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The Cervical and Caudal Vertebrae of the Cryptodiran Turtle, *Meiolania platyceps*, from the Pleistocene of Lord Howe Island, Australia

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ABSTRACT

Meiolania platyceps, a cryptodiran turtle from the Pleistocene of Lord Howe Island, Australia, has cervical and caudal vertebrae exhibiting a number of phylogenetically interesting features. The cervicals have fully formed central articulations with a formula of $(2(3(4)5)6)7)8$, interpreted as a synapomorphy of eucryptodires. Free ribs are present on cervicals two through six, a retained primitive character in *Meiolania*, lost independently in other eucryptodires, baenids, and pleurodires. The presence in *Meiolania* of cervical ribs articulating with paired intercentra shows that the supposed vestigial ribs identified by previous authors in the neck of Recent turtles are probably intercentra and not rib remnants. The neural spines of cervicals seven and eight articulate with the nuchal bone; this is interpreted as an autapomorphy, occurring independently in chelonioids.

Complete tails are unknown for *Meiolania*

platyceps, but a conservative reconstruction based on degree of serial variation and comparison with Recent turtles, yields a total of at least ten caudals plus tail club. The caudals are all opisthocoelus and have well-developed haemal spines; characters that are primitive for cryptodires. *Meiolania* has an ossified tail club consisting of a conical layer of bone surrounding and fused to the terminal caudals. *Proganochelys* has a similar, but not identical, terminal ossification, and the presence of a tail club is interpreted as a retained primitive feature in *Meiolania*, being lost independently in pleurodires and other cryptodires. The tail of *Meiolania platyceps* has a series of ventrally incomplete rings, contrasting with the complete rings found in "*Meiolania oweni* and *Niolamia argentina*". The vertebral features of *Meiolania platyceps* are consistent with its hypothesized systematic position as a primitive eucryptodire.

INTRODUCTION

The cervical and caudal vertebrae of *Meiolania platyceps* show a number of unusual

and phylogenetically interesting features. The well-developed cervical ribs and the tail club

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are found in the Triassic turtle, *Proganochelys*, and suggest the presence of very primitive chelonian features in this extinct turtle. The purpose of the present paper is to describe and systematically assess these and other features in the vertebral column of *Meiolania platyceps*.

Further information on *Meiolania platyceps*, including geographic and geologic occurrence, previous work, and cranial morphology can be found in Gaffney (1983). Lists of specimens examined are also available in that paper.

ACKNOWLEDGMENTS

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ABBREVIATIONS

AM, Australian Museum, Sydney
 BM(NH), British Museum (Natural History), London
 MM, Mining Museum, Sydney
 SMNS, Staatliches Museum für Naturkunde, Stuttgart

ATLAS

The specimens available for the atlas are as follows: AM F:49141 (complete, articulated), MM F:13825a (complete, articulated; figured in Owen, 1888, pls. 31, 32; Gaffney, 1983, figs. 42, 43), AM F:57984 (left arch, centrum fragment), AM F:61105 (arch and intercentrum), AM F:18835 (arch), AM

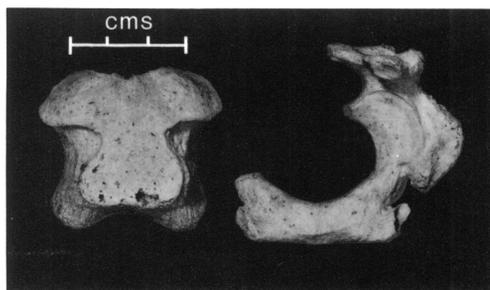


FIG. 1. *Meiolania platyceps*, AM F:61105. Left, anterior view of atlantal centrum; right, posterior view of fused atlantal intercentrum and right atlantal neural arch. See figure 5 for views of the articulated atlas.

F:5536 (centrum) and AM F:18315 (centrum fragment; figured in Anderson, 1925, pl. 37, fig. 1).

As in other turtles (and amniotes generally) the atlas of *Meiolania* (figs. 1, 5–8) consists of four elements: paired neural arches anterodorsally, an intercentrum anteroventrally, and a centrum posteriorly. The *Meiolania* atlas is generally similar to the generalized chelonian atlas, as in *Proganochelys*, but it differs in being somewhat shortened antero-posteriorly and broadened laterally.

The chelonian neural arch (see Kasper, 1903), can be roughly divided into a dorsal portion covering the neural cord and having

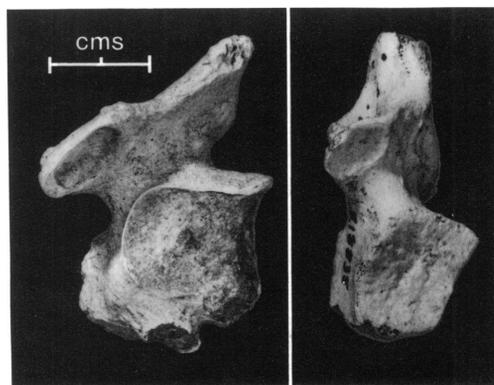


FIG. 2. *Meiolania platyceps*. Medial views of right atlantal neural arches, anterior to the left. Left, AM F:57984; right, AM F:18835.

a posteriorly directed postzygapophyseal flange articulating with the axis, and a ventral portion bearing articular facets for the occipital condyle, the atlantal centrum and the atlantal intercentrum. In *Meiolania platyceps* (figs. 1, 2) the neural arch has a particularly broad dorsal portion that inclines medially to lie almost horizontally above the space for the neural cord. The neural arches do not meet in the midline in known specimens. The postzygapophysis has a well-developed articular facet for the prezygapophysis of the axis. The very large proportion of the ventral part of the neural arch is occupied by the articular facet for the centrum of the atlas. This facet faces posteromedially and lies approximately at right angles to a smaller facet facing anteromedially that articulates with the occipital condyle of the skull. Ventral to the facet with the centrum, the neural arch has a small contact area with the atlantal intercentrum. The lateral surface of the neural arch has a transverse process with a broad base but a relatively shallow lateral extension. The transverse process extends more than in *Proganochelys* and most cryptodires but less than in pleurodires.

The transverse process of the neural arch extends ventrally to a variable extent in the direction of a short dorsal extension of the intercentrum. In MM F:13825a (see Gaffney, 1983, fig. 42, middle, for a stereophotograph) these processes join and enclose a small foramen, whereas in AM F:57984 (figs. 2, 5) they do not meet but end in surfaces that appear to have been finished in cartilage. It is possible that a cervical rib participates in the ossification of this area but no evidence of a discrete element has been seen.

The contact between the neural arch and intercentrum is fused on both sides of MM F:13825a and on the right side of AM F:61105 (fig. 1). The other specimens (including AM F:57984 and AM F:49141, which are both well preserved) show no indication of fusion. Fusion of these elements occurs in pleurodires and trionychids and it may be interpreted as characteristic of certain taxa within these groups, but I do not think its presence in *Meiolania platyceps* has systematic significance. *Meiolania platyceps* is characterized by a high degree of morphologic

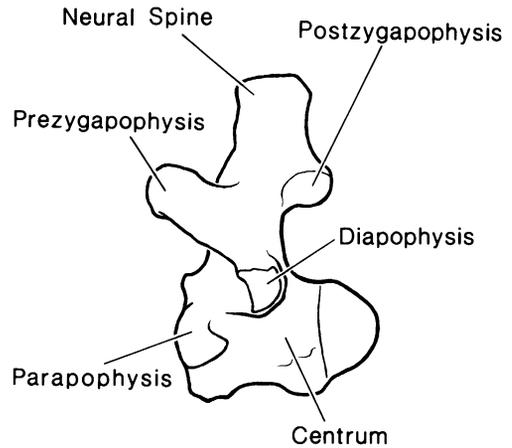


FIG. 3. Diagram showing morphologic features of cervical vertebrae. Seventh cervical of *Meiolania platyceps*.

variation in other areas and I interpret this as another example.

