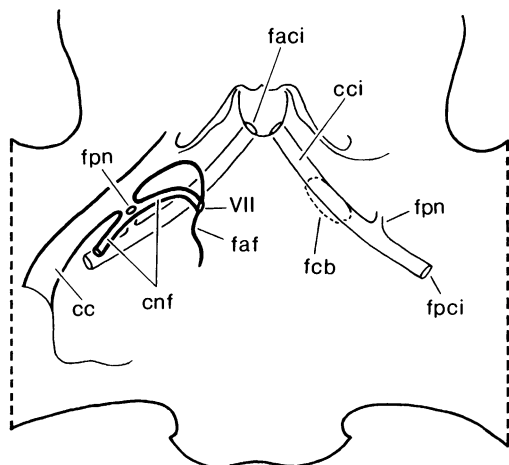


FIG. 59. *Meiolania platyceps*. Semidiagrammatic illustration of canalis caroticus internus, canalis nervi facialis, and related structures in dorsal view. See also figures 56–58. See abbreviations.

Somewhere in the vicinity of the hiatus acusticus, the prootic-opisthotic contact should occur but there is no sign of one in any specimen. Similarly, the prootic-supraoccipital suture is not identifiable.

The prootic forms the anterior part of the cavum labyrinthicum which is described elsewhere.

*Crossochelys* has a disarticulated right prootic that provides a basis for comparison with *Meiolania platyceps*. Beginning anteriorly, the *Crossochelys* prootic does not have the anterior process dorsal to the foramen nervi trigemini that articulates with the elongate epipterygoid of *Meiolania platyceps*, but the rugose nature of the bone surface above the foramen in *Crossochelys* suggests to me that such an articulation with an elongate epipterygoid was quite possible. Looking at the anterolateral prootic surface, the processus trochlearis oticum of *Crossochelys* is virtually the same as in *Meiolania platyceps*, as is the position and shape of the canalis cavernosus. Although the canalis cannot be probed in *Crossochelys*, there is a foramen in the canalis cavernosus in the same position as the one in *Meiolania platyceps* that opens into the facial nerve canal as well as a foramen pro ramo nervi vidiani on the ventral surface of the prootic. Similarly, there is a foramen in the wall separating the canalis

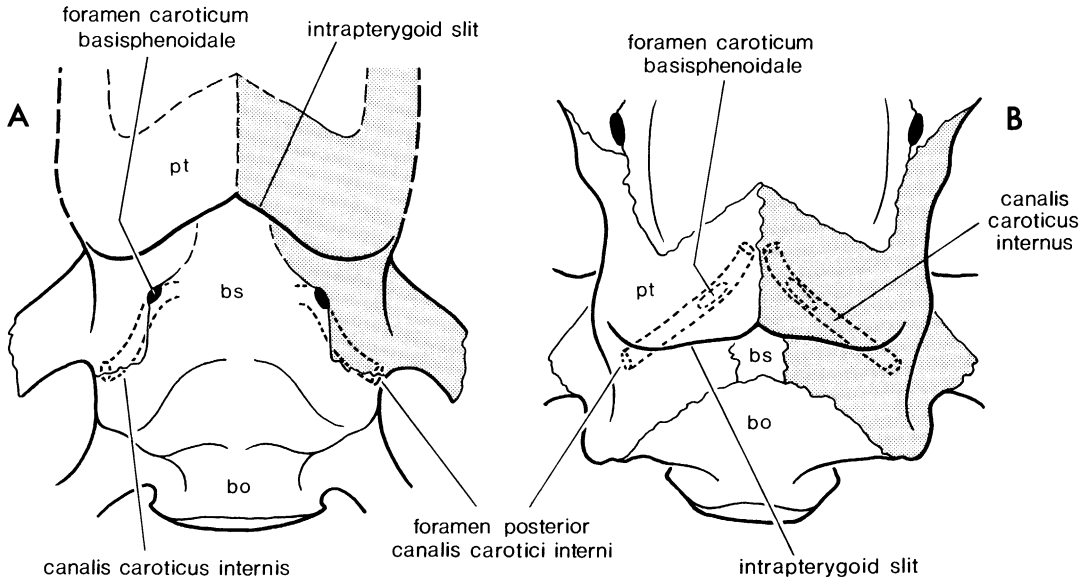


FIG. 60. Comparison of meiolaniid basicrania. A, *Crossochelys corniger*, AMNH 3161, restored by transposing left to right, basioccipital based on AMNH cast of *Niolamia argentina*; B, *Meiolania platyceps*, AM F:57984. Left pterygoids stippled, canalis caroticus internus dashed.

cavernosus from the cavum acustico-jugulare in *Crossochelys* in the same position as the facial nerve foramen in *Meiolania platyceps*. Although there is some ambiguity in the contacts, and the opisthotic is broken in the appropriate area, re-articulation of the right quadrate, prootic, and opisthotic in *Crossochelys* shows a strong similarity to *Meiolania platyceps* and suggests that the opisthotic entered the canalis stapedio-temporale. On the medial surface the foramen nervi facialis and the most anterior foramen nervi acustici are present in the fossa acustico-facialis; however, the area posterior to this in the hiatus acusticus is broken or was never ossified.

#### OPISTHOTIC

Figures 21, 37, 46, 47, 49–52

The opisthotic is preserved in the following specimens: AM F:61110, AM F:43183, AM F:57984, AM F:208b, AM F:18671, AM F:18364, AM F:1209, AM F:18370, AM F:18314, MM F:13825a, MM F:13827, BMNH R9605, BMNH R9606, and BMNH R682.

The opisthotic of *Meiolania platyceps* has a well-developed processus paroccipitalis (figs. 21, 37) that broadly articulates with the posteromedial surface of the quadrate and is even exposed within the cavum tympani (AM F:57984) where the quadrate becomes extremely thin (fig. 22). Dorsolaterally, the opisthotic reaches the squamosal in a suture (visible only in AM F:57984) that begins posteriorly at the posterolateral margin of the processus paroccipitalis of the opisthotic and extends anterodorsomedially to a position about halfway across the otic chamber where the quadrate-opisthotic contact begins. This latter suture continues in the same direction until the vicinity of the foramen stapedio-temporalis where the opisthotic contacts the prootic anteriorly. Contrary to the condition in most turtles, the opisthotic forms a major part of the foramen stapedio-temporale, canalis stapedio-temporalis, and aditus canalis stapedio-temporalis. Although the sutures are not entirely clear (see Prootic for further description), the opisthotic seems to form most of the posteromedial section of these structures.

Dorsomedially, the opisthotic-supraoccip-

ital suture is not determinable in any specimens, nor is the opisthotic-exoccipital suture which should be found along the postero-medial margin of the opisthotic. Within the cavum acustico-jugulare (see Cavum Acustico-Jugulare for further description) the opisthotic-quadrante suture can be seen extending posterolaterally from the aditus canalis stapedio-temporalis. The opisthotic forms a prominent part of the roof of the cavum acustico-jugulare (along with an undetermined amount of exoccipital) and extends medially to form the posterior part of the cavum labyrinthicum (see Cavum Labyrinthicum for further description). The opisthotic-prootic suture lies in the roof of the cavum acustico-jugulare at the anterior margin of the opisthotic and extends medially from the aditus canalis stapedio-temporalis to the dorsal rim of the fenestra ovalis. The opisthotic forms the posterior rim of this fenestra and the processus interfenestralis, which extends ventrally to meet the basioccipital (in AM F:57984 and AM F:61110 the processus does not reach the basioccipital because it was apparently capped in cartilage). In the ventromedial part of the processus interfenestralis lies the fenestra perilymphatica, which allows communication between the cavum labyrinthicum and the recessus scalae tympani. Dorsally, in the base of the processus interfenestralis, is the foramen externum nervi glossopharyngei. The opisthotic-exoccipital suture is not visible but it would presumably lie in the roof of the recessus scalae tympani as in nearly all other turtles.

The opisthotic usually forms the posterior part of the hiatus acusticus and the anterior part of the foramen jugulare anterius (fig. 45) but the sutures are not apparent. The hiatus is described under Prootic but the other features normally found in the opisthotic are described here. The foramen jugulare anterius is a C-shaped opening, concave anteriorly, that is continuous laterally with the recessus scalae tympani which is only slightly larger than the foramen. The foramen medialis nervi glossopharyngei lies near the anterior margin of the foramen jugulare anterius and parallels it to open in the cavum acustico-jugulare at the foramen externum nervi glossopharyngei. Because the nerve is in a bony canal from the cavum cranii lat-

erally, there is no foramen internum nervi glossopharyngei (see Gaffney, 1979b, p. 211 and fig. 50 for my usage of these confusing terms). Ventral to the foramen jugulare anterius what is presumably the opisthotic contacts the basioccipital.

### BASISPHENOID

Figures 21, 45, 46, 53, 55, 58

The basisphenoid of *Meiolania platyceps* is best seen in AM F:57984 (figs. 21, 22), which has sutures and is the most complete, and in AM F:18671 (fig. 58), which has sutures and much of the pterygoids broken off showing the entire ventral surface of the basisphenoid. Other specimens with the basisphenoid preserved are: AM F:208a, AM F:208b, AM F:401, AM F:18364, BMNH R682, BMNH R9605, BMNH R9606, AM F:43183, AM F:61110, MM F:13825a, MM F:13827, BMNH R675, AM F:1209, AM F:18314, and AM F:18668.

Although there is a certain amount of variation in the morphology of the dorsum sellae turcica region (figs. 45, 46, 54, 55), the features are generally consistent. The dorsum sellae is high and does not overhang the sella turcica or foramen anterior canalis carotici interni. There is a prominent paired ridge, variably developed, which begins as the processus clinoides and turns ventrally on either side of the dorsum sellae to contact each trabecula. These ridges cause the dorsum to lie in a median trough that is continuous with the sella turcica. In AM F:57984 (fig. 55) the variability of these ridges can be seen. The right ridge is very extensive, curving anterolaterally. The sella turcica is relatively small and not defined anteriorly because the ossified trabeculae are very short and do not combine to form a distinct rostrum basisphenoidale. Each foramen anterius canalis carotici interni lies in the posterolateral corner of the sella turcica. Lateral to the ridge that extends on either side of the dorsum sellae is an anterolaterally facing concavity just medial to the ventral foramen nervi abducentis. This concavity may have been an eye muscle attachment site.

In Gaffney (1976, p. 536) I argued that the following features are shared derived characters for the Chelonioidea:

(1) Dorsum sellae high and separated from sella turcica and foramina anterius canalis carotici interni by prominent bone surface that usually has a sagittal ridge.

(2) Posterior part of sella turcica not concealed by overhanging dorsum sellae.

The dorsum sellae in *Meiolania platyceph* is high and separated from the sella turcica although a sagittal ridge is not present, and the dorsum sellae does not overhang the sella turcica. There is a difference, of dubious significance, between *Meiolania platyceph* and chelonoids in that the dorsum sellae of *Meiolania platyceph* has paired parasagittal ridges, whereas chelonoids (at least plesiochelyids) have a horizontal ridge extending along the anterior margin of the dorsum.

The foramina anterius canalis carotici interni are separated by a column of bone that may be flat (AM F:57984, fig. 55) or concave (AM F:18671, fig. 53). They lie just dorso-medial of the base of each trabecula. Between the trabeculae is a connecting sheet of bone that forms the floor of the sella turcica. Both the trabeculae and the interconnecting bone end anteriorly in flat or slightly convex surfaces that have the appearance of being finished in cartilage. The rostrum basisphenoidale (trabeculae) is one of the shortest in all turtles, and this may be correlated with the relative shortness (or telescoping) of the pterygoids.

Although there is no distinct processus clinoides (except in AM F:61110, fig. 54) the area of the processus is identifiable, just lateral to the dorsum sellae and this area is pierced by the foramen nervi abducentis, as in other turtles.

The dorsal surface of the basisphenoid (figs. 52, 54, 55) is irregular, with a different set of asymmetrical holes, spicules, and short canals in each specimen. At the basisphenoid-basioccipital suture there is a cup-shaped rugosity, the basis tuberculi basalis, found in most turtles. The dorsolateral margin of the basisphenoid is covered by the prootic (suture can be seen in AM F:57984 and AM F:18671). In some specimens of *Meiolania platyceph* the basisphenoid may enter the hiatus acusticus (AM F:57984, AM F:18671) but in others (BMNH R682, AM F:18364) the hiatus is ossified except for a small area on the prootic. The pterygoid covers the ventro-

lateral surface of the basisphenoid and, as in the case of the prootic, since there are no disarticulated specimens of these elements, the nature of these contact surfaces is not known.

The posterior margin of the basisphenoid consists of a vertical transverse contact with the basioccipital, which can be seen on the latter bone in AM F:18363 (fig. 48). Most of this contact is covered ventrally by a medial sheet of the pterygoid, visible in AM F:57984 and AM F:18671. The ventral surface of the basisphenoid is exposed above the intrapterygoid slit and largely hidden in ventral view by the medial lamella of the pterygoid (see Pterygoid for description). The basisphenoid forms the medial margin of the foramen caroticum basisphenoidale and, anteromedial to this foramen, the canalis caroticus internus lies within the basisphenoid (see Canalis Caroticus Internus and Associated Structures). On the midline of the ventral surface the basisphenoid often has a short ridge that articulates with the pterygoids ventrally.

## CAVUM LABYRINTHICUM

Figures 49, 52

Although all the skulls with an otic chamber contain the cavum labyrinthicum it is actually visible to a useful extent only in a few specimens that have had the surrounding bone removed naturally or artificially. AM F:208a and AM F:208b (Anderson, 1925, pl. 33) have the cavum labyrinthicum exposed dorsally, whereas the cavum in AM F:18314 (fig. 49) is exposed ventrally.

The semicircular canals are very similar in all turtles but the degree to which they ossify varies; however, as yet, I have found no systematic significance to this variation. In *Meiolania* all the semicircular canals are contained in bone. The canalis semicircularis anterior and the canalis semicircularis posterior can be seen in dorsal view in AM F:208b (Anderson, 1925, pl. 33, fig. 5), whereas all three canals can be seen in ventral view in AM F:18314 (fig. 49). The recesses housing the ampullae are also readily seen in these specimens.

The acoustic nerve (VIII) enters the cavum labyrinthicum via one or more foramina in the medial wall of the cavum. In most turtles



much of this wall remains cartilaginous and is termed the hiatus acusticus, but in *Meiolania* it is usually ossified. The acoustic nerve foramina are, therefore, usually well defined in *Meiolania*. As in most turtles, two of the foramina nervi acustici lie in the fossa acustico-facialis along with the foramen nervi facialis. As in many other turtles (see Gaffney, 1979, fig. 71), another foramen nervi acustici enters the cavum labyrinthicum posterodorsal to the fossa.

### CAVUM ACUSTICO-JUGULARE

Figures 47, 49–52

The specimens that provide particularly useful information on the cavum acustico-jugulare are: AM F:57984, which has the most complete set of sutures; AM F:18671, which has some sutures and is broken showing internal features; and AM F:18364, which is also broken. Specimens with this area preserved are: AM F:401, AM F:208a, AM F:208b, BMNH R682, BMNH R9605, BMNH R9606, AM F:43183, AM F:61110, MM F:13825a, AM F:18668, MM F:13827, and AM F:1209.

The general morphology of the cavum acustico-jugulare in *Meiolania platyceps* is similar to that in other eucryptodires. The cranioquadrate portion is walled laterally by the quadrate which participates in the formation of the aditus stapedio-temporalis and the canalis stapedio-temporalis dorsally and the canalis cavernosum ventrally. The canalis stapedio-temporalis is nearly twice the diameter of the canalis caroticus internus suggesting that the stapedia artery was larger than the internal carotid artery, which is the primitive condition for turtles and retained in most cryptodires. The medial wall of the canalis stapedio-temporalis is formed by the prootic and is exposed in AM F:18364. The canalis cavernosus is unusually large in relation to other structures but not uniquely so. It is oval in cross section with a slight narrowing in the middle. The canalis cavernosus as it enters the cavum acustico-jugulare is formed laterally by the quadrate, medially by the prootic, and ventrally by the pterygoid, but as the canalis continues anteriorly its lateral wall is formed by the pterygoid.

The medial limits of the cavum acustico-

jugulare in *Meiolania platyceps* consist of the fenestra ovalis, the processus interfenestralis, and the recessus scalae tympani (figs. 50–52). The fenestra ovalis is somewhat irregularly shaped as in many turtles, and is almost completely formed in bone, namely, the prootic anteriorly and the opisthotic posteriorly; only a small notch in its ventral border appears to have been filled with cartilage in life. The processus interfenestralis is formed by the opisthotic and separates the fenestra ovalis anteriorly from the recessus scalae tympani posteriorly. The processus is well developed in *Meiolania platyceps*, and in all specimens except AM F:61110 and AM F:57984 it extends ventrally to the basioccipital. In AM F:61110 the basioccipital is broken off in this region but the processus ends in what appears to be a cartilaginous surface, indicating that it would not be suturally attached to the basioccipital. This condition is presumably related to the hypothesized juvenile condition of AM F:61110. The medial portion of the processus interfenestralis forms most of the fenestra perilymphatica, an opening between the cavum labyrinthicum and the recessus scalae tympani. Based on AM F:18363 it appears that a portion of the ventromedial margin of the fenestra perilymphatica is formed by the exoccipital. The hiatus postlagenum is absent. The dorsal portion of the processus interfenestralis is pierced by the glossopharyngeal nerve (fig. 49). The foramen externum nervi glossopharyngei occurs on the posterior surface of the processus and may be found above the recessus scalae tympani in some specimens (AM F:61110, AM F:18364).

Between the fenestra ovalis and the aditus canalis stapedio-temporalis is a posteriorly facing concavity (best seen in AM F:18671 and AM F:18364), presumably associated in life with the paracapsular system (see fig. 46A, Gaffney, 1979b). In AM F:43183 this concavity has been eroded to form a canal, but this is due to postmortem damage of some sort. Just medial to the foramen cavernosum in the ventral portion of the cavum acustico-jugulare lies the foramen posterius canalis carotici interni (fig. 50). This foramen lies within the cavum acustico-jugulare in the Testudinidae and a few other testudinoids. Just dorsal to the foramen posterius canalis

carotici interni and formed primarily by the prootic is the posterior opening of the canal for the hyomandibular branch of the VII nerve (for further descriptions of this structure and the canalis caroticus internus see Canalis Caroticus Internus).

The recessus scalae tympani (fig. 52) is the portion of the cavum acustico-jugulare that lies behind the processus interfenestralis of the opisthotic and anterior to the exoccipital. Medially, the foramen jugulare anterius forms an opening between the cavum cranii and the recessus which extends posterolaterally and a bit ventrally into the main part of the cavum acustico-jugulare. The foramen jugulare posterius lies in the posterior wall of the recessus scalae tympani and is apparently formed by the exoccipital, although it is possible that a portion of the pterygoid forms the ventrolateral margin. The foramen is completely enclosed only in BMNH R9605, AM F:208b, and MM F:13827 (left side, right side is either open or damaged). In AM F:57984, AM F:18671, AM F:1209, MM F:13827, AM F:43183 and MM F:13825a the foramen is only partially enclosed, the lateral margin is incomplete.

#### CANALIS CAROTICUS INTERNUS AND ASSOCIATED STRUCTURES

Among the preserved specimens of *Meiolania platyceph* (figs. 56–59) there is a good series of braincases which are variably broken and, when taken together, show nearly all the canals and connections between foramina. The entire length of the canalis caroticus internus is exposed in BMNH R9606 and AM F:208b, whereas the intact canal can be probed in AM F:57984 (left side). Although Anderson (1925, pls. 33, 35) described and figured AM F:208a and AM F:208b; other braincases, namely AM F:401, AM F:18668, AM F:18671, and AM F:18364 also provide significant basicranial information. AM F:57984 and AM F:18671, however, are virtually the only source of information on sutures in this region.

The foramen posterius canalis carotici interni in *Meiolania platyceph* (fig. 50) is situated at the ventrolateral corner of the fenestra postotica as in some testudinoids but as op-

posed to chelonoids and trionychoids, where the foramen is distinctly separated from the fenestra postotica. The position of this foramen is most similar to the position seen in testudinids (e.g., AMNH 104684) in which the foramen lies virtually on top of the pterygoid and well anterior to the margin of the fenestra postotica. The diameter of the foramen posterius canalis carotici interni is the same on both sides in most of the available *Meiolania platyceph* specimens, but in AM F:401 (fig. 56) the right foramen posterius canalis carotici interni and canalis caroticus internus are much larger than the left. Sutures are visible in both AM F:57984 and AM F:18571 which show the foramen posterius canalis carotici interni to be formed by the pterygoid. This bone curves dorsally to surround the canalis and a complex suture is formed above the canalis where the two parts of the pterygoid meet.

On both sides of AM F:208a there are indications of another structure traversing the foramen posterius canalis carotici interni. On the left, a groove is preserved and on the right a partially formed foramen can be seen. The anterior extent of this structure is not visible. The fact that the other specimens have no indication of this feature suggests to me that it is a nerve or vessel that accompanied the internal carotid in all the specimens and that its impression on the bone is an individual variant of that in AM F:208a.

The canalis caroticus internus extends anteromedially from the foramen posterius canalis carotici interni and, about midway, is formed primarily by the basisphenoid rather than by the pterygoid. There are two major foramina that occur along the canalis caroticus internus, the foramen pro ramo nervi vidiani and a ventral opening into the intrapterygoid slit, the foramen caroticum basisphenoidale (both discussed below).

Dorsal to the canalis caroticus internus but roughly paralleling it is the canalis nervi facialis, which begins anteriorly at the foramen nervi facialis, curves medially, and then posteriorly to end just above the foramen posterius canalis carotici interni (figs. 57, 59). Midway along its length this canal has a ventral branch, the foramen pro ramo nervi vidiani. The canalis nervi facialis of most cryptodires is a short structure that carries the

facial nerve laterally into the canalis cavernosus, where a branch, the hyomandibular, travels posteriorly. In pleurodires the hyomandibular nerve lies in its own canal, which may also be termed the canalis nervi facialis, above and roughly parallel to the canalis caroticus internus (Gaffney, 1975). The condition in *Meiolania platyceps* is similar to the pleurodire condition in that there is a posterior continuation of the canalis nervi facialis; whether or not the hyomandibular nerve was contained in it in *Meiolania* is conjectural. Examination of the prootic of *Crossochelys* also reveals the presence of a posterior continuation of the canalis nervi facialis, suggesting that the feature is present in all meiolaniids. The canalis nervi facialis of *Crossochelys* and *Meiolania platyceps* is formed by the prootic and pterygoid in contrast to its condition in pleurodires where the canal is formed entirely by the prootic. Furthermore, the length and position of the canal is different, being shorter and more dorsal to the canalis caroticus internus in pleurodires, whereas it is longer and close to the canalis caroticus internus in meiolaniids.

The foramen pro ramo nervi vidiani (fig. 59) is a short canal, apparently formed by both pterygoid and prootic, between the canalis nervi facialis and the canalis caroticus internus. It occurs about one-third of the way along the canalis caroticus internus from the foramen posterius canalis carotici interni. The foramen pro ramo nervi vidiani is broken open and visible in AM F:208a and BMNH R9606. In both specimens the foramen is a short canal running dorsoventrally from the canalis nervi facialis down to the canalis caroticus internus, but in BMNH R9606 the foramen pro ramo nervi vidiani is somewhat elongated anteroposteriorly, whereas in AM F:208a it is the more common circular tube.

In other cryptodires the foramen pro ramo nervi vidiani connects the canalis cavernosus and the canalis caroticus internus, and although the condition in *Meiolania platyceps* differs, it does not seem to be in a fundamental way. Other cryptodires have the dorsal opening of the foramen in the ventral surface of the canalis cavernosus, ventral to the opening of the foramen nervi facialis which is usually in the medial wall of the canalis. In *Meiolania platyceps* the foramen pro ramo

nervi vidiani begins dorsally about halfway along the length of the canalis nervi facialis (figs. 57, 59) and at this point there is a lateral opening into the canalis cavernosus. The foramen pro ramo nervi vidiani may extend posteroventrally into the canalis caroticus internus or it may extend vertically without a distinct angle.

About two-thirds of the distance along the canalis caroticus internus anterior to the foramen posterior canalis carotici interni is the second major opening of the canalis caroticus internus. This is a large opening in the floor of the canalis that communicates with the space formed by the intrapterygoid slit. The homologue of this opening is not obvious and I am coining a new term, the "foramen caroticum basisphenoidale" in allusion to its close association with the basisphenoid; the foramen is also the position where the canalis caroticus internus is formed by the basisphenoid medially. The morphology of the foramen caroticum basisphenoidale is readily seen in BMNH R682, AM F:18671, AM F:401, AM F:18364, and AM F:57984. The foramen is variable in size being relatively large in AM F:18671 and smaller in AM F:18364; generally, however, it approximates the size of the canalis caroticus internus. Associated with the foramen caroticum basisphenoidale is a smaller one that varies in its position and development. In AM F:18671 (fig. 58) it is a nearly enclosed groove lying in the posteroventral corner of the foramen caroticum basisphenoidale and continuous anteriorly with a distinct groove that marks the lateral margin of the intrapterygoid slit. In AM F:18364 and AM F:401 the groove is a completely enclosed foramen in the ventrolateral floor of the canalis caroticus internus and is separated from the foramen caroticum basisphenoidale by a short distance. In BMNH R9606 the distance is much longer and the small foramen begins directly beneath the foramen pro ramo nervi vidiani which is connected to the small foramen by a groove.

The contents of these two foramina are by no means certain although it is most likely that the foramen caroticum basisphenoidale contained the palatine artery and the small foramen the vidian nerve. The foramen caroticum basisphenoidale is formed at the juncture of the pterygoid and basisphenoid

bones, which is the usual position of the branching-off of the canalis caroticus lateralis (containing the palatine artery) from the canalis caroticus internus. The canalis caroticus lateralis is usually formed between the basisphenoid and the pterygoid in cryptodires and in *Meiolania platyceps* this would be the lateral area of the intrapterygoid slit. The intrapterygoid slit of *Meiolania platyceps* opens anteriorly around the margins of the rostrum basisphenoidale, whereas the usual position of the foramen caroticum laterale in other cryptodires is between the pterygoid and rostrum basisphenoidale. The small foramen/canal is less convincingly identified as the container of the vidian nerve (VII) but this seems the most likely possibility. The vidian nerve is usually contained in a canal formed entirely within the pterygoid and this could be envisioned by the fusion of the intrapterygoid slit in *Meiolania platyceps*. However, the slit really does not seem to extend as far laterally as the canalis nervi vidiani of other cryptodires, furthermore, the canalis nervi vidiani usually terminates in the vicinity of the foramen palatinum posterius which is not the case of the pterygoid slit in *Meiolania platyceps*. Again, however, the small foramen in BMNH R9606 has a distinct groove connecting it with the foramen pro ramo nervi vidiani, and, considering the variability of the vidian nerve in recent turtles, it still seems the best identification.

At the position of the foramen caroticum basisphenoidale the canalis caroticus internus turns more anteriorly and somewhat dorsally so that as it enters the sella turcica each canal is nearly parasagittal (see AM F:208b).

#### COLUMELLA AURIS

Both stapes are present in MM F:13825a although the basis columellae is visible only on the right side. The stem of the columella is straight and rodlike, very much as in other turtles. The distal end, on the left side of MM F:13825a, is a bit thicker than the remaining portion. The basis columellae or footplate is expanded into a cone, as in baenids, trionychids, and *Dermatemys* (see Gaffney, 1979b, fig. 90, for the *Dermatemys*). The inside of the cone cannot be seen, although it is presumably hollow.

#### LOWER JAWS

Figures 61–63

There are relatively few preserved lower jaws of *Meiolania platyceps*. The best one, AM F:57984, is associated with a skull, has most of the sutures preserved, and is the only specimen to provide useful information about the posterior part of the jaw. Most of the description is based on this specimen. MM F:13825a is the only other jaw associated with a skull but only part of it has been freed from the skull. AM F:58099 lacks the posterior part of the jaw but is still well preserved and shows the splenials and interior parts of the fossa meckelii to good advantage. AM F:186, AM F:18365, and an uncatalogued specimen in the Lord Howe Island Museum (a cast is AMNH 20976) are fragments of dentaries.

#### DENTARY

The dentary has the following contacts: coronoid posterodorsally, surangular posterolaterally, angular posteroventrally, and splenial posteromedially. A prearticular-dentary contact is barely prevented by a very narrow exposure of the coronoid between the processus coronoideus and a large foramen lying above the splenial.

The triturating surface of the lower jaw is formed entirely by the dentary; there is no contribution from the coronoid as in baenids. The triturating surface is unexpanded, the labial and lingual ridges are parallel, there are two troughs and an accessory ridge, and the form of the triturating surface is very similar to that in testudinids, in particular *Hesperotestudo*. The labial ridge is lower than the lingual ridge and begins anteriorly at a variably developed median cusp. This cusp is relatively low in AM F:57984 but is distinct and well developed in MM F:13825a. When the jaws are closed the cusp fits into a median concavity formed by the premaxillae. The labial ridge curves upward slightly as it extends posteriorly, and ends in a small spur, seen in other turtles. The labial ridge is bordered medially by a shallow trough that forms about half the width of the triturating surface. Medial to this trough is an accessory or intermediate ridge that is distinct from the lingual ridge and separated from it by a smaller trough. The lingual ridge, accessory ridge, and

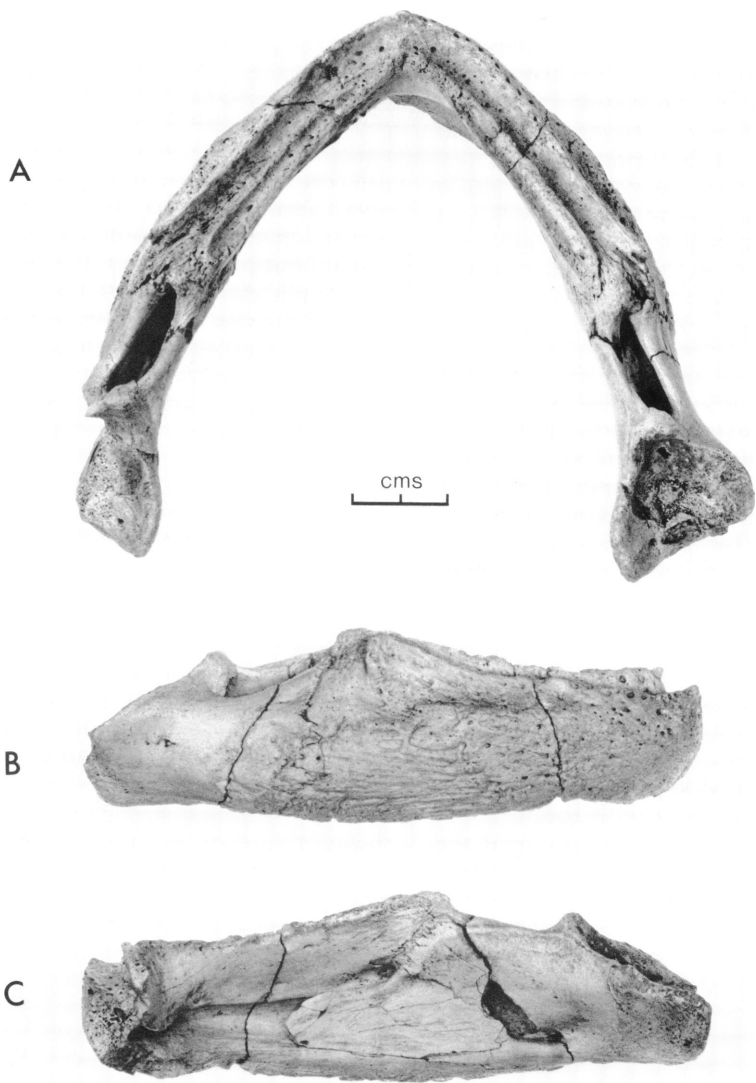
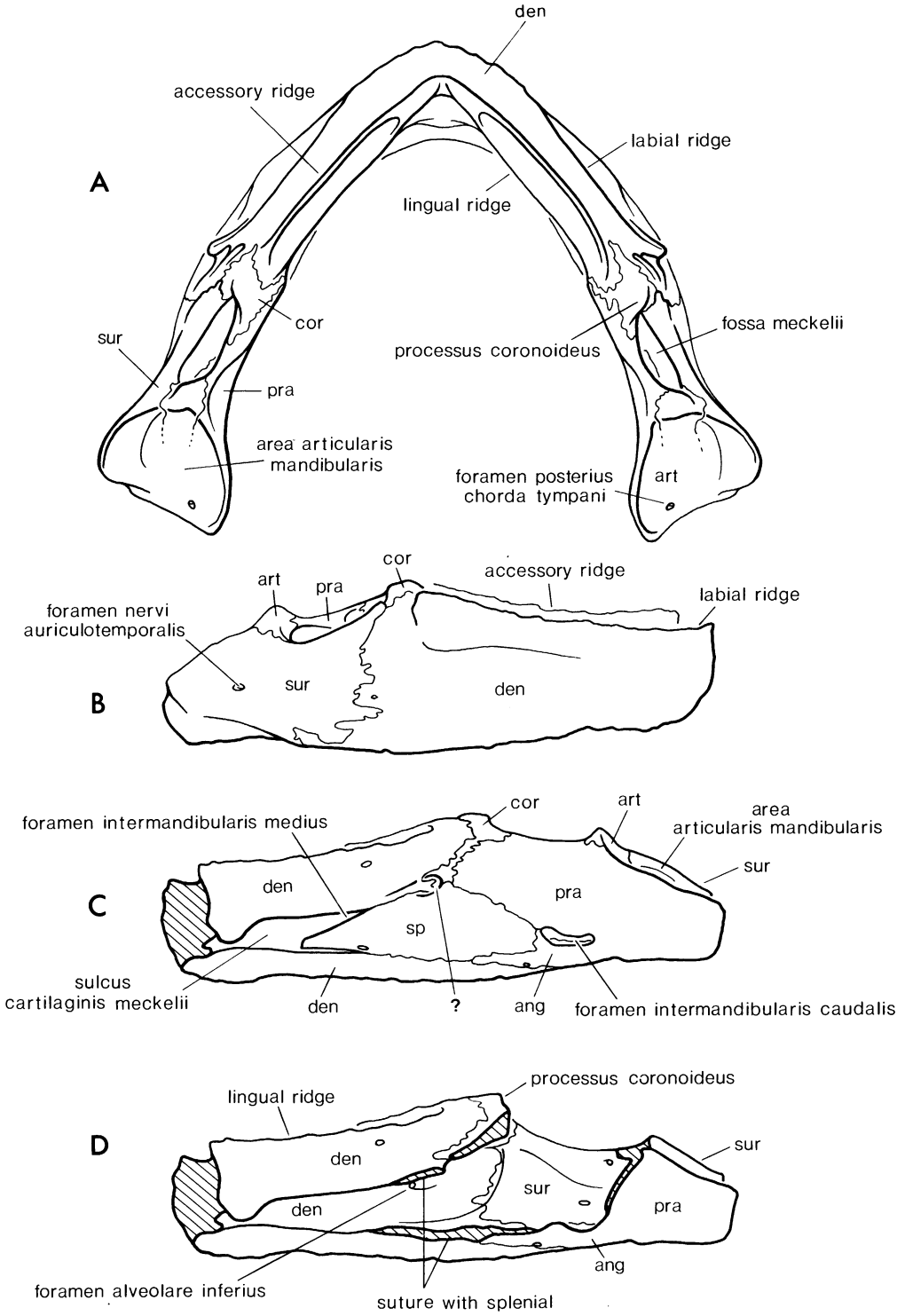