An unassociated neural arch, AM F:18835 (fig. 2) is not so easily interpreted as individual variation, but I see no other alternative. This is a right neural arch, roughly similar to the others but about a third narrower in lateral view. The dorsal process that extends over the neural cord is a cylindrical process rather than a broad plate as in the other specimens. The ventral portion of the arch has the central and occipital facets but much of the surrounding bone is reduced in comparison to other neural arches. The arch is clearly *Meiolania*; it has no particular similarities to sea turtles or pleurodires. It could be from a juvenile but the dorsoventral dimension is the same as in AM F:57984.

The intercentrum of the atlas in *Meiolania platyceps* (figs. 1, 5) is a crescentic element, connecting the bases of the neural arches, and forming the ventral third of the atlantal ring. It articulates with the occipital condyle anteriorly and with the atlantal centrum posteriorly. The intercentrum of *Meiolania* is narrow transversely, being distinctly wider than long, in contrast with most turtles which have a more equidimensional intercentrum. The intercentrum of *Proganochelys*, however, is similar to *Meiolania*, suggesting that this is the primitive chelonian condition. The

intercentrum is fused to the neural arch in MM F:13825a and on the right side of AM F:61105 (fig. 1) but it is unfused in the remaining specimens. There is a concavity on the posterolateral corner of the intercentrum directly below a similar area on the neural arch, discussed above.

The atlantal centrum (figs. 1, 5) is relatively short anteroposteriorly but broad and equidimensional laterally and dorsoventrally. The anterior articulation is broadly convex, ending in a low midline projection that faces the shallow concavity on the condylus occipitalis of the skull. The articular surface is roughly T-shaped, the two dorsolateral areas articulate with the posterior facets of the neural arches and the ventral area articulates with the posterior facet of the intercentrum. The posterior articular surface of the atlantal centrum is concave and articulates with the convex centrum of the axis. The atlantal centrum has a paired projection extending posteroventrolaterally that bears an articular facet for the capitulum of the first cervical rib (fig. 11). The tuberculum of this rib articulates with the transverse process (diapophysis) of the second cervical vertebra.

CERVICAL VERTEBRAE TWO TO EIGHT

Figures 3-9

CENTRA: The centra of the cervicals of *Meiolania platycephs* all have fully formed articulations, with cervicals two and three opisthocoeilus, cervical four biconvex, and cervicals five to eight procoelus. This pattern is common in eucryptodires and also occurs in some baenids (*Chisternon*). The anterior convexity in the second cervical (axis) is less pronounced than the convexity in any of the other cervicals. The degree of development of the central surface is about the same in the other cervicals. The ventral surface of the centrum has two, low parasagittal ridges in cervicals two to four, they are indistinct in cervical five, and they are absent in cervicals six to eight, which have a curved ventral surface. The centrum main body is slightly constricted in the cervicals of *Meiolania* but not to the extent seen in baenids and pleurodires. There is no indication of double articulations or saddle-shaped surfaces.

Meiolania platycephs has well-developed cervical ribs (figs. 9, 11) that are freely articulated on cervicals two to seven. There is no free rib on cervical eight. The free ribs are double-headed and articulate with a laterally projecting transverse process (diapophysis) dorsally and a less-pronounced ventral articulation (parapophysis). The diapophysis is about equally developed on cervicals two to seven and is situated at the junction of the centrum and neural arch midway along the length of the centrum. The lateral margin of the transverse process bears a posteroventrally facing articular facet for the tuberculum of the rib. The articular facet is always larger than the ventral parapophyseal articulation with the capitulum of the rib. The diapophyseal articulation decreases in area posteriorly to a slight extent.

The ventral rib articulation (fig. 9) is with an element that I interpret as an intercentrum. This element in *Meiolania* may be fused to the centrum or it may be separated by a suture. The intercentra occur in pairs and may be fused on one side and separate on the other (as in the fifth cervical of AM F:57984). The intercentra are associated with the centra in a unique manner. The first intercentrum is single, C-shaped, and part of the atlas (see above), whereas the second are paired and attached (fused in all known specimens) to the atlantal centrum at its posterolateral margins. Paired intercentra are also attached (by a suture in all known specimens) to the posterolateral margins of cervicals two and three, but cervical four has no intercentra attached to it, instead cervical five has the intercentra attached to its anterolateral margin rather than the posterolateral margin. This position change continues posteriorly and the sixth, seventh, and eighth cervicals also have the intercentra attached to the anterior margin. The intercentral attachment position is correlated with the central articulation pattern so that the intercentra always attach to the margin of the centrum that has the concave articular surface. Thus cervical four, which is biconvex, lacks intercentral attachments. I see no particular explanation for this correlation. Another aspect of this serial change in intercentra attachments are the rib articulations. In cervicals five through seven the

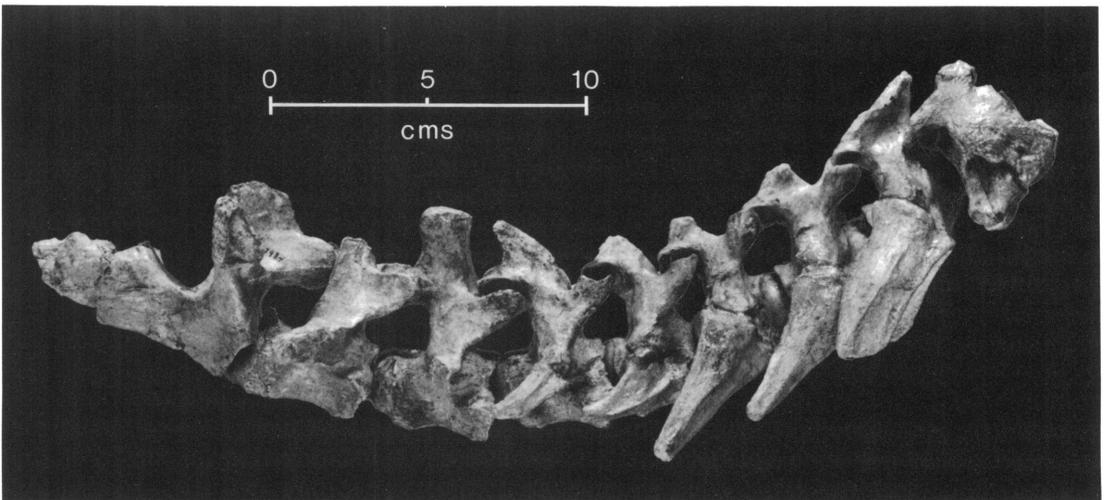


FIG. 4. *Meiolania platyceps*. Right lateral view of articulated cervicals from atlas to eighth plus first thoracic. Anterior on right. Reconstructed neck based primarily on AM F:57984.

tuberculum and capitulum of each rib articulates with the diapophysis and parapophysis of the same vertebra, but for cervicals two and three the rib articulates with the diapophysis of one vertebra and parapophysis of the vertebra anterior to it, thus the two anterior ribs each articulate with two vertebrae and cervical four has no rib articulation.