FIG. 61. *Meiolania platyceps*, AM F:57984, lower jaw. A, dorsal view; B, lateral view; C, medial view.

FIG. 62. *Meiolania platyceps*, AM F:57984, lower jaw. A, dorsal view; B, lateral view; C, medial view; D, medial view with splenial and portions of prearticular removed. See abbreviations.



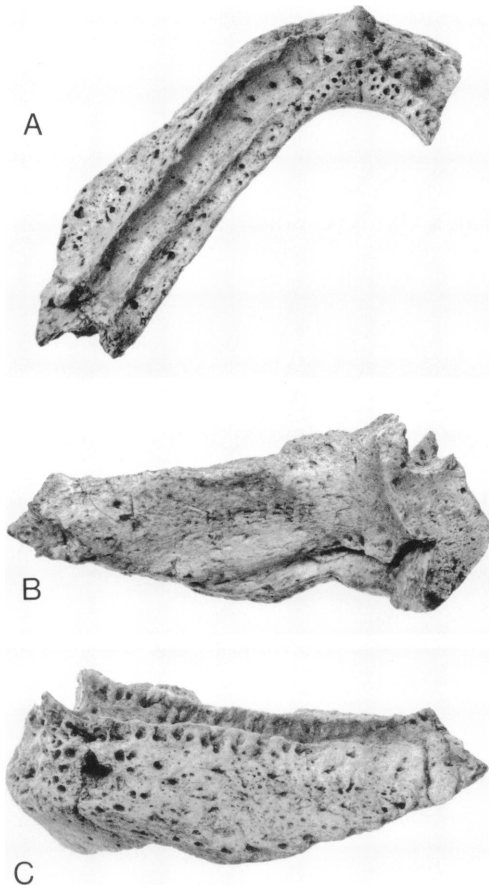


FIG. 63. *Meiolania platyceps*, MM F:13825a, partial lower jaw. A, dorsal; B, medial; C, lateral.

the trough lying between them are all higher than the labial ridge and the larger trough separating labial ridge and accessory ridge. The lingual ridge and accessory ridge merge at the symphysis to form a single ridge. These features are all found in the Tertiary testudinid *Hesperotestudo* (see Hay, 1908, fig. 569).

The external surface of the dentary is heavily pitted and grooved, presumably due to the presence in life of the horny beak. About midway along the dentary on the external surface is a low shelf or ridge (fig. 62A) developed ventral to the labial ridge and not on the triturating surface. This low ridge marks the extent of overlap of the maxilla when the jaws are closed.

In most turtles there is a distinct foramen on the outer surface of the dentary, the foramen dentofaciale majus. This foramen is absent in *Meiolania*. In most turtles the foramen dentofaciale majus joins the canalis alveolaris inferior, a nutrient canal that begins in the fossa meckelii at the foramen alveolare inferius and extends anteriorly along the main axis of the jaw ramus. The canalis alveolaris inferior in *Meiolania* can be seen in section in AM F:18365 and the foramen alveolare inferius can be seen in the other jaws but the foramen dentofaciale majus and the short canal connecting it with the canalis alveolaris inferior are absent, a condition that may be unique to *Meiolania*. Its systematic significance remains to be seen.

The sulcus cartilaginis meckelii of *Meiolania* is open from its beginning at the symphysis to the point where it is covered by the splenial just anterior to the fossa meckelii. The sulcus is close to the ventral edge of the dentary. The dorsal margin overhangs the sulcus, particularly at the symphysis, but the lower margin is a broad slope that extends to the ventral margin of the jaw.

#### ANGULAR

The angular is not clearly defined in the material of *Meiolania* available at present. There is an anterior contact with the dentary on the ventral surface of the jaw. On the medial surface the angular sends a process forward to partially separate dentary and splenial. Behind this contact the angular forms the lower margin of the foramen intermandibularis caudalis. Posterior to the foramen nearly all sutures are fused, a common condition in turtles, but it is likely that the angular continues posteriorly to underlie the jaw until it meets the articular. The angular of *Meiolania* differs from most other cryptodires, particularly eucryptodires, in being less extensive anteriorly. Its relations are similar, however, to the condition in *Plesiochelys* (Gaffney, 1976, figs. 48, 49).

#### SURANGULAR

The surangular covers the lateral surface of the posterior portion of the jaw and has an interdigitating suture with the dentary at its anterior margin. The surangular is more



extensive anteriorly than in most other eucryptodires but it is comparable to *Portlandemys* (Gaffney, 1976, fig. 50) and baenids. There is a small opening in the surangular that appears to be the foramen nervi auriculotemporalis but it has not been probed. The surangular forms the entire lateral wall of the fossa meckelii, a large space in the posterior part of the lower jaw.

### CORONOID

The coronoid of *Meiolania* is relatively inconspicuous; it is not exposed on the triturating surface and the processus coronoideus is very low. The coronoid is a blocklike element lying in the dorsal part of the jaw ramus about halfway along its length. It contacts the dentary anteriorly and laterally, the prearticular medially, and the splenial ventromedially. The coronoid forms the anterior margin of the fossa meckelii and the anterior part of the roof of the fossa. The relatively small size of the coronoid bone in *Meiolania* is unusual in turtles but I do not see that it has systematic significance. Among other turtles, even forms that have a low processus coronoideus have a relatively well-developed coronoid and so the small size of the coronoid may be unique to *Meiolania*.

### ARTICULAR

The articular bone and the other elements forming the posterior part of the jaw in turtles tend to have the sutures fused, and *Meiolania* is no exception. The articular lies in the area articularis mandibularis and forms most of this region. The more lateral section of the area articularis mandibularis, however, appears to be formed by the surangular as in most other turtles. Sutures are visible anteriorly and show the articular lying with the prearticular medially and the surangular laterally. The articular forms a small part of the posterior rim of the fossa meckelii. The area articularis mandibularis is visible only on the right side of AM F:57984 and is damaged. The surface is broadly concave with no development of a retroarticular process. Posteriorly, there is a foramen posterius chorda tympani as in most turtles. A posteromedial flange is developed that presumably was formed by the articular and prearticular.

### PREARTICULAR

The prearticular forms the medial margin of the rim of the fossa meckelii and most of the medial wall of the fossa. The fossa meckelii of *Meiolania* is a bit larger than the fossa in most turtles but not uniquely so. The size of the fossa does not seem to have particular systematic significance. The prearticular also forms a small part of the posterior margin of a large foramen, here questionably identified as the foramen intermandibularis oralis.

### SPLENIAL

The splenial is a large, platelike bone lying on the medial surface of the jaw anterior to the prearticular. Lateral to the splenial is the fossa meckelii posteriorly and the sulcus (or canalis) cartilaginis meckelii anteriorly. Posterioventrally, the splenial reaches the angular and barely enters the margin of the foramen intermandibularis caudalis. Anteriorly, the splenial forms the posterior margin of the foramen intermandibularis medius which in *Meiolania* is simply the space created by the noncontinuation of the splenial as the medial wall to the sulcus cartilaginis meckelii. There is another, relatively large foramen in the suture between dentary, splenial, and coronoid that does not seem to occur in most other turtles, even ones with large splenials. This foramen is in the same position as the foramen intermandibularis medius of other cryptodires, that is, just ventral to the coronoid and at the anterodorsal margin of the fossa meckelii. The homology of these foramina would be clarified if their contents were known. It is likely that one or more of the structures, such as the ramus intermandibularis medius of  $V_3$ , that run through the foramen intermandibularis medius in other turtles, is in its own foramen in *Meiolania* because the foramen intermandibularis medius lies so far forward due to the large splenial. The foramen is labeled with a question mark in figure 61.

## RELATIONSHIPS

Another assessment of meiolaniid phylogeny will be attempted after completion of work on the Triassic turtle *Proganochelys* and on meiolaniid postcranial morphology. Now, however, a discussion of relationships based on *Meiolania platyceps* cranial features and what I know at present of *Proganochelys*, as well as other turtles, is appropriate. I will first state the argument for meiolaniid relationships and follow it by more detailed discussion.

It is not too difficult to find unique features to support Anderson's (1925) and Simpson's (1938) conclusions that the Meiolaniidae form a natural group. Using characters that can be seen in currently available specimens of *Meiolania platyceps*, "*Meiolania*" *oweni*, *Niolamia argentina*, and *Crossochelys corniger* we have the following unique features for the Meiolaniidae.

(1) Squamosal and supraoccipital produced into large posteriorly and posterolaterally directed processes that extend clear of the skull roof.

(2) Medial plate of pterygoid separated ventrally from basisphenoid to form the intrapterygoid slit.

(3) Broad squamosal-quadratojugal contact ventral to the quadrate.

Accepting the Meiolaniidae as monophyletic, the taxon can then be identified as Cryptodira based on the possession of:

(1) A processus trochlearis oticum on the anterior edge of the otic chamber.

(2) A pterygoid that extends posteriorly between quadrate and braincase.

(3) A descending process of the prefrontal that meets the vomer ventromedially.

Within the Cryptodira, the meiolaniids can be identified as Eucryptodira based on the posterior position of the foramen posterius canalis carotici interni (Gaffney, 1975). The absence of other eucryptodiran features in meiolaniids would further suggest that they are the sister taxon to all or nearly all remaining Eucryptodira.

Although work on the Triassic turtle, *Proganochelys* (fig. 64), is still in progress, a preliminary description of the skull is available (Gaffney and Meeker, 1983), and will allow

comparison with most of the cranial areas in *Meiolania platyceps*. Because *Meiolania platyceps* has conspicuously retained some characters that seem to be primitive for all turtles or for Casichelydia, it would be useful to attempt to assess the distribution of these characters more accurately by comparison with *Proganochelys*. The order of treatment of the various elements follows the main body of the text.

**DERMAL ROOFING ELEMENTS:** The nasal bone in *Meiolania platyceps* is very large, larger in relation to the skull than in any other turtle that I am aware of. The nasal of *Proganochelys* approaches the relative size of the *M. platyceps* nasal but does not reach it. *Meiolania platyceps* has a hypertrophied fossa nasalis and a nasomaxillary sinus partially formed by the nasal (the nasomaxillary sinus also occurs in "*Meiolania*" *oweni* from Queensland and is presumably a meiolaniid feature). The large size of the nasal in *M. platyceps* and the associated structures would appear to be autapomorphous for *Meiolania platyceps* (or the Meiolaniidae if the size of the nasal were known in the other members of the group). However, a relatively large nasal, widely separating the prefrontals, and forming a prominent portion of the fossa nasalis is nonetheless a feature that is primitive for all turtles, it is only the extreme size of the nasal in *Meiolania platyceps* that is autapomorphous. Even *Glyptops*, *Mesochelys*, and baenids (Gaffney, 1979a) have nasals that are proportionally smaller than in *Meiolania platyceps* or *Proganochelys*. The baenids, *Hayemys*, *Trinitichelys*, and possibly *Dorsetochelys*, have what would be the relatively largest nasals after *Meiolania platyceps* and *Proganochelys*, and in these forms the prefrontals are widely separated. Therefore, the large nasal in *Meiolania platyceps* is consistent with the hypothesis that *Meiolania* is the sister group to all other casichelydians. However, in view of other characters, I would interpret this feature as a reversal or as a retained primitive character in *Meiolania platyceps*, and argue that in the latter case reduced nasals evolved independently in cryptodires and pleurodires.

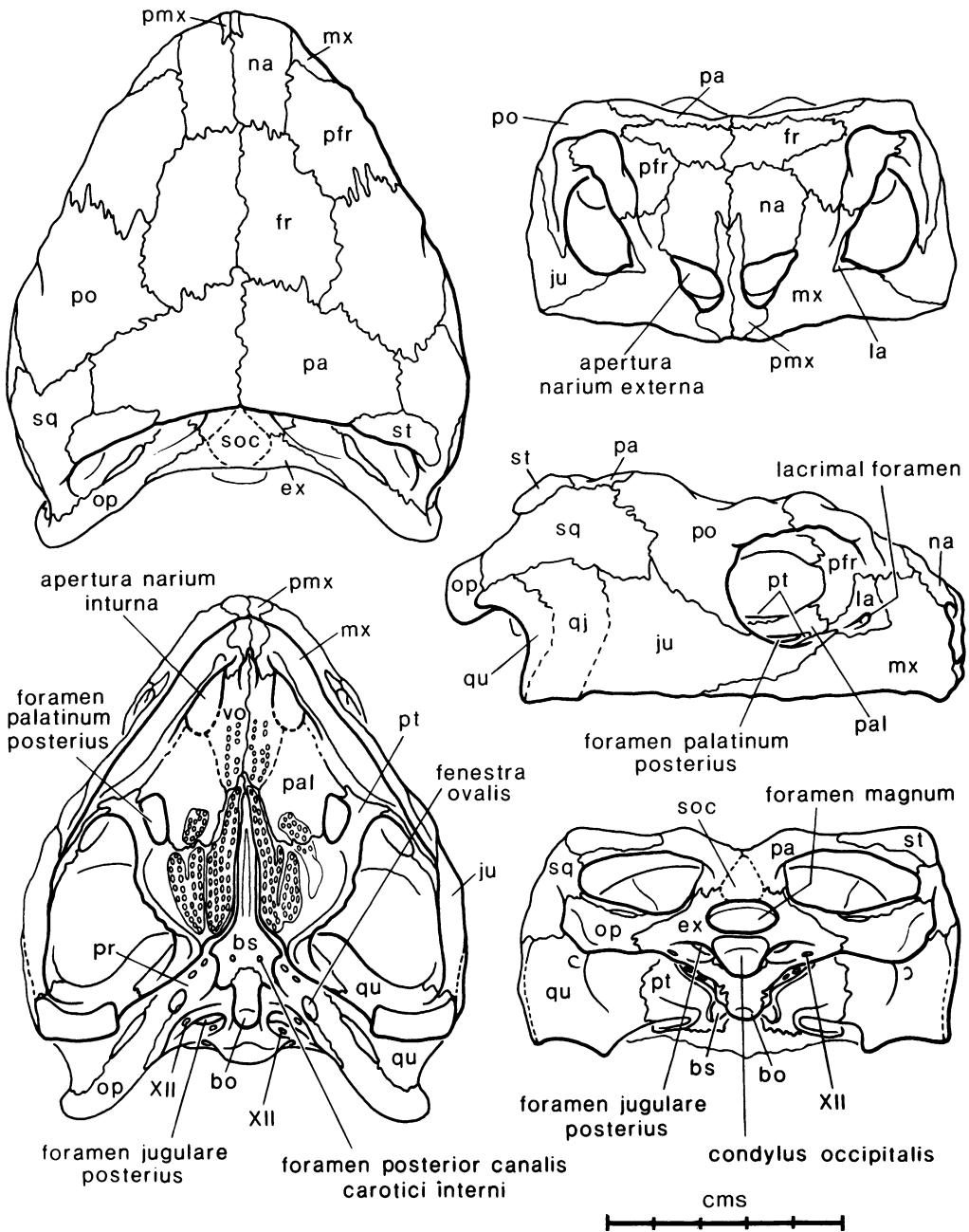


FIG. 64. *Proganochelys quenstedti*, Staatliches Museum für Naturkunde, 16980, Late Triassic, Trossingen, Germany. From Gaffney, and Meeker (1983). See abbreviations.

The divided external nares in most (but not all) *Meiolania platyceps* is formed by ventral processes of the nasals and dorsal processes

of the prefrontals, whereas in *Proganochelys* the external nares is divided by dorsal processes of the prefrontals that actually extend

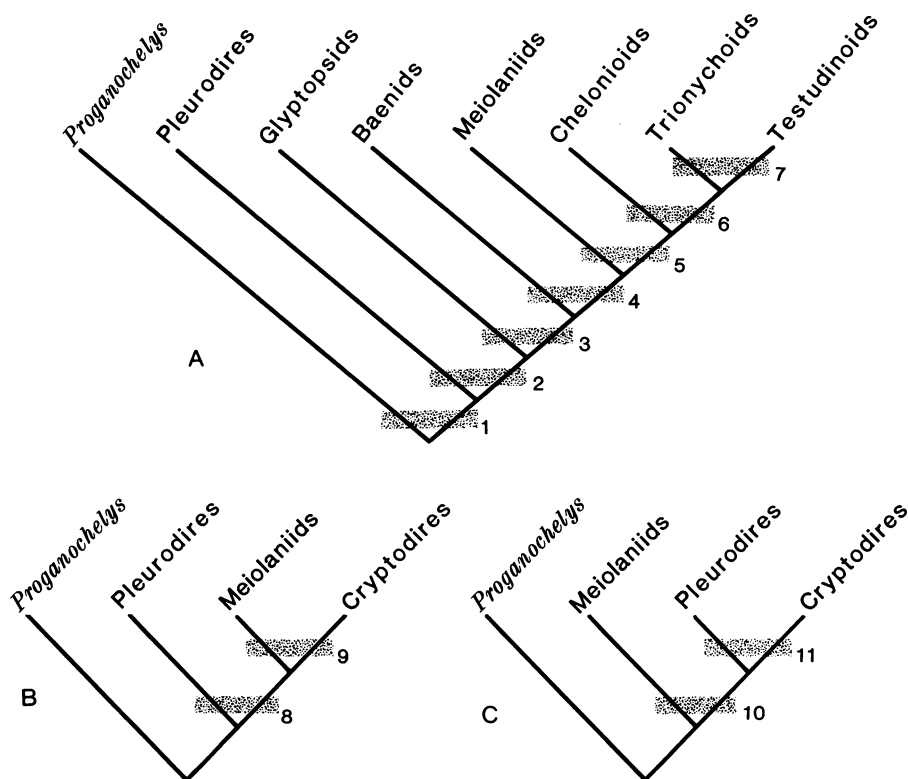


FIG. 65. Three phyletic hypotheses relating meiolaniids to other turtles. A. The hypothesis preferred here, meiolaniids are considered the sister group of other eucryptodires. The numbers refer to the following taxa with characters in parentheses: 1. Testudines (see Gaffney, 1975; Gaffney and Meeker, 1983). 2. Casichelydia (see Gaffney, 1975; Gaffney and Meeker, 1983). 3. Cryptodira (see Gaffney, 1975). 4. Unnamed taxon (posterior temporal emargination separates or nearly separates parietal and squamosal, see Gaffney, 1979a, for discussion). 5. Eucryptodira (see Gaffney, 1975, 1979a). 6. Unnamed taxon (small or absent nasals, prefrontal dorsal lappet meeting or nearly meeting in midline). 7. Unnamed taxon (well-developed vertical neck retraction in which skull is at least partially withdrawn into carapace). B. Alternate phylogenetic hypothesis in which meiolaniids are considered as the sister group to all cryptodires. 8. Casichelydia (as above). 9. Cryptodira (as above), but the monophyly of all cryptodires minus meiolaniids would have to be based on lack of temporal emargination, small nasals, absence of intrapterygoid flange, see text for discussion. C. Alternate phylogenetic hypothesis in which meiolaniids are considered as the sister group to Casichelydia. 10. Casichelydia (as above). 11. Unnamed taxon (absence of intrapterygoid slit, small nasals, partial temporal emargination, see text for discussion).

onto the skull roof and fit into V-shaped indentations on the nasals. Although the morphology of the nasal in *Meiolania platyceps* differs distinctly from the condition in *Proganochelys*, the nasal-premaxilla contact may be considered a character held in common between *Meiolania platyceps* and *Proganochelys*. Again, like the large nasal, this is a generalized amniote feature that could be used to support the hypothesis that *Meiolania* is

the sister group to all other Casichelydia. I would, however, interpret the nasal-premaxilla contact as a retained primitive character lost independently in cryptodires and pleurodires or as a reversal.

In the specimens of *Proganochelys* I am studying the prefrontal has not been prepared internally so the comparison must be limited to the external shape, which in general agrees with *Meiolania platyceps*. In both forms the

prefrontal is relatively large, widely separated from the other prefrontal by a broad nasal-frontal contact, and does not enter the margin of the apertura narium externa. *Proganochelys* is unique among turtles in having a lacrimal bone and duct between the prefrontal and maxilla. In generalized Casichelydia, such as glyptopsids and baenids, the prefrontal is relatively smaller than in *Proganochelys* and *Meiolania platyceps* and the postorbital contact is reduced or lost (see below), but the other relations are the same. Eucryptodires usually have a large prefrontal that morphologically replaces the missing nasal, and this is a distinctly different condition, but the prefrontal of *Meiolania platyceps* is consistent with all the alternative phylogenies that are considered here.

The frontal of *Meiolania platyceps* and *Proganochelys* is similar in that it is relatively small and widely separated from the orbits by a broad contact of the postorbital and prefrontal. This feature is another one that can be interpreted as a generalized amniote character. Furthermore, although it occurs widely in other casichelydians (for example, some emydids, chelydrids, *Dermochelys*), forms that I would consider to be generalized cryptodires (glyptopsids, baenids) have a widely separated prefrontal-postorbital. The absence of a clear distribution of this feature suggests that we are dealing in fact with more than one character. The degree of postorbital-prefrontal contact and the relative size of the frontal are closely involved with the position of the orbits and the general shape of the skull. *Meiolania platyceps* and *Proganochelys* have short, wide skulls with widely spaced orbits facing anterolaterally and having no dorsal exposure. Glyptopsids and primitive baenids have elongate skulls with narrow interorbital distances and the orbits have some degree of dorsal exposure. In pleurodires the situation is unclear although narrow interorbital distances and dorsal orbital exposures are generally the rule. Small frontals, widely separated from the orbits by a broad prefrontal-frontal contact would be best interpreted as primitive for turtles but large frontals with narrow interorbital distances lacking a prefrontal-postorbital contact appears to have evolved a number of times, and the character does not form a group consistent

with other features. The presence of the generalized condition in both *Meiolania platyceps* and *Proganochelys* is therefore consistent with a number of phylogenetic hypotheses.

The ventral surface of the skull roofing bones are not yet accessible in the material of *Proganochelys* that I am working on. Therefore, such features as the fissura ethmoidalis, processus inferior parietalis, and sulcus olfactorius must wait for future comparisons.

The parietal in *Proganochelys* is what would be expected in the sister group of Casichelydia; there is no temporal emargination and the retained supratemporal is present posterolaterally. The parietal of *Meiolania platyceps* on the other hand is very unusual among turtles in that it is entirely surrounded by bone, the squamosal and supraoccipital in particular. The shape of the parietal is equidimensional in *Meiolania platyceps* but distinctly wider than long in *Proganochelys* so there are not even superficial similarities between them. In glyptopsids, primitive baenids, and most pleurodires the parietal is distinctly longer than wide, suggesting that as the generalized casichelydian condition. The parietal shape in *Meiolania platyceps* is best interpreted as apomorphic for all meiolaniids, as the condition also occurs in *Crossochelys*. If meiolaniids are hypothesized as the sister group to other eucryptodires then the feature used to argue baenid-eucryptodire monophyly, namely well-developed temporal emargination (Gaffney, 1979a) is contradicted. Meiolaniids can be interpreted as having lost this emargination and secondarily evolving a squamosal-parietal contact and that is the point of view that I would favor.

The jugal of *Proganochelys* is relatively large and has a squamosal contact, rare but not unknown conditions in Casichelydia (*Dermochelys*, for example), whereas the jugal of *Meiolania platyceps* is smaller, has no jugal contact, and is not noticeably different from other Casichelydia.

The limits of the quadratojugal in *Proganochelys* are not completely known, but the bone, as understood to date, is a relatively elongate element lying anterior to the quadrate. The quadratojugal of *Meiolania platyceps* is more like other turtles than *Progan-*

*ochelys*, but I do not think that this resemblance is distinctive enough to be useful in a phylogenetic argument because of the great variation in quadratojugal morphology in Casichelydia.

*Meiolania platyceps* (and presumably the other meiolaniids) is unique among turtles in having a broad quadratojugal-squamosal contact ventral to the cavum tympani and quadrate.

The squamosal of *Meiolania platyceps* bears the prominent horns and is the largest bony element of the skull extending from the parietal-postorbital down to the quadratojugal ventrally and behind the parietal to meet the supraoccipital posteriorly. There are no features of the squamosal in common between *Meiolania platyceps* and *Proganochelys* suggesting that *Meiolania platyceps* has any vestige of a generalized chelonian condition in that bone. The prevention of a parietal exposure posteriorly in *Meiolania platyceps* is not primitive for turtles and the clear participation of the squamosal in a well-developed antrum postoticum and cavum tympani are definite casichelydian derived features.

The postorbital of *Meiolania platyceps* agrees with other casichelydians but that bone in *Proganochelys* differs from most other turtles only in being relatively larger and that seems to be a function of skull shape.

**PALATAL ELEMENTS:** As discussed above the premaxillae of *Proganochelys* and (most) *Meiolania platyceps* have dorsal processes that reach the nasals and this appears to be a retained primitive or reversed character in *Meiolania platyceps* as it is not definitely known to occur in any other turtles.

The maxilla of *Proganochelys* does not appear to differ significantly from other turtles (except in having a lacrimal contact, a bone absent in all other turtles). The triturating surfaces of the premaxillae and maxillae are relatively narrow in *Proganochelys* (as in many other turtles) and are moderately expanded in *Meiolania platyceps* with the addition of accessory ridges. However, these features are not of significance in determining sister group relations among turtle higher taxa.

The vomer of *Proganochelys* is paired, a generalized amniote condition not found in other turtles. The vomer of *Meiolania pla-*

*tyceps* is similar to that in other casichelydians and it has a prefrontal contact that is a unique contact for cryptodires. There is not yet sufficient information to determine definitely that *Proganochelys* lacks a vomer-prefrontal contact but it does seem likely at present.

The anterior portion of the palatine bone is not particularly well preserved in *Proganochelys*, but the posterior parts are much as in other turtles. The foramen palatinum posterius is formed by the palatine and pterygoid in *Proganochelys*, most pleurodires, and in generalized cryptodires such as *Glyptops* and baenids. Its formation by the maxilla and palatine in *Meiolania platyceps* does not appear to be significant with regard to the hypothesis being tested here.

**PALATOQUADRATE ELEMENTS:** The bones making up the palatoquadrate region are among the most useful in testing phylogenetic hypotheses among chelonians, and it is in this area that characters occur that clearly resolve questions of relationships among *Meiolania platyceps*, *Proganochelys*, and other turtles.

The quadrate in *Meiolania platyceps* has a well-developed cavum tympani, medial wall, and incisura columellae auris, as in other casichelydians, but in contrast to *Proganochelys* which has a more generalized amniote type of quadrate. The more internal areas of the quadrate and basicranium are not yet accessible in *Proganochelys* so further comparison must be delayed. Among Casichelydia, *Meiolania platyceps* has an incisura columellae auris that is fully enclosed by bone and the stapes and eustachian tube are enclosed together, a condition found both in baenids and in pleurodires. This feature may be interpreted as primitive for all Casichelydia or as independently derived in pleurodires and baenids. The hypothesis that *Meiolania platyceps* is a eucryptodire would require a third independent derivation in the latter case. Earlier workers (see Previous Work) have allied *Meiolania platyceps* and baenids on primitive characters but this condition of the incisura columellae auris is the only relatively strong baenid feature I have found in *Meiolania platyceps*. Other baenid synapomorphies are the expanded posterior triturating surface with accessory ridge, possibly interpretable as present in *Meiolania*

TABLE 2  
Measurements (in Centimeters) of *Meiolania platycephs* Skulls

	MM F:13825a	AM F:43183	AM F:57984	AM F:61110	AM F:1209	AM F:18668
Length from anterior margin of premaxillae to posterior margin of occipital condyle	14.3	13.3	16.0	12.5	—	12.5
Length from anterior margin of nasals to posterior margin of skull roof	19.2 <sup>a</sup>	18.5	20.0	14.4	—	—
Skull width measured at base of "A" horn cores	22.0 <sup>a</sup>	17.0	16.0	16.3	19.0	—
Skull width measured at lateral margin of area articularis mandibularis	19.0 <sup>a</sup>	15.5	17.0 <sup>a</sup>	14.2	17.5	13.0 <sup>a</sup>
Skull height measured from skull roof to ventral margin of cheek at position of cavum tympani	10.5 <sup>a</sup>	9.0	—	—	10+?	—

<sup>a</sup> Estimated.

*platycephs*, and the small prefrontal lappet, absent in *Meiolania platycephs*. Another significant derived character of the quadrate is the processus trochlearis oticum formed by the quadrate and prootic and synapomorphic for the Cryptodira. *Meiolania platycephs* has a well-developed processus, *Proganochelys* has none.

The pterygoid, however, shows the clearest indications of relationships of *Meiolania platycephs*. In *Proganochelys* the generalized amniote condition of movable basiptyergoid articulation (Gaffney, 1983; Gaffney and Meeker, 1983) is present but all other turtles (Casichelydia) have this articulation fused. In cryptodires the pterygoid extends posteriorly to cover the basiptyergoid articular region and connects the neurocranium and quadrate. *Meiolania platycephs* has the cryptodire condition.

*Meiolania platycephs* (and the other meiolaniids) also have the intrapterygoid slit, a structure (described in the main body of the text) that I have interpreted as synapomorphic for the Meiolaniidae. In the light of *Proganochelys* could this structure be interpreted instead as primitive at some higher level within turtles? The intrapterygoid slit covers the rostrum basisphenoidale ventrally and, if removed, would show the rostrum basisphenoidale separating the two pterygoids. In *Proganochelys* the cultriform process of the basisphenoid is visible ventrally because the pterygoids are separated by a space. In other amniotes the cultriform process and the rostrum basisphenoidale seem to have different

embryologic origins (the latter is the ossified remnant of the trabeculae, whereas the former is membrane bone ossifying ventral to the trabeculae) but this may not be significant as the rostrum basisphenoidale of turtles is extended into and perhaps combined with the cultriform process. Nonetheless, the ventral pterygoid flanges covering the rostrum basisphenoidale in other Casichelydia are still present in meiolaniids even though they are not fused onto the rostrum. Is this a primitive condition or just different?

It could be argued from a derivationist point of view that the unfused condition would precede the fused condition although there is as yet no evidence for this. There is some support, however, from the glyptopsids, which are characterized by an elongate basisphenoid that completely separates the pterygoids. I have argued (Gaffney, 1979a) that by comparison with the out-group for cryptodires, the pleurodires, this condition is derived because pleurodires have pterygoids that meet ventrally beneath the rostrum basisphenoidale. But if we accept the glyptopsid condition as primitive for cryptodires on the basis of its similarity to *Proganochelys*, then the meiolaniid condition might be considered as intermediate between glyptopsids and other cryptodires. For this hypothesis the medially meeting pterygoids would have to be independently derived in pleurodires and, if meiolaniids are accepted as eucryptodires, in baenids also. It seems most parsimonious to regard the intrapterygoid slit of meiolaniids as a synapomorphy for this family.