Although the morphology of the transverse process (diapophysis) is relatively stable from cervical two to cervical seven, the parapophysis (intercentrum) shows some variation along the column. Anteriorly, the parapophyses of the atlantal centrum, second and third cervicals, project posterolaterally and bear the rib articulation facet on the posterolateral surface. The articulation facets are of about the same size. The fourth cervical completely lacks a parapophysis. Cervicals five through seven have their parapophyses extending anterolaterally from the anterior central margin (as described above) and the capitulum articulation facet lies on the posterolateral edge of the parapophysis. The parapophyseal facet is smaller on the fifth than on the third cervical and is more reduced on the sixth and seventh cervicals where it may only be a rugosity (as in AM F:57984).

The eighth cervical has a much longer

transverse process than any of the other cervicals, about three times in length. The process curves posterolaterally. There is a parapophysis that is smaller than in any of the other cervicals. The cervical rib appears to be absent, the long transverse process bears no evidence of being a fused rib. *Proganochelys* has fused ribs on cervicals six through eight and these retain the dorsal and ventral attachments with a foramen between them. In *Meiolania* there is no evidence of a persistent rib shaft, only an elongate diapophysis.

NEURAL ARCH: The neural arch is described in three general headings: prezygapophyses, postzygapophyses, and neural spines (fig. 3). The prezygapophysis of the second cervical is small, much smaller than the prezygapophysis of any other cervical, and articulates with the postzygapophysis of the atlantal neural arch. The prezygapophysis is missing on available specimens except AM F:49141 where it can be seen preserved on both sides. It lies on a short projection from the neural arch about midway up the arch. The prezygapophysis of the second cervical differs from all other cervicals in facing dorsolaterally rather than dorsomedially. This is the usual situation for the axis in other turtles, including *Proganochelys*, as well as other am-

notes. The prezygapophyses of cervicals three to seven are similar to each other, they face dorsomedially with the facets on cervicals three and four facing slightly more anteriorly than in the others. The prezygapophyses are separated from each other to a greater extent in cervicals three to six than in the other cervicals, the prezygapophyses begin to approximate each other in cervical seven, and they are only barely separated from each other in cervical eight. The surface area of the prezygapophyseal articulation facet is relatively small in the second cervical but uniformly larger in the remaining cervicals.

The postzygapophyses generally parallel the orientation and size of the prezygapophyses, they all face ventrolaterally with the farther anterior ones more separated from each other than the farther posterior postzygapophyses. The postzygapophyses of cervical seven nearly join at their base. Unfortunately, the neural spine and postzygapophyses of cervical eight are not preserved in any available specimen. Whereas the prezygapophyses are borne on short processes extending anteriorly from the neural arch, the postzygapophyses are nearly integral elements of the neural spine and are not as discrete.

One of the differences between living cryptodires and pleurodires lies in the wide separation of the zygapophyses in cryptodires and their close approximation in pleurodires. Although there are exceptions due to the wide diversity of vertebral morphology in turtles, it is possible to make broad comparisons. *Meiolania* and *Proganochelys* both have zygapophyseal positions that are intermediate between the two extremes seen in the living turtle groups and are similar to baenids.

The neural spines of the cervicals in *Meiolania platyceps* exhibit considerable serial variation. The neural arch of the second cervical virtually lacks a neural spine, instead it is a broad, flat platform, that seems to articulate with the underside of the skull roof. The skull roof of *Meiolania* has a flat area just posterior to the crista supraoccipitalis and anterior to the posterior skull margin (Gaffney, 1983, figs. 38, 40). The second cervical fits in this area when the neck is articulated (as seen in MM F:13825a; Gaffney, 1983, figs. 42, 43). The postzygapophyses of the second cervical extend just beyond the skull

margin. The third cervical has a slight boss for a neural spine and this is a larger, discrete knob in the fourth cervical. The neural spine of the fifth cervical begins the development of a posterodorsal extension which becomes best developed in cervical six. All the neural spines have rugose dorsal surfaces, suggesting the presence of well-developed ligaments. Cervicals five and six have posterior concavities, most extensive in cervical six, that are also rugose and may have been involved in ligament attachment. The concavity on the neural spine of cervical six is divided down the midline by a longitudinal ridge in AM F:49141 but not in AM F:57984. The neural spine of the seventh vertebra (best seen in AM F:49141) is high and compressed laterally in contrast to the anterior cervicals. Most of the neural spine of the eighth cervical is missing in available specimens, but from the preserved material a thin, compressed spine is indicated.

The nuchal bone of *Meiolania platyceps* has two oval articular facets on the midline of its ventral surface; the top of the neural spine of cervical seven articulates with the anterior facet and it seems likely that the eighth cervical neural spine articulates with the posterior facet. These facets indicate a movable joint rather than a sutured one, as in *Proganochelys*, which has a sutured articulation between the neural spine of the eighth cervical but no articulation between the seventh cervical and the nuchal. Some turtles, for example, chelonoids, have a close ligamentous association of the eighth cervical and the nuchal, but turtles which have well-developed neck retraction mechanisms seem to lack them.

CERVICAL RIBS

Figures 6–9, 11

Meiolania platyceps is unusual in having well-developed cervical ribs, elements absent in nearly all turtles. There are five free cervical ribs in *Meiolania* with a very small sixth that may be partially fused. The atlas may have a small rib element associated with it (see above) but it is not freely articulating nor discrete in the available material. The first well-developed rib belongs to the second cervical (the ribs will be referred to by the

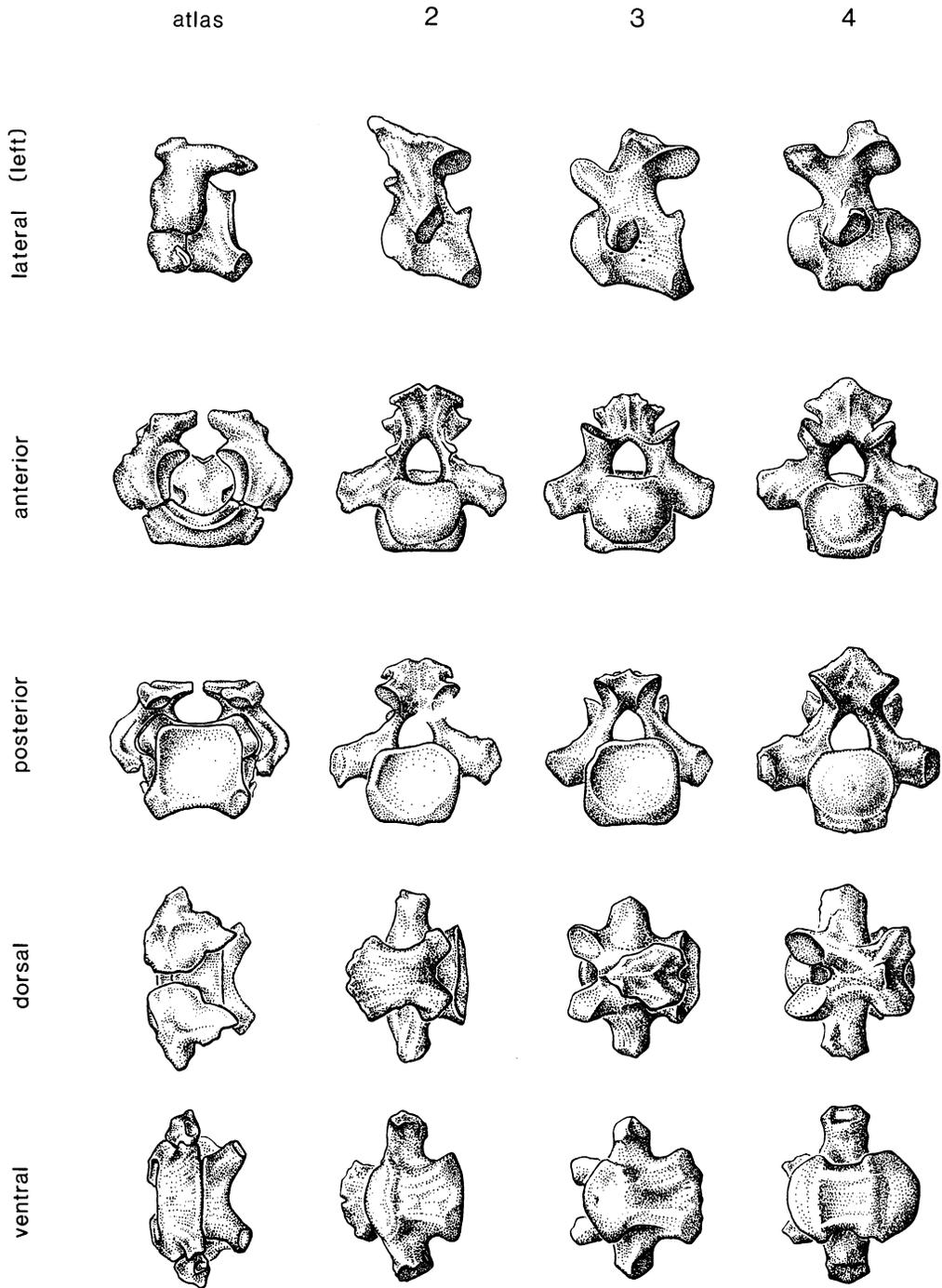


FIG. 5. *Meiolania platyceps*. Cervical vertebrae, AM F:57984, except for atlas centrum (AM F:61105) and second cervical (AM F:5547).

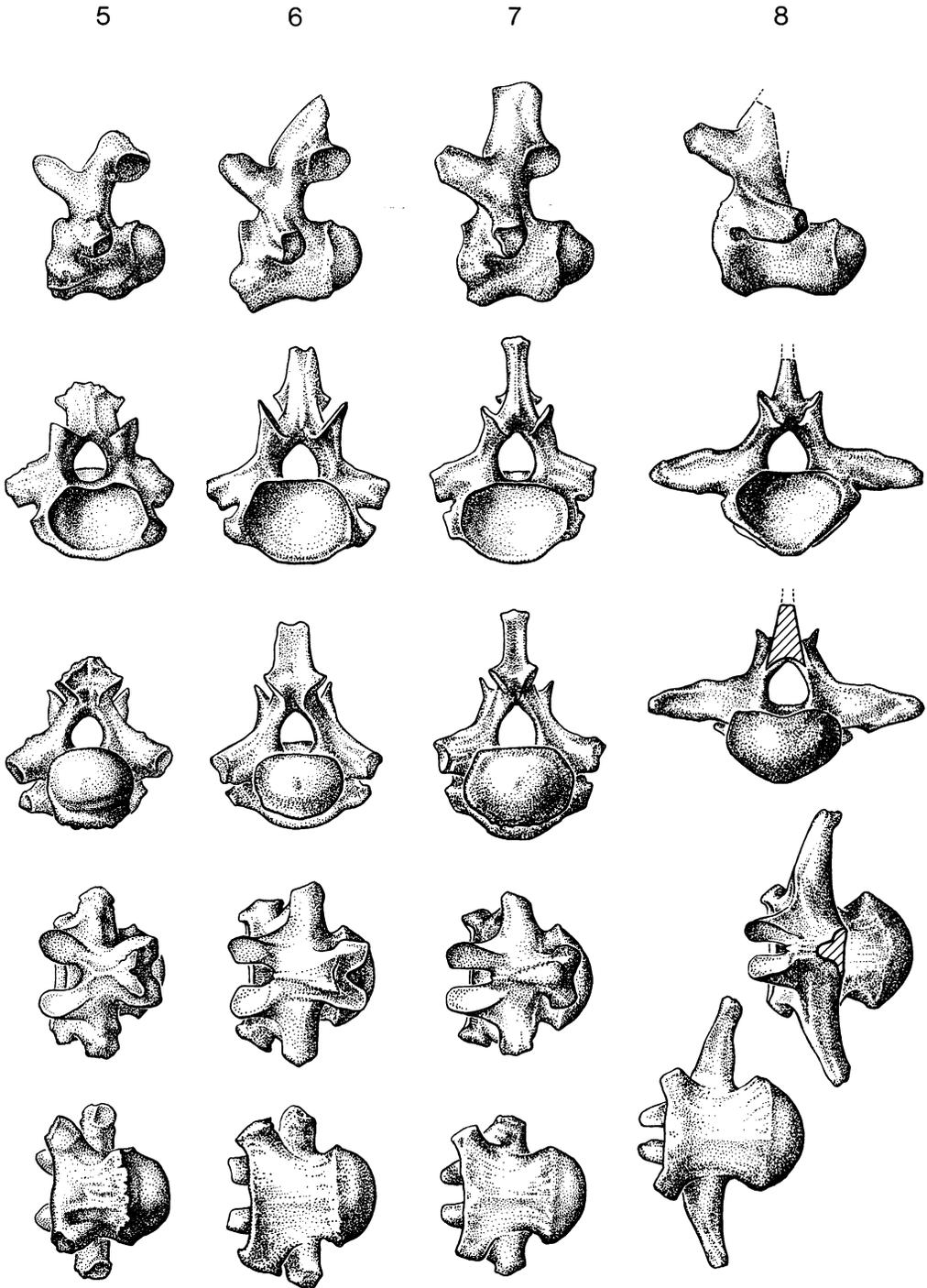


FIG. 5. Continued.

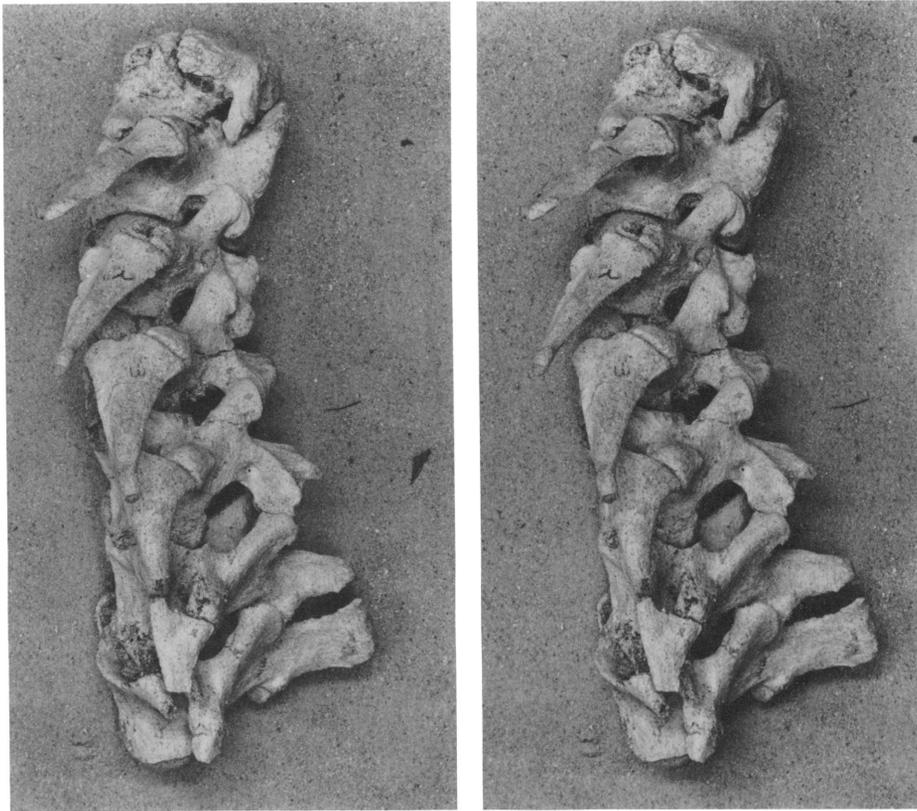


FIG. 6. *Meiolania platyceps*. Left lateral view of AM F:49141, cervicals one through seven, in natural articulation.

cervical they articulate with). This rib, and the two behind it, are the largest in the series, extending posteriorly well onto the posterior cervicals. The rib of the second cervical differs from the others in being relatively broad and spatulate in shape rather than tapering as in the more posterior ribs. The free cervical ribs of *Proganochelys* are also broad and flat rather than acutely tapering but they are not as broad as the second cervical rib of *Meiolania*. The free cervical ribs of *Proganochelys* are also much shorter, not extending very far beyond the centrum. The third and fourth cervicals in *Meiolania* are very similar in size and shape and would be very difficult to tell apart, one reason why the disarticulated ribs in the collection are questionably identified as to cervical.