TABLE 3  
A Comparison of the Five Most Complete Skulls of *Meiolania platyceph*

	MM F:13825a	AM F:43183	AM F:57984	AM F:61110	AM F:18668
Locality	"Lord Howe Island"	Ned's Beach Cliff	Swimming pool of Ocean View Guest House	Old Settlement Beach	Trader Nick's
Collector	Collector unknown, but collected before 1880	Purchased from Phyllis M. Ross in 1947, possibly collected by her husband, Patrick Gaffney, 1979b	Alan Wilson and Cec Tompkins, 1971	Alex Ritchie, Oct. 5, 1977	Max Nicholls and Reg Hines, purchased 1926
Figures and literature	Owen, 1888	Gaffney, 1979b	Gaffney, 1982	Ritchie, 1978	None
Skull areas preserved	Most of skull roof weathered off, external surface generally damaged. Only intact palate known to date. Stapes and hyoid associated	Nearly complete, but most of central section of palate gone	Badly broken during discovery but originally complete. Some of palate remaining, good braincase, most of both cheeks missing	Lower margin of cheek, all of palate, and some of braincase lost to erosion	Snout, braincase, and left cheek preserved
Other elements preserved	Lower jaws, hyoid, first and second cervical vertebrae	None	Lower jaws and much of skeleton <sup>a</sup>	Carapace and much of skeleton <sup>b</sup>	None
Sutures	Nearly all fused except in floor of orbit, epipterygoid, and some of palate	Nearly all fused except in part of cavum cranii	Nearly all open except squamosal-parietal-supraoccipital contacts	Nearly all fused except in part of basicranium	Cheek and palatal sutures open, remainder fused
Bone thickness	Intermediate	Intermediate	Thick	Thin	Intermediate
Scale expression	Much of bone surface eroded off, some scales visible in anterior half of skull	Poor, although most of skull roof mechanically prepared with consequent removal of bone	Good	Extremely good	Good

TABLE 3 — (Continued)

	MM F:13825a	AM F:43183	AM F:57984	AM F:61110	AM F:18668
C-horn	Badly eroded but apparently as in AM F:61110	Barely visible	Very well developed	Distinct but not as developed as in AM F:57984	Indeterminant
Bulge in D-scuta area	Indeterminant	Low, thin bone	Bone thickened into well-developed convex bulge	Low, thin bone	Indeterminant
Preorbital "boss" in scale area F	Intermediate	Low	Intermediate	Well developed	Well developed
B-horn	Eroded bases preserved	Not curved	Not curved	Curved posteroven- trally	Indeterminant
B horn length <sup>c</sup>	Indeterminant	32 mm.	60 mm.	35 mm.	Indeterminant
B horn width	Indeterminant	32 mm.	42 mm.	46 mm.	Indeterminant
Internarial septum	Complete	Complete	Naturally incom- plete	Naturally incom- plete, septal pro- cesses closer than in AM F:57984	Naturally incom- plete, septal pro- cesses as in AM F:57984
Nasal overhang	Overhang slight but present	No overhang	Very well devel- oped overhang	No overhang	No overhang
Choanal grooves on vomer and palatine	Deepest anteriorly	Indeterminant	Deepest midway along their length	Indeterminant	Indeterminant
Labial ridge	Low and thick	Intermediate	High and thin	Broken but looks intermediate	High, but thicker than in AM F:57984
Processus trochlearis	Moderate	Moderate	Moderate	Well developed	Moderate
Processus interfen- stralis of opisthotic	Indeterminant	Broken	Ventral margin par- tially fused	Ventral margin free	Ventral margin par- tially fused

<sup>a</sup> The postcranial remains of AM F:57984 consist of: nearly complete cervical series, anterior and central areas of carapace with costal rib heads 1–8, anterior lobe of plastron, nearly complete left and right scapulae with portions of coracoids, nearly complete right forelimb and right hindlimb, head of left humerus, left femur, and two caudals. This specimen was restored in 1980–1981 at the AMNH, casts are now in New York, the Australian Museum, and the Lord Howe Island Museum.

<sup>b</sup> The postcranial remains of AM F:61110 consist of: nearly complete carapace, both shoulder girdles, both humeri, right and left femur, left tibia, left fibula, caudal, tail ring, and phalanges. Found nearby, but given number AM F:61412, were a left radius, cervical rib, and dermal ossicles; probably part of AM F:61110.

<sup>c</sup> Measurements in millimeters, average of left and right.

The meiolaniids have a foramen posterior canalis carotici interni contained within the pterygoid and formed near the posterior end of the pterygoid. This is an advanced condition that I have argued characterizes a group, the Eucryptodira, containing the living cryptodires. The condition is quite clear in *Crossochelys* and *Meiolania platyceps* (see text for description) but there is also an opening that I have termed the foramen caroticum basisphenoidale covered by the intrapterygoid slit in *Meiolania platyceps* but apparently exposed ventrally in *Crossochelys*. Is this foramen the same as the foramen posterior canalis carotici interni in baenids and in glyptopsids or even in *Proganochelys*? The general position of these foramina is certainly similar: on or near the suture between basisphenoid and pterygoid and leading into that portion of the canalis caroticus internus formed at least in part by the basisphenoid. *Meiolania platyceps* might be interpreted as an intermediate form having the baenid foramen as well as the eucryptodire foramen and consistent with a derivationist argument that would derive baenids from a *Meiolania*-like ancestor by the loss of the eucryptodire foramen and eucryptodires by loss of the baenid foramen. One particular problem with this hypothesis is the more precise testing of homology of the foramina in these groups. In glyptopsids and baenids the branching of the palatine artery, the canalis caroticus lateralis, takes place in the sutural area between pterygoid and basisphenoid as it does in most, if not all, eucryptodires. In *Meiolania platyceps* this split takes place in the intrapterygoid slit, as it would in a eucryptodire with the pterygoid flange lifted off the basisphenoid. In glyptopsids and baenids the canalis caroticus lateralis also splits from the canalis caroticus internus with the pterygoid-basisphenoid suture rather than at the foramen posterior canalis carotici interni as it should if the latter foramen were the same as the foramen caroticum basisphenoidale of meiolaniids. Actually, the various alternative interpretations of the foramen involved here does not alter the position of *Meiolania platyceps* as a eucryptodire, rather these alternatives will change the position of the glyptopsids and baenids regarding the use of this morphology

as a derived character testing baenid monophyly, glyptopsid plus baenid monophyly, or baenid plus eucryptodire monophyly.

There is a character contradiction with a derived feature of pleurodires that is also found in *Meiolania platyceps* and *Niolamia* (the type of *Crossochelys corniger*, Simpson, 1937). The facial (VII) nerve sends a branch posteriorly, the hyomandibular, which in cryptodires enters the canalis cavernosus and travels posteriorly in that structure, whereas in pleurodires the hyomandibular branch usually lies in its own canal. In meiolaniids (*Meiolania platyceps* and *Crossochelys*) the canalis nervi facialis also extends posteriorly presumably with the hyomandibular nerve as in pleurodires. In view of the other cryptodiran features of *Meiolania platyceps* it would be most parsimonious to interpret this character as independently derived or primitive for Casichelydia (see Gaffney, 1975) rather than to hypothesize meiolaniids as pleurodires.

The epipterygoid is known in only one specimen of *Proganochelys* and it is not yet fully prepared for study. The epipterygoid appears to be a large, relatively loose element not particularly similar to other amniotes or to turtles. The large epipterygoid of *Meiolania platyceps* is probably primitive for cryptodires but whether it is best interpreted as primitive for all turtles, for all Casichelydia, or just cryptodires remains to be seen.

**BRAINCASE ELEMENTS:** The ossified neurocranium of *Proganochelys* shows a number of unusual features, such as the very large foramen jugulare posterius, apparently hypertrophied cavum labyrinthicum, and large tuberculum basisphenoidale, whose significance has not yet been determined. Preparation in this area is still incomplete, but excepting the features already discussed, such as the basisphenoid, the neurocranial region of *Meiolania platyceps* is quite similar to that in other cryptodires and would not particularly benefit from comparison with *Proganochelys* at this time. I find no *Meiolania platyceps* characters that differ significantly from the expected eucryptodiran condition in this region with the exception of the supraoccipital. As discussed above, the supraoccipital in meiolaniids is enlarged to form a promi-

ment part of the skull roof, a condition approached by the chelid, *Pseudemydura*, but very unusual in cryptodires.

In summary, although new information from *Proganochelys* does reveal similarities between it and *Meiolania platycephs*, the hypothesis that meiolaniids are the sister group to the remaining Casichelydia is inconsistent with a number of compelling characters. It is

very difficult to accept the hypothesis that meiolaniids are not clearly cryptodires and that the sister group of cryptodires are pleurodires. Within the Cryptodira there are more contradictory characters or perhaps more accurately, the characters are not as well understood, so that I am less confident of the sister group relations of glyptopsids, baenids, and eucryptodires, and therefore meiolaniids.

## SUMMARY OF CRANIAL FEATURES OF *MEIOLANIA PLATYCEPS*

### DERMAL ROOFING ELEMENTS

Nasals present, relatively larger than in all other turtles.

Naso-maxillary sinus branching laterally from apertura narium externa.

Fossa nasalis very well developed, larger than in any other turtle.

Descending process of prefrontal meeting maxilla, palatine, and vomer as in most cryptodires.

Prefrontal with well-developed dorsal plate in contrast to baenids but not meeting in midline as in most eucryptodires.

Apertura narium external partially or (more commonly) completely divided by a ventral nasal process and a dorsal premaxillary process.

Frontal widely separated from margin of fossa orbitalis by broad contact of postorbital and prefrontal.

Parietal relatively small, entirely surrounded by bone, and widely separated from posterior margin of skull by broad contact of squamosal and supraoccipital.

Squamosal forms most of posterolateral portion of skull, beginning medially with a broad suture with the supraoccipital and extending laterally and ventrally to reach the quadratojugal ventral to the cavum tympani; posterior margin of squamosal downturned to occlude portion of fossa temporalis; squamosal forms distinctive posterolaterally directed horns that are usually recurved.

Processus inferior parietalis small in comparison with most turtles, barely enters foramen interorbitale in contrast to most tur-

ties in which the process is a major constituent of the foramen.

### PALATAL ELEMENTS

Labial ridge of premaxilla and maxilla relatively high and sharp, paralleled by a lower intermediate ridge running between the labial ridge and the lingual margin, a second intermediate ridge as in "*Meiolania*" *oweni* generally absent but may be poorly developed on posterolateral portion of triturating surface.

Lingual margin of triturating surface without a ridge, evenly expanded medially, and without local expansions as seen in baenids.

Paired labial cusps form the anterior margin of low parasagittal ridges that extend posteriorly to connect the labial and intermediate ridges and form the lateral margin of a deep median concavity.

Palate similar to testudinids and consists of a broad arch with two longitudinal troughs formed by the vomer and palatines and separated by a thin median ridge formed by the vomer.

Sulcus vomeri and fissura ethmoidalis relatively broad in comparison to other turtles.

### PALATOQUADRATE ELEMENTS

Cavum tympani and incisura columellae auris completely enclosed by dermal skull roof (squamosal and quadratojugal) as in no other turtle outside the Meiolaniidae.

Incisura columellae auris with stapes and eustachian tube confluent.

Fossa cartilaginous epipterygoidei present as in nearly all cryptodires.

Processus trochlearis oticum formed by prootic and quadrate as in other cryptodires, no distinct anterior projection as in many cryptodires, but developed to the extent seen in most baenids.

Processus pterygoideus externus with parasagittal anterior extension and vertical plate lacking as in testudinids.

Prootic and epipterygoid contact prevents exposure of pterygoid in foramen nervi trigemini.

Intrapterygoid slit present, formed by medially meeting flanges of pterygoid ventral to basisphenoid, unique to Meiolaniidae.

Intrapterygoid slit covers foramen basisphenoidale ventrally.

Foramen posterius canalis carotici interni is in eucryptodiran position, at the posterior margin of the pterygoid, it also lies in posterolateral edge of cavum acustico jugulare in contrast to most eucryptodires except testudinids.

Epipterygoid very large, extending from the skull roof to the pterygoid, occupying nearly all of the braincase wall between the foramen nervi trigemini and the foramen interorbitalis.

#### BRAINCASE ELEMENTS

Crista supraoccipitalis relatively small when compared with other turtles; dorsal portion much expanded horizontally, comparable to *Pseudemidura*.

Margin of foramen magnum inclined so that dorsal part is more anterior than ventral part.

Condylus occipitalis formed equally from exoccipitals and basioccipital as in most turtles, with exoccipitals meeting or nearly meeting in midline.

Pterygoid has broad contact with basioccipital posteromedially as in cryptodires.

Opisthotic enters posteromedial portion of foramen stapedio-temporale, canalis stapedio-temporalis, and aditus canalis stapedio-temporalis in contrast to most turtles in which these structures are formed only by the quadrate and prootic, foramen stapedio-temporale formed only by prootic and opisthotic in *Meiolania platyceps*.

Dorsum sellae high, does not overhang sella turcica or foramen anterior canalis carotici interni.

Paired ridges lie on either side of dorsum sellae extending from processus clinoides to base of rostrum basisphenoidale (trabeculum).

Foramen anterius canalis carotici interni lies in posterolateral corner of sella turcica.

Sella turcica relatively small and not defined anteriorly due to the absence of a distinct rostrum basisphenoidale such as occurs in most other turtles.

Canalis stapedio-temporalis nearly twice the diameter of the canalis caroticus internus, implying that a well-developed stapedia artery was present, the primitive chelonian condition.

Fenestra perilymphatica present and distinct, hiatus postlagenum absent.

Foramen canalis nervi facialis separated from canalis cavernosus as in pleurodires.

#### APPENDIX 1.

##### REPORT BY DR. JOHN FOULIS IN: NEW SOUTH WALES PARLIAMENTARY ACCOUNTS AND PAPERS—LORD HOWE ISLAND: PROPOSED NEW SETTLEMENT, 1853

Statement of circumstances in reference to Lord Howe's Island, situated off the coast of New South Wales, between the Heads of Port Jackson and Norfolk Island, furnished by Dr. Foulis, of Sydney.

I shall endeavor in supplying the information I possess relative to Lord Howe's Island, to confine myself to facts that came under my notice while

residing there, and shall refer to a plan<sup>1</sup> attached to this statement, which I have drawn as correctly

<sup>1</sup> I have examined this very rough approximation of the island's features and find no geologic information worth noting. No reference is made on it to fossils or bones.

as my memory would enable me, having lived on the Island about three years.

I believe the Island is about 450 miles from Sydney, and with a fair wind can be reached in three or four days, although sailing vessels with contrary winds are often fourteen days making the trip.

It is about thirty-five miles in circumference, and only about two and a half miles across in the widest part. On reference to the plan attached, it will be seen that on one side of the Island there is a coral reef extending nearly two miles from the shore, and stretching from the northern to the southern extremity, and being about ten miles in length.

It is only within this reef that any safe anchorage for small vessels can be found; and I would beg leave to observe that there are two entrances through the reef (as shown in the plan) by which vessels of fifty or sixty tons can enter, drawing from seven to eight feet of water. All large ships, such as whalers, which visit the Island for provisions, have to stand off and on, and communicate with the Island by lowering boats.

The entrance through the reef marked No. 1, is the best for vessels to go in at as the water seems scarcely to be disturbed here when it is blowing hard outside, nor is there any ground swell observable, although frequently a heavy swell and surf is breaking on the reef.

The water inside this reef is in most places about five feet deep at half tide, and in some parts, from ten to twelve, with a fine sandy bottom.

I may here observe that there are abundance of fine fresh easily obtained in the lagoon formed by the reef, the principal being a beautiful blue fish shaped somewhat like the bream of this harbour, averaging about 4 lbs. There are also mullet, rock cod, guard fish, salmon, king fish, etc. Whales are in the habit of breeding near the reef at certain seasons.

With reference to the Island itself, I would first remark that some of the hills are considered to be upwards of 4,000 feet above the level of the sea, and are visible on a clear day at eighty or ninety miles distance, and are usually sighted by vessels passing between Sydney and Norfolk Island.

The slopes of these hills are very thickly wooded, and the soil on the cleared land, consisting of about forty acres, is very rich, being composed of disintegrated trap rock and coral sand; it is very productive, as is evident by the very abundant and large cabbage trees which flourish on all the flats.

There are many varieties of hardwoods, some being very large and durable and fit for building purposes.