The rib of the fifth cervical is nearly half the length of the anterior three ribs but still

extends past the limits of its cervical. The rib is acuminate and curves dorsally. The rib of the sixth cervical is shorter than any anterior to it and is a bit more irregular in shape, though still triangular and tapering, its acuminate point is relatively blunt. The seventh cervical of AM F:57984 has a transverse process (diapophysis) with an articular facet at its end, whereas in AM F:49141 there appears to be a small conical knob of bone separated from the diapophysis by a partial suture. All of this indicates that there is a cervical rib attached to the seventh cervical but that it is small and placed on the tip of the transverse process (as restored in fig. 9). As I interpret the eighth cervical, it lacks a rib and has a large transverse process. It is possible that part of the transverse process consists of a fused rib. In *Proganochelys* the cervicals two through five have free ribs, whereas the

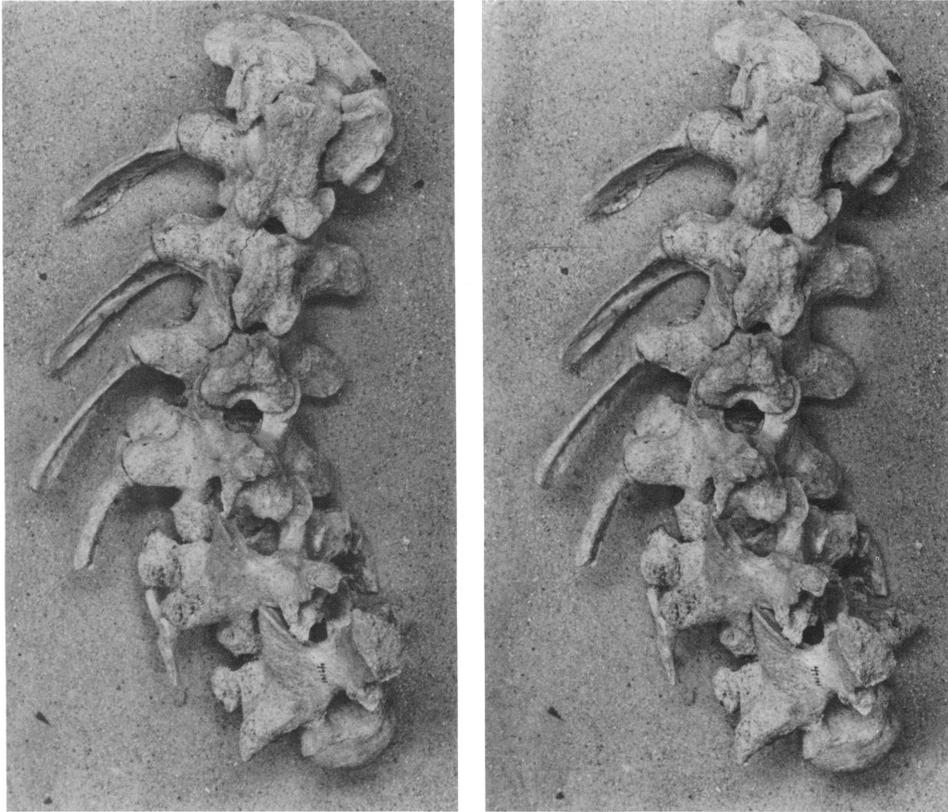


FIG. 7. *Meiolania platyceps*. Dorsal view of AM F:49141, cervicals one through seven, in articulation as found. First four ribs on right side have been removed.

more posterior ones do not. Cervicals six and seven of *Proganochelys* clearly have fused ribs, the tuberculum and capitulum are separated by an opening. But the eighth cervical of *Proganochelys* is similar to that in *Meiolania* in the very long transverse process that has no sign of distinct rib heads or foramen. Thus, the long transverse process in the eighth cervical of both *Meiolania* and *Proganochelys* may not have a rib component.

The articulations of the cervical ribs in *Meiolania* are described above but they might be compared here with *Proganochelys*. Both turtles have double-headed ribs but in *Proganochelys* the ventral articulation does not articulate with anything. There are facets, although small in comparison with *Meiolania*, where cartilaginous intercentra might be present on either side of the centra in *Proganochelys*. It is likely that *Proganochelys* had

cartilaginous intercentra but they were probably smaller than the ossifications in *Meiolania*.

Most of the cervical ribs (except the rib on cervical two) have a small unfinished surface at the distal tip suggesting continuation in cartilage.

PHYLOGENETIC SIGNIFICANCE OF CERVICAL VERTEBRAL CHARACTERS

Free cervical ribs are present throughout the Amniota as a primitive feature of the group and their absence or fusion in turtles is an advanced or derived condition. The presence of free cervical ribs in *Proganochelys* is consistent with the hypothesis that it is the sister group of all other turtles (Gaffney and Meeker, 1983), but their presence in *Meiolania* contradicts the assertion that

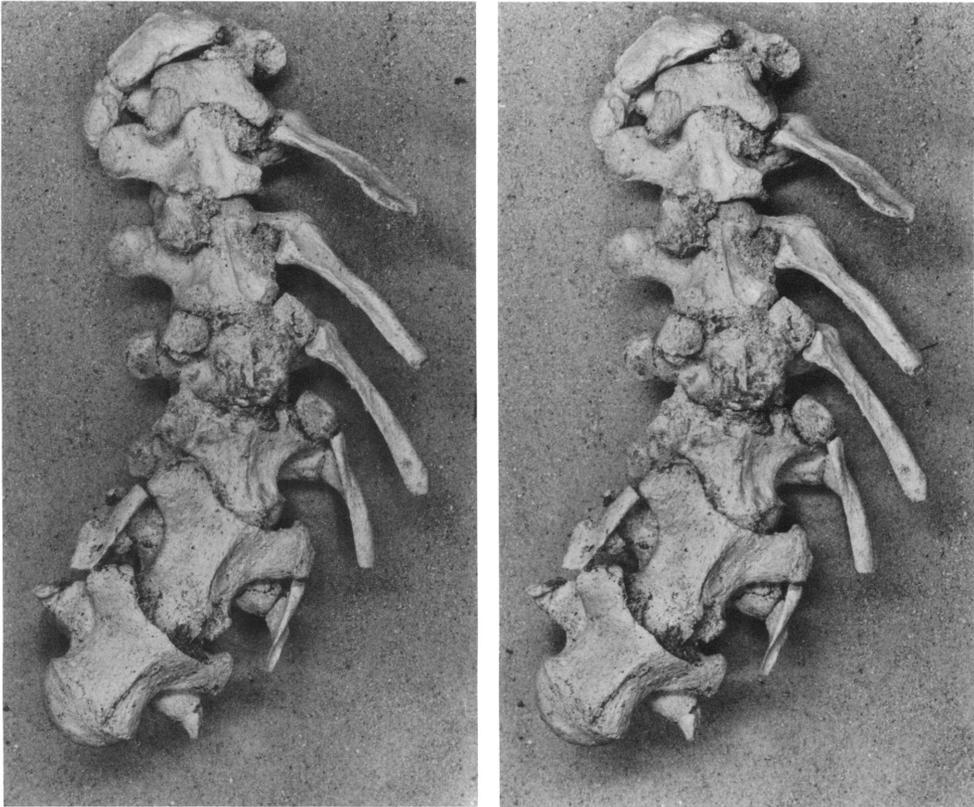


FIG. 8. *Meiolania platyceps*. Ventral view of AM F:49141, cervicals one through seven, in articulation as found. First four ribs on right side have been removed.

Meiolania is a eucryptodire (fig. 22). The systematic position of *Meiolania* is of some interest because it involves questions of the relationships of the major groups of turtles. I have discussed the history of phylogenetic work on *Meiolania*, developed a series of systematic hypotheses, and tested them with cranial characters in Gaffney (1983). The vertebral characters described here are discussed in the context of this earlier work and the reader should have access to that paper. One problem with this extension of comparisons from skulls to vertebrae is that the vertebral structure of many extinct taxa is less known than the skull.

The generalized amniote condition appears to consist of a cervical rib for each centrum, including the axis. Presumably the double-headed condition with articulations

on the intercentrum and diapophysis of the centrum are also primitive for amniote cervical ribs. All turtles, including *Proganochelys*, lack the atlantal rib (or may have a small, fused one at best). *Proganochelys* has well-developed double-headed ribs on cervicals two through five but is advanced over the primitive amniote condition by having fused ribs on cervicals six, seven, with the rib fused or absent on eight. In terms of cervical rib fusion, *Meiolania* is more generalized than *Proganochelys* because it has free ribs on cervical six as well as on cervicals two through five. There are other turtles with free cervical ribs, although the distribution of this feature is not well understood so far. *Pleurosternon* (described as *Mesochelys* by Evans and Kemp, 1975), has associated with it a cervical having well-developed diapophyseal and parapoph-

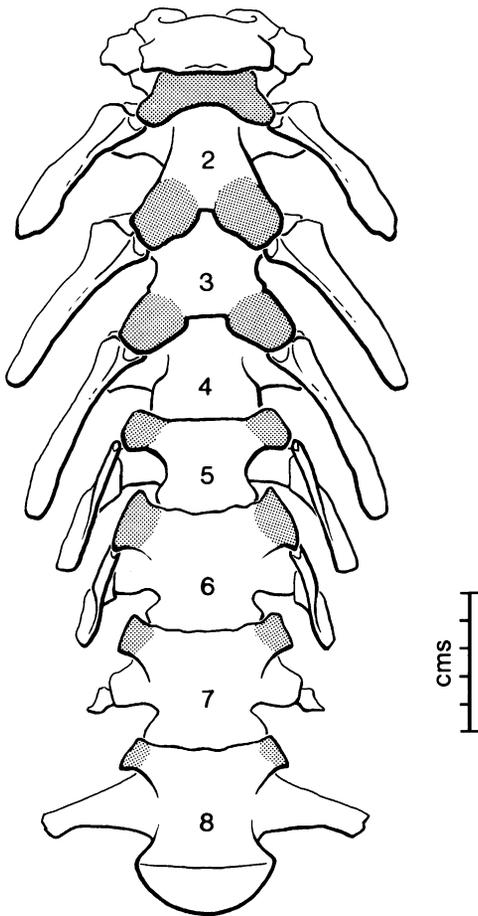


FIG. 9. *Meiolania platyceps*. Ventral view of cervicals one through eight, intercentra shown in stipple. Partially restored, based on AM F:49141.

yseal processes and facets, although an actual rib is not preserved. A similar cervical, but also lacking preserved ribs, has been found with the as yet undescribed Early Jurassic cryptodire from the Kayenta Formation of Arizona. The cervicals of such primitive cryptodires as baenids and *Glyptops*, however, clearly lack well-developed free cervical ribs. It is thus the case that postulation of one-time loss of free cervical ribs in turtles is inconsistent with nearly all other available derived characters. It is also possible that the presence of embryologic anlagen of cervical ribs (see below) would allow the development of free ribs, but this is extremely speculative.

In any case, the presence of free cervical

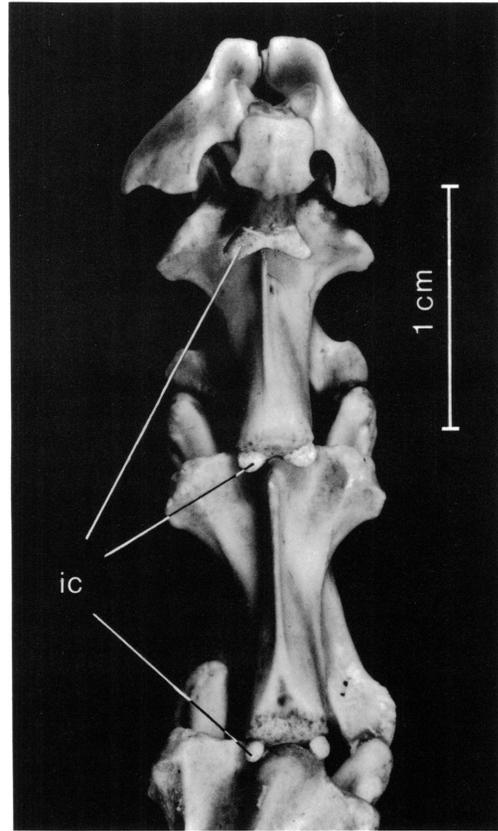


FIG. 10. *Pseudemys scripta*. Ventral view of cervicals one through four (part), intercentra indicated as IC. Compare with figure 9. The elements identified here as intercentra are identified as rib remnants by Williams (1959).

ribs in *Meiolania* is most compatible with alternative C (in Gaffney, 1983, fig. 65) in which *Meiolania* is hypothesized as a casichelydian but as the sister group of all other cryptodires and pleurodires. This would still require rib loss/fusion once in pleurodires and once in cryptodires due to the presence of ribs in *Pleurosternon* (*Mesochelys*). If my preferred hypothesis of *Meiolania* as an eucryptodire is chosen (alternative A in fig. 65, Gaffney, 1983), loss/fusion of free cervical ribs would be required at least four times: pleurodires, *Glyptops*, baenids, and living eucryptodires. Considering that even *Proganochelys* has some degree of autapomorphic fusion of cervical ribs, a case can be made for the multiple development of this feature.