All kinds of vegetables can be produced in great

abundance, potatoes, pumpkins, and other garden provisions are reared twice a year and sometimes oftener from the same ground.

Maize and wheat grow well and have yielded large crops as also the sweet potatoe, which seems very well adapted for the more sandy parts.

The banana grows luxuriantly and ripens very well; and some vines which I planted on my arrival on the Island flourished exceedingly well and were producing fruit before I left.

With respect to water, I am of opinion that any quantity could be obtained by sinking wells or forming dams. There are many good springs on the hills, and I caused one or two wells to be sunk at a very moderate expense. They were about 15 feet deep, and contained about 10 feet of water and never failed in the driest weather in supplying the settlement with abundance of pure and wholesome water.

It is very rare to have a period of more than a month at any time of the year without rain, and the usual rainy season corresponds with the winter months in this Colony. I consider it will be of some importance to notice here the prevalent winds at different seasons of the year, as vessels attempting to enter through either of the passages in the reef require a leading wind.

During the winter months northerly and north-westerly gales prevail, and it is from the months of September to January or February that the southerly and south-easterly winds are almost constant, and as the reef faces these points it is at this season that there is the greatest facility for vessels entering the harbour, a fair wind being necessary in consequence of the narrowness of the passages, through the reef, which precludes the possibility of vessels beating in, but this difficulty could be obviated by the employment of a steamer of light draught.

In the heat of the summer the thermometer seldom ranges higher than 80°, nor in the winter lower than 50°, and I am of opinion that owing to this great equality of temperature it would be difficult to find a more healthy spot for European constitutions.

There are few birds that belong to the Island, the only valuable kind being a large blue pigeon which is tolerably numerous; there are also numbers of small parrots, very destructive to the crops, and a kind of bird called the woodhen, which is much like the landrail in its habits and shape, but which cannot fly; a few large eagles occasionally visit the Island, and gannets and tropic birds build on the cliffs.

The mutton bird (which serves as an article of food, and is much esteemed by the inhabitants), visits the Island at certain seasons in flocks of

thousands to lay its eggs in the ground, at which time it is caught in great numbers for the sake of its feathers.

It is only the young unfledged birds that are eaten, as they are free from any fishy rankness. There are considerable numbers of wild pigs running in the Bush, and also several large herds of goats, both of which were hunted with dogs and used as food. There are no snakes, rats, mice, native cats, nor other wild animals except the pigs and goats. I have no doubt plenty of land could be found to support a small flock of sheep (say 500), at a time, and also a few head of cattle, and I think they would thrive well, and find abundance of food from the natural grasses which spring up wherever the land is cleared, and it is so thickly timbered that there could be no want of wood for building, as well as domestic purposes. I believe there are at present about 16 persons residing on the Island, some of them having their wives and families, and they enjoy uninterrupted good health. I saw lately in Sydney, one of the married women who came up in a whaler for provisions, she had been nearly nine years there, and was most anxious to return. The settlers all have gardens and huts which they have built of the cabbage tree. They live by trading with whalers, catching pigs and fish, and growing vegetables and fruits, and although few in number, I should consider the Island sufficiently large and fertile to support a population of 5,000 souls if under control, and capable of supplying them with all the usual necessities of life. Some coal might probably be required after a time, although at present, and for some years, there would be abundance of firewood, and sides of the hills which are not capable of being brought under cultivation, being thickly wooded down to the waters edge.

The storms of wind and rain are sometimes very severe, and I have known the water to rush down from the hills in such torrents as to flood the gardens and the flats, although this only happened once during my residence.

The higher hills of Howe's Island are all volcanic, and in some parts form perpendicular basaltic cliffs, many hundred of feet above the level of the sea. The middle and lower parts consist of

soft sandstone hills and cliffs composed of granulated coral, which seems to have been stratified under water, as the bones of turtles and sea shells are found embedded in them.

The arable soil is mixed with sand derived from the decomposition of these soft rocks, and this, in my opinion, is a great cause of its fertility. There are extensive and deep beds of clay on some parts of the low lands; on one spot where a well was sunk, the stratum of clay was not cut through at a depth of 14 feet. I should consider it well adapted for brickmaking if mixed with a portion of a kind of ferruginous earth which is abundant in the same neighborhood. (See plan.)

There is a conical hill near the southern extremity of the Island, which was used by the settlers as a look-out station, as from its commanding position it overlooks all the other heights, except the Big Hills, which are inaccessible perpendicular cliffs, and above 4,000 feet high. From this hill all vessels may be seen approaching when at a considerable distance.

There are several small islands of three or four acres in extent, within a mile and a half of the northern extremity of the mainland called the Admiralty Rocks. They are quite bare of all vegetation, except coarse grass, which affords breeding places for vast numbers of mutton birds and gannets.

Howe's Island has for many years been a place of resort for whalers to procure wood, water, and fresh provisions, to enable them to prosecute their voyage without the necessity of going into port. There were generally from 60 to 80 vessels in the course of the year that touched there for the above purpose, and it not unfrequently happened that we had English news from American vessels some weeks before the same was known in this Colony.

Having now noticed the principal features of the Island, I would beg to add that any further particulars that might be considered useful to the Government which I may not have alluded to, I shall at any time, be most happy to afford, if in my power.

[Signed] JOHN FOULIS, M.D.  
Sydney, September 1, 1851

## APPENDIX 2.

### *MEIOLANIA PLATYCEPS* SPECIMENS IN THE AUSTRALIAN MUSEUM, SYDNEY, NEW SOUTH WALES

AM F:182-215 were collected by Robert Etheridge and were catalogued during 1888, but they may have been collected in 1887.

AM F:182—phalange

AM F:184—a group number including a nuchal, first costal, set of articulated costals and peripherals, peripherals, left anterior portion of skull, and shell fragments



AM F:186—right ramus of lower jaw  
 AM F:189—right pelvis with horn core  
 AM F:190—broken acetabulum of pelvis  
 AM F:191—horn core with skull fragment  
 AM F:192—five horn core fragments  
 AM F:193—seven fragments of tail rings and “A” horn cores  
 AM F:194—tail fragments in matrix  
 AM F:205—a group number with a femur head, two heads of humeri or femora, two fragments of humeri or femora  
 AM F:206—three caudals with label in Etheridge’s handwriting: “Lord Howe Island, reptilian lumbar vertebrae associated with *Meiolania*”  
 AM F:207—two right radii, a right ulna  
 AM F:208a—braincase, figured in Anderson (1925, pl. 33, fig. 6)  
 AM F:208b—braincase, figured in Anderson (1925, pl. 33, fig. 5; pl. 35)  
 AM F:209—three right tibia, one left tibia and an upper portion of right fibula  
 AM F:210—glenoid fragment  
 AM F:211—pathologic caudal  
 AM F:212—proximal end of humerus  
 AM F:213—distal end of left tibia, and two posterior thoracics and/or sacrals  
 AM F:215—caudal fragment

AM F:217–232 were collected by E. H. Saunders and purchased from him in 1888.

AM F:217—large sacral rib  
 AM F:219—right acetabulum  
 AM F:220—six carapace fragments including a nuchal fragment  
 AM F:222—? scapula fragment  
 AM F:223—proximal end of left ulna  
 AM F:225—two dermal ossicles  
 AM F:226—one haemal spine and one caudal centrum  
 AM F:227—three bone fragments, one indeterminate, two humeral fragments  
 AM F:228—five tail club fragments  
 AM F:229—five tail ring fragments  
 AM F:230—horn core fragment  
 AM F:232—identified as tail but seems to be three shell vertebrae fused  
 AM F:241—(probably an error on label, 241 in catalogue is an invertebrate) bridge peripherals and costal fragment

AM F:366–375 were purchased from Captain G. Garth in 1888. Garth was captain of the schooner *Mary Ogilvie* and apparently acted as agent for Saunders on Lord Howe Island.

AM F:366—right anterior peripherals, costal, and other peripherals  
 AM F:367—two specimens, a sacral and a middle

caudal; note by Etheridge says “vertebrae called by Owen caudal of *Meiolania*, but having nothing to do with it.” I have been unable to find an Owen reference that obviously pertains to this specimen

AM F:368—proximal end of femur  
 AM F:369—glenoid portion of shoulder girdle  
 AM F:370—right radius  
 AM F:372—caudal  
 AM F:374—dorsal part of tail ring showing sutures on both edges, and posterior part of a skull  
 AM F:375—three horn cores.

AM F:398–406 are from Fitzgerald, 1888.

AM F:398—anterior portion of skull, figured in Anderson (1925, pl. 31, figs. 1, 2)  
 AM F:399—tail sheath fragment  
 AM F:402—horn core  
 AM F:403—two “A” horn cores  
 AM F:404—scapula fragment  
 AM F:405—right humerus figured in Anderson (1925, pl. 38, figs. 4, 5), and a left femur  
 AM F:406—left radius

AM F:921–928 were transferred from the Department of Mines, Mining and Geological Museum, Sydney, in September 1940.

AM F:921—not *Meiolania*, possibly Recent mammal  
 AM F:922—not *Meiolania*, possibly Recent mammal  
 AM F:923—anterior part of plastron with articulated posterior cervicals and manus  
 AM F:924—scapula with glenoid part of coracoid  
 AM F:925—proximal end of a very large left humerus  
 AM F:926—femur and other bones in matrix  
 AM F:927—egg in matrix  
 AM F:928—egg in matrix

Unless otherwise indicated the following specimens (AM F:1048–1219) were all purchased from William Nichols, 1889–1890.

AM F:1048—horn core, caudal, proximal portion of humerus, and a peripheral  
 AM F:1049—egg, figured in Anderson (1925, pl. 40, fig. 5)  
 AM F: “1059”—damaged humerus, in catalogue this number is a kangaroo, but label says “pur. W. Nichols, 1903”  
 AM F:1194—two tail sheath fragments  
 AM F:1195—two horn cores  
 AM F:1196—a tail ring fragment and an “A” horn core fragment  
 AM F:1197—portion of snout, left side used in

conjunction with AM F:5473 in Anderson (1925, pl. 32, fig. 1)  
 AM F:1198—two caudals  
 AM F:1199—three vertebrae  
 AM F:1200—damaged vertebral centrum  
 AM F:1201—?anterior sacral  
 AM F:1202—left tibia, incorrectly labeled “?lizard”  
 AM F:1203—damaged right femur, figured in Anderson (1925, pl. 40, fig. 1, part of composite with AM F:16858), left femur  
 AM F:1204—left humerus, figured in Anderson (1925, pl. 38, figs. 2, 3)  
 AM F:1205—one left acetabulum, one right acetabulum with portion of ischium  
 AM F:1206—three shell vertebrae  
 AM F:1207—costal and other carapace fragments  
 AM F:1208—plastron, figured in Anderson (1925, pl. 30)  
 AM F:1209—posterior half of skull, figured in Anderson (1925, pl. 34, pl. 33, figs. 2–4)  
 AM F:1210—horn core  
 AM F:1211—tail ring fragment  
 AM F:1214—left ilium  
 AM F:1216—proximal end of right humerus  
 AM F:1217—posterior sacral and other vertebral fragments  
 AM F:1219—right pubis and (?) ischium  
 AM F:1459—damaged humerus and head of femur; from T. E. Icelly, 1891  
 AM F:“1788”—distal end and left femur; no date, number pre-occupied in catalogue  
 AM F:1948—damaged humerus  
 AM F:2804—mold of egg  
 AM F:3296—left pelvis; “from Mr. Berry, Surveyor, General Office, 1878?” Another label says: “A3296”

AM F:5472–5478 were purchased from William Nichols, April 1898.

AM F:5472—two horn cores  
 AM F:5473—left snout, figured in Anderson (1925, pl. 32, fig. 1)  
 AM F:5475—two damaged left humeri  
 AM F:5476—left acetabulum  
 AM F:5477—right tibia  
 AM F:5478—damaged (?) humerus

AM F:5522–5543 were collected by Robert Etheridge and E. R. Waite in 1898.

AM F:5522—posterior half of plastron, same individual as AM F:5523  
 AM F:5523—anterior half of plastron, same individual as AM F:5522  
 AM F:5526—left tibia  
 AM F:5527—left radius  
 AM F:5528—right radius

AM F:5529—both pubes  
 AM F:5531—three bridge peripherals  
 AM F:5532—bridge peripherals  
 AM F:5533—complete bridge with AM F:18326 added to it and belonging to same individual  
 AM F:5534—right fibula  
 AM F:5535—shoulder girdle fragments  
 AM F:5541—a group number of 44 dermal ossicles. It is possible that AM F:5541, AM F:5542, and AM F:5543 were found associated in some manner. I have not found any definite duplication that would demonstrate more than one individual. Preservation and labeling suggests that these numbers were used for one lot artificially segregated  
 AM F:5542—a group number of 39 manus and pes elements, including: two centrales, right and left radials, right and left intermedium, left ulnars, right metacarpal II and phalange, right metacarpal III and phalange, right metacarpal IV, left metacarpal IV, left metacarpal II and phalange and ungula, possibly two V ungual and phalange of manus (can't tell right or left of these), left distal carpal III and IV, right distal carpal III, four distal carpals that could be I or II, right metatarsal I, left metatarsal III and phalange and ungual, left metatarsal I and phalange and ungual, left metatarsal I (?), five penultimate phalanges of fore or hind foot, three presumed distal tarsals, left astragalus, small (?) metatarsal. (All ungulas were originally from AM F:5543, associated by trial and error, no original associations)  
 AM F:5543—eight ungual phalanges, originally 13, but five were added to AM F:5542

AM F:5750–5758 were purchased from William Nichols in 1898.

AM F:5750—tail club  
 AM F:5751—horn core fragment  
 AM F:5752—shell fragment  
 AM F:5754—tail ring fragment  
 AM F:5755—damaged right humerus  
 AM F:5756—right acetabulum and portion of ilium  
 AM F:5757—(?) cervical  
 AM F:5758—proximal end of humerus or femur

AM F:9025–9067 were purchased from William Nichols in 1903.

AM F:9025—horn core  
 AM F:9051—tail club with two articulated caudals and tail rings  
 AM F:9053—horn core  
 AM F:9054—horn core  
 AM F:9055—horn core

AM F:9056—peripheral  
 AM F:9057—right ilium plus acetabulum  
 AM F:9058—distal end left humerus  
 AM F:9059—damaged humerus  
 AM F:9060—proximal end of femur  
 AM F:9061—proximal end right ulna  
 AM F:9065—glenoid portion scapula  
 AM F:9067—two sacral vertebrae, figured in Anderson (1925, pl. 37, figs. 4, 5)

AM F:10773–10788 were purchased from William Nichols in 1906.

AM F:10773—femur  
 AM F:10776—horn core  
 AM F:10777—horn core  
 AM F:10778—horn core  
 AM F:10779—bone fragment  
 AM F:10780—sacral vertebrae  
 AM F:10781—caudal vertebrae  
 AM F:10782—caudals  
 AM F:10784—scapula  
 AM F:10785—scapula  
 AM F:10786—scapula  
 AM F:10787—proximal end femur  
 AM F:10788—?femur fragment

AM F:16846–16870 are without data other than "Lord Howe Island."

AM F:16846—damaged right humerus  
 AM F:16847—distal end right humerus  
 AM F:16848—distal end right humerus  
 AM F:16849—proximal end right humerus  
 AM F:16850—proximal end right humerus  
 AM F:16851—distal end humerus  
 AM F:16852—damaged left humerus  
 AM F:16853—distal end right femur  
 AM F:16854—distal end left femur  
 AM F:16855—distal end right femur  
 AM F:16856—distal end left femur  
 AM F:16857—distal end femur  
 AM F:16858—right femur, figured in Anderson (1925, pl. 40)  
 AM F:16860—anterior end of skull  
 AM F:16863—centrum of shell vertebra  
 AM F:16864—skull fragment  
 AM F:16865—(?) skull fragment  
 AM F:16866—left cranial horn core, figured in Anderson (1925, pl. 32)  
 AM F:16867—tail sheath  
 AM F:16868—caudal  
 AM F:16870—distal end of femur or humerus

AM F:17726–17736 are from R. V. Hines, 1922.

AM F:17726—horn core  
 AM F:17727—horn core  
 AM F:17728—horn core

AM F:17729—horn core  
 AM F:17730—distal end humerus  
 AM F:17731—distal portion humerus  
 AM F:17732—damaged humerus  
 AM F:17733—bridge peripheral  
 AM F:17734—proximal end femur  
 AM F:17735—left acetabulum  
 AM F:17736—shoulder or pelvic girdle fragment

AM F:18249–18254 are from E. Troughton, 1923.