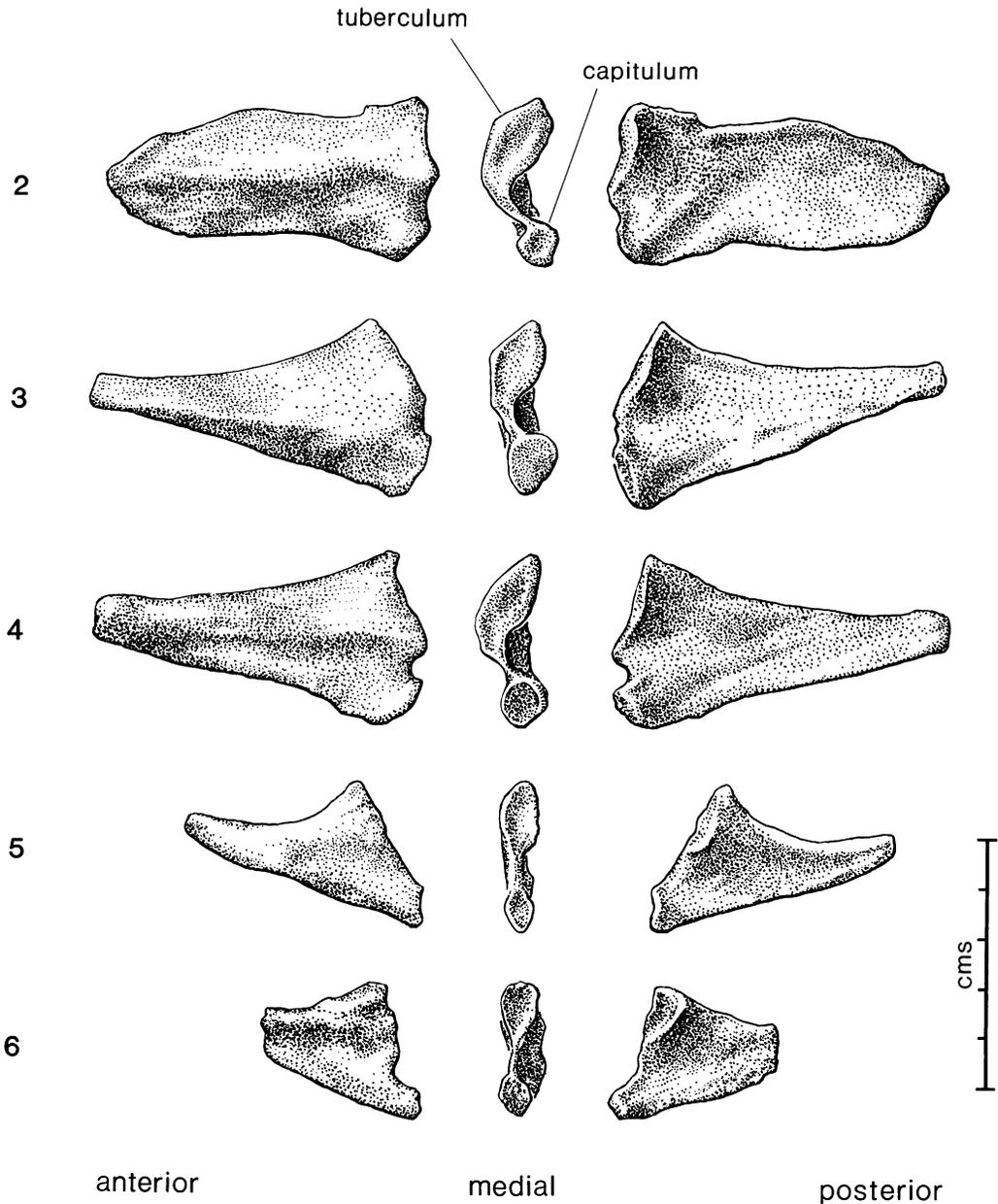


FIG. 11. *Meiolania platyceps*, AM F:49141. Cervical ribs from right side, shown in three views. Numbers on left indicate vertebra rib articulates with.

The identification of intercentra in *Meiolania* also has ramifications for our understanding of some poorly known features in Recent turtle cervicals. Williams (1959) described small nodules found in the intervertebral tissue of Recent turtles. These nodules

have been noted by earlier authors (see Williams for references) and I have seen them in both cryptodires (fig. 10) and pleurodires. Bojanus (1819, pl. 8, fig. 18 and pl. 14, fig. 51) figured three pairs in the neck of *Emys orbicularis*. Williams identified the nodules as

TABLE 2
Comparison of Cervical Vertebrae of *Meiolania* With Other Turtles

	<i>Proganochelys</i>	<i>Meiolania</i>	Baenids	Eucryptodires	Pleurodires
Formed central articulations	No	Yes	Yes and no	Yes and no	Yes
Biconvex 4th cervical	No	Yes	Yes and no	Yes	No
Well-developed free cervical ribs	Yes	Yes	No	No	No
Intercentra	Apparently unossified, but a wedge-shaped area is present	Paired, well developed, variably fused to centra	Apparently absent	Present as loosely ossified nodules	Present as loosely ossified nodules
Ventral median ridge	Absent	Absent	Present	Generally present	Generally present
Articulation of 8th cervical neural spine with carapace	Yes	Yes	No	Present only in chelonoids	No
Transverse processes	Present and well developed, middle of centrum	Present and well developed, middle of centrum	Present, usually well developed, middle of centrum	Usually absent, anterior edge of centrum	Usually present, middle of centrum
Centrum	Short	Short	Intermediate	Elongate	Elongate

cervical rib rudiments and based his identification on comparisons with early developmental stages of cryptodiran embryos. He thought he could identify tissue concentrations that were homologous with the tuberculum, capitulum, and main body of cervical ribs in these early developmental stages. In the adult of Recent turtles Williams identified the commonly occurring intervertebral nodules (termed the gamma elements by Williams) as the rudiments of rib capitula or ventral rib heads. Williams also found less common nodules, beta elements, slightly lateral to the gamma elements, which he identified as the cervical rib main body. The developmental evidence seems ambiguous to me; the various cell concentrations are consistent with a number of possible identifications. The discovery that *Meiolania* has a series of well-developed paired intercentra suggests comparison with these and the intervertebral ossicles of living turtles (figs. 9,

10). The gamma elements of Williams are in the same morphologic position as the intercentra of *Meiolania*. The fact that *Meiolania* also has well-developed free cervical ribs substantiates the identification of intercentra in *Meiolania*. Also, the paired intercentra found in other amniotes are similar to and in the same position as the gamma elements of turtles. Therefore, the best interpretation of the paired, intervertebral ossicles commonly found in the neck of Recent turtles would be as intercentra. It is also likely that the less common beta elements are rib rudiments, but whether main body, capitulum, or tuberculum cannot be determined. But the previous idea that cervical rib elements are common throughout turtles must be questioned.

The central articulation pattern of *Meiolania* may shed some light on the distribution of this condition in turtles. It is apparent from *Proganochelys* and pleurosternids (Hay, 1908, cf. *Glyptops*) that amphicoelus cervicals are



FIG. 12. *Proganochelys quenstedti* (Triassic, Germany), SMNS 17204. Nearly complete tail consisting of caudals 4 through 13, tail club at end, and series of osteoderms preserved in articulation. Left lateral view, anterior to left.

primitive for cryptodires, but the distribution of formed central patterns (Williams, 1950) are complex within the known extinct cryptodires, such as baenids. *Trinitichelys*, a baenid, has amphicoelus cervicals and *Plesiochelys* (Bräm, 1965), a chelonioid, also has amphicoelus cervicals. Other baenids and chelonioids, however, have formed central articulations (although different from each other) suggesting that formed articulations have arisen more than once within cryptodires. It is extremely likely that they arose independently in pleurodires as well. If the appearance of a biconvex fourth cervical in some, but not all, baenids (the distribution of central patterns in this family is still not well known, *Macrobaena* and possibly *Neurankylus* may not be baenids) is interpreted as an independent acquisition, then a case can be made for the (2(3(4) 5) 6) 7) 8) pattern as a eucryptodiran synapomorphy. This pattern occurs in chelydrids, testudinoids, chelonioids, and trionychoids and may be hypothesized as the primitive condition for each group. If *Meiolania* is the sister group of remaining eucryptodires then the occurrence of this feature in it is consistent with the hypothesis that this pattern is a eucryptodiran synapomorphy.