AM F:18249—proximal end femur  
 AM F:18250—head of right humerus  
 AM F:18251—left acetabulum and ilium  
 AM F:18252—left acetabulum  
 AM F:18253—scapula and glenoid portion of coracoid  
 AM F:18254—caudal

AM F:18258–18323 are without data other than "Lord Howe Island" unless otherwise indicated.

AM F:18258—left acetabulum and ilium  
 AM F:18314—braincase  
 AM F:18315—eight articulated cervicals, figured in Anderson (1925, pl. 37, fig. 1)  
 AM F:18316—distal end of femur  
 AM F:18317—damaged femur  
 AM F:18318—right tibia  
 AM F:18319—left tibia  
 AM F:18320—posterior peripheral, from Nicholls and Hines, 1926  
 AM F:18321—shell fragment  
 AM F:18322—tail club fragment and shell fragment  
 AM F:18323—fragment of epiplastron and entoplastron  
 AM F:18325—plastron and other shell fragments, purchased from W. Nichols, 1889  
 AM F:18326—plastral fragments that belong to same individual as AM F:5533, Etheridge and Waite, 1898  
 AM F:18361—tail club, A. R. McCulloch, 1924

Unless otherwise indicated AM F:18363–18390 were purchased from R. V. Hines in 1924.

AM F:18363—braincase, figured in Anderson (1925, pl. 33, fig. 1)  
 AM F:18364—braincase  
 AM F:18365—left ramus of lower jaw  
 AM F:18366—horn core  
 AM F:18367—horn core  
 AM F:18368—horn core  
 AM F:18369—scapula fragment  
 AM F:18370—caudal  
 AM F:18371—caudal  
 AM F:18373—fragments of a caudal centrum

- AM F:18374—damaged right humerus  
 AM F:18375—left tibia  
 AM F:18376—glenoid fragment  
 AM F:18377—glenoid  
 AM F:18378—coracoid fragment  
 AM F:18379—girdle fragment  
 AM F:18380—girdle fragment  
 AM F:18381—shell fragments  
 AM F:18382—shell fragment  
 AM F:18383—shell fragments  
 AM F:18384—three tail ring fragments  
 AM F:18390—six peripheral fragments  
 AM F:18494—cervical, figured in Anderson (1925, pl. 37, fig. 2), no data  
 AM F:18495—cervical, figured in Anderson (1925, pl. 37, figs. 2, 3), no data  
 AM F:18496—coracoid and glenoid portion of scapula, figured in Anderson (1925, pl. 38, fig. 1); same individual as AM F:1208; purchased W. Nichols, 1890  
 AM F:18497—pelvis, figured in Anderson (1925, pl. 30 and pl. 39), no data. Same individual as AM F:1208  
 AM F:18538—horn core, south end of Ned's Beach, R. E. Baxter, 1924  
 AM F:18540—peripheral, R. V. Hines, 1925  
 AM F:18541—(?) scapula, Hines's garden, R. V. Hines, 1925  
 AM F:18542—right femur, R. V. Hines, 1925  
 AM F:18543—eggs, Hines's garden, R. V. Hines, 1925  
 AM F:18544—left femur, Old Settlement Beach, Geo. Nichols, 1925  
 AM F:18545—glenoid or acetabulum fragment, A. R. McCulloch, 1925  
 AM F:18546—(?) stem of scapula, A. R. McCulloch, 1925  
 AM F:18547—left tibia, A. R. McCulloch, 1925  
  
 AM F:18668–19362 were all purchased from Max Nicholls and R. V. Hines in 1926.  
 AM F:18668—partial skull, originally separated into three pieces and registered as AM F:18669 and AM F:18670, as well as AM F:18668  
 AM F:18671—braincase  
 AM F:18673—horn core  
 AM F:18674—horn core  
 AM F:18675—horn core  
 AM F:18676—horn core  
 AM F:18677—eight fragments, including cervicals  
 AM F:18677a—humerus  
 AM F:18678—two caudals  
 AM F:18681—cervical  
 AM F:18682—caudal  
 AM F:18686—fifth cervical  
 AM F:18688—caudal  
  
 AM F:18689—sacrals  
 AM F:18691—sacral vertebra  
 AM F:18695—sacral vertebra  
 AM F:18696—fifth cervical  
 AM F:18699—caudal  
 AM F:18701—vertebra  
 AM F:18703—sacral vertebra  
 AM F:18705—caudal  
 AM F:18706—caudal  
 AM F:18707—caudal  
 AM F:18708—caudal  
 AM F:18709—caudal  
 AM F:18710—caudal  
 AM F:18712—caudal  
 AM F:18713—caudal  
 AM F:18714—caudal  
 AM F:18715—caudal  
 AM F:18716—caudal  
 AM F:18717—caudal  
 AM F:18718—caudal  
 AM F:18720—tail club  
 AM F:18721—tail club  
 AM F:18722—tail club  
 AM F:18723—tail club  
 AM F:18724—tail club  
 AM F:18725—tail club, cervicals and shell fragments prepared from same lump of matrix  
 AM F:18726—scapula fragment  
 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 portions of scapula  
 AM F:18732—scapula  
 AM F:18733—coracoid  
 AM F:18734—glenoid  
 AM F:18735—coracoid  
 AM F:18736—scapula  
 AM F:18737—coracoid  
 AM F:18738—humerus  
 AM F:18739—humerus  
 AM F:18740—damaged humerus  
 AM F:18741—humerus  
 AM F:18742—left humerus  
 AM F:18743—distal portion of humerus  
 AM F:18744—damaged humerus  
 AM F:18746—damaged humerus  
 AM F:18747—left humerus  
 AM F:18748—damaged right humerus  
 AM F:18749—damaged humerus  
 AM F:18750—right humerus, figured in Anderson (1930, pl. 48); belongs to same individual as AM F:18756, AM F:18827, AM F:18833, AM F:18834  
 AM F:18751—left femur  
 AM F:18752—right femur  
 AM F:18753—damaged left femur

- AM F:18755—right femur  
 AM F:18756—left femur, figured in Anderson (1930, pl. 49, fig. 1), belongs to same individual as AM F:18750, AM F:18827, AM F:18833, AM F:18834  
 AM F:18757—damaged left femur  
 AM F:18758—shaft of femur  
 AM F:18759—left femur  
 AM F:18760—damaged (?) femur  
 AM F:18761—right femur  
 AM F:18762—caudal  
 AM F:18762a—right femur  
 AM F:18763—distal end of femur  
 AM F:18764—ungual  
 AM F:18765—ungual  
 AM F:18766—ungual  
 AM F:18767—ungual  
 AM F:18768—ungual  
 AM F:18769—ungual  
 AM F:18770—dermal ossicle  
 AM F:18771—ungual  
 AM F:18772—ungual  
 AM F:18773—costal (?) fifth right  
 AM F:18774—shell fragment  
 AM F:18775—nearly complete plastron, lacking only buttresses and bridge areas. Comprised of the following catalogue numbers: AM F:18774 (part), AM F:18775, AM F:18776, AM F:18778, AM F:18779, AM F:18781 (part), AM F:18784, AM F:18786, AM F:18787, AM F:18788 (part), AM F:18789, AM F:18790, AM F:18794, AM F:18795 (part), AM F:18801, AM F:18806, AM F:18808, AM F:18809  
 AM F:18777—shell fragment  
 AM F:18779—costal  
 AM F:18781—plastron fragment  
 AM F:18782—shell fragments  
 AM F:18783—shell fragment  
 AM F:18785—shell fragment  
 AM F:18791—nuchal  
 AM F:18792—shell fragments  
 AM F:18793—shell fragment  
 AM F:18795—shell fragment  
 AM F:18796—shell fragment  
 AM F:18798—shell fragment  
 AM F:18799—peripheral, costal  
 AM F:18800—costal, probably seventh left  
 AM F:18802—shell fragment  
 AM F:18803—shell fragment  
 AM F:18804—right posterior peripheral  
 AM F:18805—shell fragment  
 AM F:18807—left posterior peripheral  
 AM F:18810—shell fragment  
 AM F:18811—right posterior peripheral  
 AM F:18812—dermal ossicle  
 AM F:18813—dermal ossicle  
 AM F:18814—dermal ossicle  
 AM F:18815—dermal ossicle  
 AM F:18816—dermal ossicle  
 AM F:18817—dermal ossicle  
 AM F:18818—dermal ossicle  
 AM F:18819—dermal ossicle  
 AM F:18823—left acetabulum plus ilium  
 AM F:18824—right acetabulum  
 AM F:18825—right pelvis  
 AM F:18826—left acetabulum  
 AM F:18827—right ulna, right radius, figured in Anderson (1930, pls. 47, 48), belongs to same individual as AM F:18750, AM F:18756, AM F:18833, AM F:18834; part of articulated forearm, along with five dermal ossicles  
 AM F:18828—right radius  
 AM F:18829—left ulna  
 AM F:18830—right ulna  
 AM F:18831—right ulna  
 AM F:18832—"right tibia and fibula found attached by matrix" (label), now separated  
 AM F:18833—left tibia, fibula, three metatarsals, two penultimate phalanges, one ungual, and six dermal ossicles associated with AM F:18756 and AM F:18834 in an articulated hind foot, figured in Anderson (1930, pl. 49), belongs to same individual as AM F:18750 and AM F:18827  
 AM F:18834—astragalo-calcaneum, figured in Anderson (1930, pl. 49), associated with AM F:18756 and AM F:18834 in an articulated hind foot, belongs to same individual as AM F:18750 and AM F:18827  
 AM F:18835—group number of possibly associated elements: ilium, vertebral spine, arch of axis, three penultimate phalanges of manus or pes, two distal carpals, right second metacarpal with associated penultimate phalanx, and right intermedium  
 AM F:18836—left tibia  
 AM F:18837—right fibula and radius  
 AM F:18839—left ulna  
 AM F:18841—right tibia, proximal portion damaged  
 AM F:18842—right tibia  
 AM F:18843—right ulna  
 AM F:18844—right tibia  
 AM F:18845—sacral rib  
 AM F:18846—left radius  
 AM F:18847—left ulna  
 AM F:18848—left pubis  
 AM F:18849—coracoid  
 AM F:18850—scapula fragment  
 AM F:18851—(?) scapula fragment  
 AM F:18853—right xiphiplastron  
 AM F:18855—shell fragment  
 AM F:18856—two plastron fragments, two carapace fragments, one cervical vertebra, one thoracic vertebra

AM F:18857—costal  
 AM F:18858—second left peripheral  
 AM F:18859—shell fragments  
 AM F:19360—scapula  
 AM F:19361—damaged right humerus  
 AM F:19362—right humerus  
 AM F:19775—shoulder girdle, purchased from W. Nichols in 1906

AM F:20505–20514 were collected by E. Troughton in 1928 from “R. V. Hines’ garden.”

AM F:20505—right humerus (“20505 and 20506 believed to form a pair”). It seems likely that AM F:20505 through and including AM F:20513 (and possibly AM F:20514) all belong to a single individual  
 AM F:20506—left humerus (“20505 and 20506 believed to form a pair”)  
 AM F:20507—right femur (same individual as 20506)  
 AM F:20508—glenoid portion of scapula (“?belongs to same individual as 20505”)  
 AM F:20509—right pubis (“?belongs to same individual as 20505–20508”)  
 AM F:20510—right radius (“believed to belong to same individual as 20505–20507”)  
 AM F:20511—right radius  
 AM F:20512—right fibula (“believed to belong to same individual as 20505–20510–20513”)  
 AM F:20513—left fibula (“believed to belong to same individual as 20505–20510–20513”)  
 AM F:20514—five dermal ossicles  
 AM F:33741—left posterior lobe of plastron  
 AM F:43183—complete skull—purchased from Mrs. Phyllis M. Ross, 1947, found in Ned’s Beach Cliff

AM F:47538–47545 were collected by E. Troughton in 1941.

AM F:47538—anterior peripheral  
 AM F:47539—horn core  
 AM F:47540—horn core  
 AM F:47541—tail club  
 AM F:47542—right horn core  
 AM F:47543—horn core  
 AM F:47544—lump  
 AM F:47545—horn core  
 AM F:49141—partial skeleton lacking skull but including complete set of cervicals, most of the peripherals, partial plastron and some articulated limb elements. Collected by Elizabeth Pope at Ned’s Beach Cliff in 1959

AM F:50635—tail ring  
 AM F:50636—carapace fragments, dermal ossicles  
 AM F:50637—caudal  
 AM F:52080—eggs “Sand cliff at Ned’s Beach,” presented by Pastor D. H. Watson, 1967 (probably collected in 1964)  
 AM F:50638—fibula  
 AM F:57984—nearly complete skull, cervicals, partial carapace, plastral fragments, partial shoulder and pelvic girdles, right fore- and hind-limbs, left femur, head of left humerus, and two caudals. This specimen was restored at AMNH in 1980–1981 and casts are now in New York, the Australian Museum, and Lord Howe Island Museum  
 AM F:61104—pieces, questionably associated with AM F:61110  
 AM F:61105—first cervical with fused arch, and intercentrum  
 AM F:61106—hyoid and pterygoid fragment  
 AM F:61107—miscellaneous weathered specimens associated with carpals  
 AM F:61108—left parietal  
 AM F:61110—skull, carapace, both shoulder girdles, both humeri, both femora, left tibia and fibula, caudal, tail ring, and phalanges  
 AM F:61401—eggs, collected by AMNH–AM party, June 1980, Ned’s Beach Cliff  
 AM F:61402—anterior margin of carapace with first thoracic vertebra, collected by Jim Dorman at base of Ned’s Beach Cliff  
 AM F:61404—tail club, presented by Mrs. Ilma Sainsbury, December 1979  
 AM F:61405—left humerus, presented by Mrs. Ilma Sainsbury, December 1979  
 AM F:61406—caudal, presented by Mrs. Ilma Sainsbury, December 1979  
 AM F:61407—caudal, presented by Mrs. Ilma Sainsbury, December 1979  
 AM F:61408—caudal, presented by Mrs. Ilma Sainsbury, December 1979  
 AM F:61412—radius and cervical rib, probably associated with 61110  
 AM F:64434—plastron, Old Settlement Beach, AMNH–AM party, 1980  
 AM F:64435—tail club, Old Settlement Beach, AMNH–AM party, 1980  
 AM F:64471—skull, Ned’s Beach, 45 ft. W of boat ramp, AMNH–AM party, 1980

### APPENDIX 3.

#### *MEIOLANIA PLATYCEPS* SPECIMENS IN THE MINING AND GEOLOGICAL MUSEUM, SYDNEY, NEW SOUTH WALES

The figured and referred specimens are known to have come from Lord Howe Island, all the other specimens have been identified as Lord Howe Island on the basis of preservation.

- MM F:13823—right cranial horn core (Owen, 1888, pl. 31). This specimen seems to be the horn core from the skull (MM F:13825a) in this figure. Presumably MM F:13823 and MM F:13825a are the same individual
- MM F:13824—femur
- MM F:13825—left femur (Anderson, 1925, pl. 40, fig. 2)
- MM F:13825a—nearly complete skull (Owen, 1888, pls. 31, 32; Gaffney, 1979, fig. 269). The right horn core from this skull appears to be MM F:13823
- MM F:13826—eggs
- MM F:13827—posterior portion of skull (Owen, 1888, pls. 33, 34)
- MM F:13828—posterior margin of skull (Anderson, 1925, pl. 32, fig. 2)
- MM F:13829—portion of tail ring (Owen, 1888, pl. 36, figs. 7–9)
- MM F:13830—plaster model of skull (Anderson, 1925)
- MM F:13831—a, tail club; b, c, vertebral fragments (Owen, 1888, pl. 37)
- MM F:13832—tail club
- MM F:13833—tail club
- MM F:13834—tail club
- MM F:13835—tail club
- MM F:13836—left cranial horn core
- MM F:13837—left cranial horn core
- MM F:13838—left cranial horn core
- MM F:13839—cranial horn core
- MM F:13840—cranial horn core
- MM F:13844—left tibia (Owen, 1888, pl. 36, figs. 1–4)
- MM F:13845—right radius (Owen, 1888, pl. 36, figs. 5, 6)
- MM F:13847—fifth cervical (Owen, 1888, pl. 35, figs. 1–3)
- MM F:13848—anterior caudal
- MM F:13849—caudal
- MM F:13850—caudal
- MM F:13851—caudal
- MM F:13852—caudal
- MM F:13853—caudal
- MM F:13860—dermal ossicle (Owen, 1888, pl. 36, fig. 10)
- MM F:13861—horn core in matrix
- MM F:13862—caudal covered with matrix
- MM F:13884—quadrate
- MM F:13885—peripheral
- MM F:13886—peripheral
- MM F:13887—peripheral
- MM F:13888—tail ring fragment
- MM F:13891—tail ring fragment
- MM F:13892—shell fragment
- MM F:13893—(?) skull fragment
- MM F:13894—tail ring fragment
- MM F:13895—dermal ossicle
- MM F:13896—posterior peripheral fragment
- MM F:13897—dermal ossicle
- MM F:13959—tail ring fragment
- MM F:13960—tail ring fragment
- MM F:13961—tail ring fragment
- MM F:13965—(?) peripheral fragment
- MM F:13974—dermal ossicle

### APPENDIX 4.

#### *MEIOLANIA PLATYCEPS* SPECIMENS IN THE BRITISH MUSEUM (NATURAL HISTORY), LONDON

- BMNH R675—partial skull, type of *Meiolania platycephs*, Owen (1886, pl. 30, fig. 1; pl. 31, fig. 1. Also figured in Huxley, 1887, fig. 3). Along with this skull are four horn cores: one “A” two “Bs” and a core tip
- BMNH R675a—“B” horn core (Owen, 1886, pl. 30, fig. 2)
- BMNH R675b—right half of posterior skull margin
- BMNH R675c—three “B” horn cores, two “A” horn cores, and two osteoderms
- BMNH R675d—not *Meiolania*, probably Recent mammal
- BMNH R677—left maxilla and premaxilla
- BMNH R677a—left premaxilla
- BMNH R677b—left premaxilla, maxilla, and vomer fragment
- BMNH R678—damaged caudal (probably the “cervical” mentioned by Lydekker, 1889, p. 163)
- BMNH R678a—caudal vertebra
- BMNH R678b—vertebral fragment

BMNH R678c—vertebral fragment  
 BMNH R678d—caudal chevron  
 BMNH R679—tail club (Owen, 1886, pl. 31, fig. 4)  
 BMNH R680—tail club in matrix (Owen, 1886, pl. 31, fig. 4)  
 BMNH R681—coracoid and other elements in matrix  
 BMNH R682—braincase, broken sagittally. This specimen is possibly the basis of the figure in Owen (1886, pl. 29, figs. 1, 2), but it does not match precisely nor are there any references supporting this identification  
 BMNH R683—eleven shell fragments  
 BMNH R684—distal end left humerus  
 BMNH R684a—distal end left femur  
 BMNH R685—right tibia  
 BMNH R686—scapula fragment  
 BMNH R687—ilium  
 BMNH R689—neural arch of a posterior cervical  
 BMNH R690—caudal  
 BMNH R691—(?) caudal  
 BMNH R692—thoracic vertebrae in matrix  
 BMNH R693—this is a large group number that in May 1981 had many of its elements re-registered (see BMNH R9605 below). The vertebral centrum referred to by Lydekker (1889, p. 162) is retained as BMNH R693  
 BMNH R693a—posterior caudal centrum  
 BMNH R693b—glenoid area of scapula  
 BMNH R693c—distal end of humerus  
 BMNH R693d—scapular process  
 BMNH R693e—according to label, 693e, 693g, 688, and 689 are all glued together to form this ilium and acetabulum  
 BMNH R693f—sacral rib no ilium  
 BMNH R693g—see R693e  
 BMNH R693h—(does not appear in either the collection or in Lydekker)  
 BMNH R693i—distal part of a sacral rib; not a cervical rib as indicated by Lydekker (1889, p. 166)  
 BMNH R693x—one tail ring fragment, three peripherals, one lump  
 BMNH R846b—distal end femur

BMNH R9605—R9655 were formerly BMNH R693.

BMNH R9605—braincase  
 BMNH R9606—left otic and basicranial region  
 BMNH R9607—left side of posterior skull roof  
 BMNH R9608—supraoccipital and right parietal descending process  
 BMNH R9609—right cheek  
 BMNH R9610—right supraorbital region  
 BMNH R9611—left prefrontal  
 BMNH R9612—right prefrontal

BMNH R9613—left nasal  
 BMNH R9614—left naso-maxillary region  
 BMNH R9615—right postorbital  
 BMNH R9616—right naso-maxillary region  
 BMNH R9617—dorsal portion of otic chamber  
 BMNH R9618—midline portion of posterior skull roof margin  
 BMNH R9619—supraoccipital-parietal fragment  
 BMNH R9620—left maxilla-pterygoid fragment  
 BMNH R9621—right maxilla-pterygoid fragment  
 BMNH R9622—right maxilla fragment  
 BMNH R9623—right maxilla fragment  
 BMNH R9624—right premaxilla  
 BMNH R9625—quadratojugal fragment  
 BMNH R9626—left quadrate articular region, and portion of cheek showing ventral cheek margin  
 BMNH R9627—three cavum tympani fragments  
 BMNH R9628—five sub-quadratic portions of cheek  
 BMNH R9629—left quadrate articular fragment  
 BMNH R9630—left quadrate articular fragment  
 BMNH R9631—left quadrate articular fragment  
 BMNH R9632—right quadrate articular fragment  
 BMNH R9633—right quadrate articular fragment  
 BMNH R9634—right quadrate articular fragment  
 BMNH R9635—right quadrate articular fragment  
 BMNH R9636—bone fragment  
 BMNH R9637—bone fragment  
 BMNH R9638—vertebral centrum, (?) cervical  
 BMNH R9639—scapular fragment  
 BMNH R9640—epiplastral fragment  
 BMNH R9641—ischium fragment  
 BMNH R9642—caudal chevron  
 BMNH R9643—caudal fragment  
 BMNH R9644—postzygapophyses  
 BMNH R9645—thoracic vertebral fragment  
 BMNH R9646—thoracic vertebral fragment  
 BMNH R9647—proximal section of sacral rib  
 BMNH R9648—fused posterior thoracic centra  
 BMNH R9649—distal end of (?) fibula  
 BMNH R9650—neural fragment  
 BMNH R9651—neural fragment  
 BMNH R9652—neural fragment  
 BMNH R9653—neural fragment  
 BMNH R9654—scapular fragment  
 BMNH R9655—plastron fragment

The following five numbers were formerly BMNH R675.

BMNH R9657—"A" horn core  
 BMNH R9658—"B" horn core  
 BMNH R9659—"B" horn core  
 BMNH R9660—"B" horn core  
 BMNH R9661—limb bone  
 BMNH 43493—one limb fragment, two pieces of matrix, one with a *Meiolania* shell frag-



ment, the other with a (?) bird bone. The matrix is hard sandstone, the piece with the *Meiolania* fragment also has a gastropod shell in it. The label, "Pres'd by Rev. Clarke, 1872, Beach deposit, Lord Howe

Island" indicates that this is the only Lord Howe Island material sent to the British Museum by someone other than Fitzgerald

## APPENDIX 5.

### *MEIOLANIA PLATYCEPS* SPECIMENS IN THE AMERICAN MUSEUM OF NATURAL HISTORY, NEW YORK

AMNH 20892–20895, AMNH 20921–20997 were collected by the joint Australian Museum–American Museum of Natural History Expedition of 1980, while AMNH 20896–20920 were collected by the American Museum of Natural History Expedition of 1982.

AMNH 20892—portion of shell (bridge); Ned's Beach, 240 ft. W of boat ramp

AMNH 20893—peripheral; Ned's Beach, 240 ft. W of boat ramp

AMNH 20894—first thoracic vertebra; Ned's Beach, 240 ft. W of boat ramp

AMNH 20895—partial femur; Ned's Beach, 240 ft. W of boat ramp

AMNH 20896—? *Meiolania* eggs; Wilson's Hole locality, W side from fall blocks of *Meiolania* bearing sand unit

AMNH 20897—bone fragment; Old Settlement, approx. 10 yd. S of specimen collected by A. Ritchie, same level

AMNH 20900—shell fragment; from a beach pebble collected on Middle Beach

AMNH 20901—two ossicles; Jim's Point locality

AMNH 20902—shell fragment; Jim's Point locality

AMNH 20903—ossicle; Jim's Point locality, 2 ft. above water level

AMNH 20904—shell fragment; Wilson's Hole locality, from *Meiolania*-bearing sand unit

AMNH 20905—portion of shell; Wilson's Hole locality, W side; from *Meiolania*-bearing sand unit

AMNH 20906—partial lower jar; Wilson's Hole locality, W side; from fall-block of *Meiolania*-bearing sand unit

AMNH 20907—bone fragment; Wilson's Hole locality, W side; from fall-block of *Meiolania*-bearing sand unit

AMNH 20908—second cervical vertebra; Wilson's Hole locality, W side; from fall block of *Meiolania*-bearing sand unit

AMNH 20909—cervical vertebra; Wilson's Hole locality, W side; from fall-block of *Meiolania*-bearing sand unit

AMNH 20910—partial horn core; Wilson's Hole

locality, W side; from *Meiolania*-bearing sand unit, 2 ft. below upper contact

AMNH 20911—portion of horn core; first bay E of Ned's Beach; from fall block of ledge-forming sandstone

AMNH 20912—cross section of shell (plastron) in matrix; (silicone rubber peel), Ned's Beach, approx. 25 ft. W of boat ramp, approximately 10 ft. from embankment

AMNH 20913—portion of ?shell; Headland, E of Ned's Beach, 12 ft. above low water, from "reddish zone" below ledge sandstone

AMNH 20914—fragment of pelvis; Headland E of Ned's Beach, from low angle cross-set block in karst collapse breccia, 4 ft. above low water

AMNH 20915—ossicle; Headland E of Ned's Beach, from cross-sets in karst collapse breccia, 4 ft. above low water

AMNH 20916—portion of tail ring; Headland E of Ned's Beach, from karst collapse breccia, 2 ft. above low water

AMNH 20917—portion of shell; Headland E of Ned's Beach, from karst collapse breccia, 18 in. above low water

AMNH 20918—femur; Ned's Beach Cliff, approx. 15 ft. W of Pope specimen locality

AMNH 20919—ungual; W end of Ned's Beach, W-most exposures of calcarenite, near base of Malabar Hill

AMNH 20920—bone fragment; W end of Ned's Beach, near base of Malabar Hill, W-most exposure of calcarenite, near contact

AMNH 20921—quadrate; Ned's Beach, 240 ft. W of boat ramp

AMNH 20922—portion of carapace, Ned's Beach, intertidal zone, W of boat ramp

AMNH 20923—claw; Old Settlement Beach

AMNH 20924—portion of tail ring; Old Settlement Beach

AMNH 20925—portion of snout; Trader Nick's garden

AMNH 20926—maxillary fragment; Trader Nick's garden

AMNH 20927—portion of snout; Trader Nick's garden

- AMNH 20928—portion of skull fragment; Pit 16, Ilma Sainesbury's garden
- AMNH 20929—horn core, left, A and B horns; Pit 4, Trader Nick's garden
- AMNH 20930—horn core, B horn; Pit 4, Trader Nick's garden
- AMNH 20931—horn core, right, B horn; Pit 4, Trader Nick's garden
- AMNH 20932—right horn core, with A and B horns; Pit 4, Trader Nick's garden
- AMNH 20933—horn core fragment; Pit 4, Trader Nick's garden
- AMNH 20934—partial caudal vertebra; Pit 4, Trader Nick's garden
- AMNH 20935—second cervical vertebra; Pit 4, Trader Nick's garden
- AMNH 20936—partial caudal vertebra; Pit 16, Ilma Sainesbury's garden
- AMNH 20937—caudal vertebra; Pit 4, Trader Nick's garden
- AMNH 20938—fragment of vertebral centrum; Pit 4, Trader Nick's garden
- AMNH 20939—fragment of vertebral centrum; Pit 4, Trader Nick's garden
- AMNH 20940—portion of scapula; Pit 4, Trader Nick's garden
- AMNH 20941—partial humerus; Pit 4, Trader Nick's garden
- AMNH 20942—partial humerus; Pit 4, Trader Nick's garden
- AMNH 20943—humerus shaft; Pit 4, Trader Nick's garden
- AMNH 20944—distal humerus; Pit 4, Trader Nick's garden
- AMNH 20945—fragment of distal humerus; Pit 4, Trader Nick's garden
- AMNH 20946—fragment of proximal humerus; Pit 4, Trader Nick's garden
- AMNH 20947—partial ischium, adhering to root cast; Pit 4, Trader Nick's garden
- AMNH 20948—portion of pelvis; Pit 4, Trader Nick's garden
- AMNH 20949—portion of pelvis; Pit 4, Trader Nick's garden
- AMNH 20950—fragmentary proximal femur; Pit 4, Trader Nick's garden
- AMNH 20951—fragment of limb bone shaft; Pit 4, Trader Nick's garden
- AMNH 20952—claw (ungual); Trader Nick's garden
- AMNH 20953—claw; Pit 9, Trader Nick's garden
- AMNH 20954—portion of first costal and two fragments; Pit 14, Trader Nick's garden
- AMNH 20955—peripheral fragment; (float) from creek bed S of Trader Nick's at small waterfall approx. 75 ft. E of road
- AMNH 20956—fragment of peripheral; Pit 4, Trader Nick's garden
- AMNH 20957—nine fragments, incl. ossicle, shell fragments, etc.; Pit 12, Trader Nick's garden
- AMNH 20958—seven miscellaneous fragments; Trader Nick's garden
- AMNH 20959—approximately two dozen shell fragments; Pit 5, S of Trader Nick's
- AMNH 20960—miscellaneous bone fragments; Pit 5, S of Trader Nick's
- AMNH 20961—five bone fragments; Pit 5, S of Trader Nick's
- AMNH 20962—two limb bone fragments; Pit 5, S of Trader Nick's
- AMNH 20963—two bone fragments; Pit 5, S. of Trader Nick's
- AMNH 20964—portion of tail ring; Pit 5, S of Trader Nick's
- AMNH 20965—portion of tail ring; Pit 5, S of Trader Nick's
- AMNH 20966—small horn, fragment of tail ring; Pit 5, S of Trader Nick's
- AMNH 20967—fragment of tail ring; Pit 5, S of Trader Nick's
- AMNH 20968—first cervical rib; Pit 5, S of Trader Nick's
- AMNH 20969—phalanx; Pit 5, S of Trader Nick's
- AMNH 20970—carpal bone: radiale/ulnare; Pit 5, S of Trader Nick's
- AMNH 20971—five limb bone fragment; Pit 5, S of Trader Nick's
- AMNH 20972—bone fragment; Pit 5, S of Trader Nick's
- AMNH 20973—three girdle bone fragments; Pit 5, S of Trader Nick's
- AMNH 20974—bone fragment; Pit 5, S of Trader Nick's
- AMNH 20975—five vertebral fragments; Pit 5, S of Trader Nick's
- AMNH 20976—left dentary (cast); Ned's Beach Cliff (original in Lord Howe Island Museum, not catalogued)
- AMNH 20977—right metatarsal I; soil horizon, N of middle Beach
- AMNH 20978—bone fragment (?limb or girdle); from supratidal outcrops (below bench) between Ned's Beach and Hell's Gate
- AMNH 20979—shell fragment; Ned's Beach, 240 ft. W of boat ramp
- AMNH 20980—tail club; Ned's Beach, 240 ft. W of boat ramp
- AMNH 20981—caudal vertebra; Ned's Beach, 240 ft. W of boat ramp
- AMNH 20982—partial second cervical vertebra; ? Ned's Beach

- AMNH 20983—fragments of shell; Ned's Beach, 240 ft. W of boat ramp
- AMNH 20984—portion of scapula, with part of glenoid; Ned's Beach, 240 ft. W of boat ramp
- AMNH 20985—portion of distal femur; Ned's Beach, 240 ft. W of boat ramp
- AMNH 20986—portion of distal humerus shaft; Ned's Beach, 240 ft. W of boat ramp
- AMNH 20987—fragment of ?limb bone; Ned's Beach, 240 ft. W of boat ramp
- AMNH 20988—limb bone fragment; Ned's Beach, 240 ft. W of boat ramp
- AMNH 20989—partial posterior peripheral; Ned's Beach, 240 ft. W of boat ramp
- AMNH 20990—portion of bridge; Ned's Beach, 137 ft. W of boat ramp
- AMNH 20991—peripheral; Ned's Beach, 240 ft. W of boat ramp
- AMNH 20992—proximal portion of costal; Ned's Beach, 240 ft. W of boat ramp
- AMNH 20993—proximal portion of costal; Ned's Beach, 240 ft. W of boat ramp
- AMNH 20994—nasal and preorbital bones; Ned's Beach, 137 ft. W of boat ramp
- AMNH 20995—portion of plastron and fragments; Ned's Beach Cliff, approx. 5 ft. above beach
- AMNH 20996—humerus shaft; Ned's Beach Cliff, E end, 6 ft. above beach level
- AMNH 20997—seven miscellaneous fragments, plastron fragments, two ossicles, horn core, foot bone; Ned's Beach Cliff, E end, below lower soil horizon

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