CAUDAL VERTEBRAE

There are no articulated tails in the collections of *Meiolania platyceps* and the only

specimen with as many as two articulated caudals is AM F:9051 (see discussion under Tail Rings). The reconstruction of a tail (fig. 13) has been entirely speculative and based on analogy with chelydrids and baenids and on the degree and kind of variation seen in the disarticulated *Meiolania* caudals. The restored skeleton (Burke et al., 1983, fig. 18) has what I believe are the fewest number of caudals given the amount of serial variation seen in the available caudals, and that is 10. It is quite possible that more caudals were present but fewer caudals would be unlikely. The number of caudals in *Meiolania* is hard to compare with other turtles because the distal caudals in *Meiolania* are fused into the tail club (which may represent four to five vertebrae), whereas the distal caudals of most other turtles are often greatly reduced and more numerous for a given length than the anterior ones. The total tail length, as restored for *Meiolania*, is similar to that in chelydrids, which is relatively long compared with other Recent turtles.

In the absence of articulated material, the relative position of caudal vertebrae has been determined by comparison with chelydrid and baenid caudals, which are most similar to the caudals of *Meiolania*, and by trial articulation of *Meiolania* caudals. The restored tail consists of the following caudals, beginning with the most anterior: AM F:61409, AM F:57984, AM F:18704, AM F:57984, AM

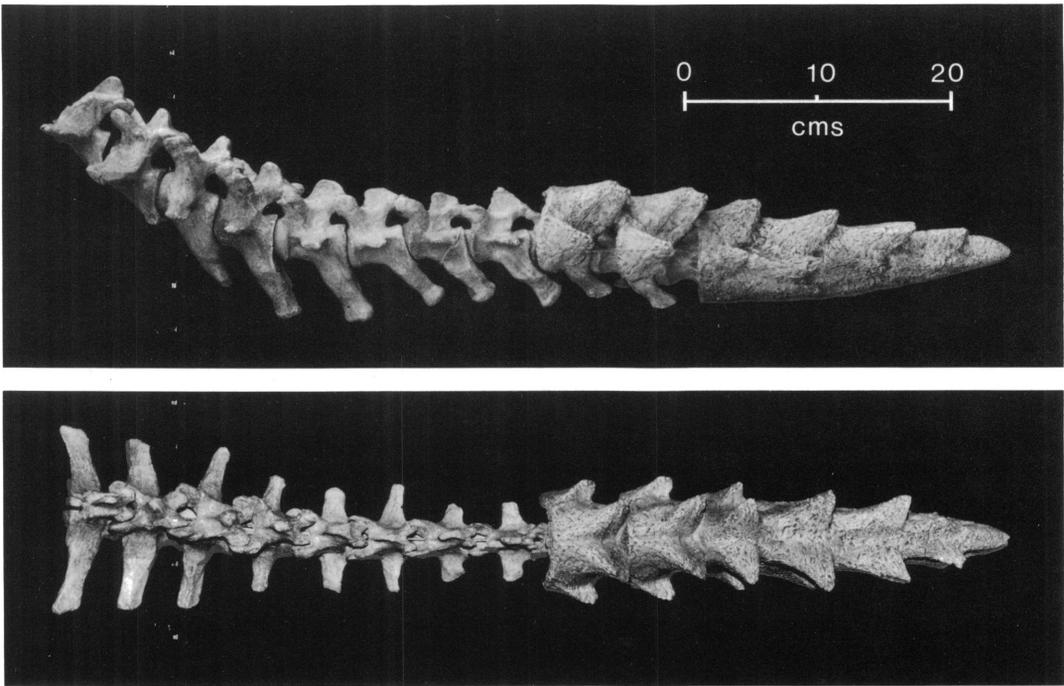


FIG. 13. *Meiolania platyceps*. Reconstructed tail consisting of ten caudals, tail club, and two tail rings. Upper, left lateral view; lower, dorsal view. Anterior to left. Compare with figure 12.

F:18716, AM F:18710, and AM F:18706. Two casts of the same caudal (AM F:18706) were used to bring the number to 10 as the last two caudals are largely obscured in our reconstruction by tail rings. Two caudals, the first and the fourth are from the same specimen, AM F:57984, that makes up most of the restored skeleton. Nonetheless, they were found disarticulated and their position in the tail is based on analogy as with other caudals.

The identification of sacral vertebrae in *Meiolania* shows that the anterior central articulation of the first caudal (fig. 14) is convex but very shallow and wider than high. AM F:61409 meets these conditions and is hypothesized as the first caudal in the reconstruction. This vertebra has wide transverse processes, wider than in any other preserved caudal, and they curve anteriorly to a slight extent rather than extend laterally at right angles to the centrum or curve posteriorly as in the other caudals. There are only low, blunt processes at the posteroventral margin of the centrum, rather than a haemal arch. The pre-

zygapophyses are comparable with those on the other caudals. The centrum is short in comparison to posterior caudals and has its longitudinal axis inclined so that the posterior central articulation is lower than the anterior central articulation.

The second caudal chosen for the reconstruction is a vertebra from AM F:57984. This centrum has a somewhat shallow and broad anterior central articulation but it is more convex than in AM F:61409. The zygapophyses and most of the transverse processes are broken off this caudal and it is possible that it is a first rather than a second caudal. However, the processes in the position of the haemal arch attachment are larger than in AM F:61409, suggesting that AM F:57984 is a more posterior vertebra.

The third caudal in the restoration is AM F:18704, and it bridges the morphologic gap between the extreme anterior caudals which lack haemal arches and the more "typical" caudals which have well-developed haemal arches. In AM F:18704 a haemal arch is pres-

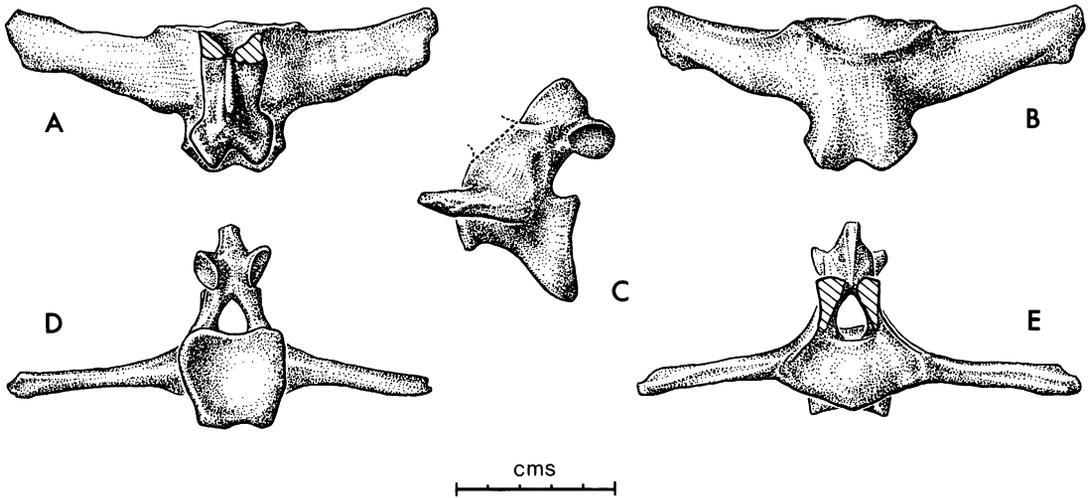


FIG. 14. *Meiolania platyceps*. First caudal vertebra, AM F:61409. A, dorsal; B, ventral; C, left lateral; D, posterior; E, anterior.

ent with paired basal attachments, but the arch is relatively small, inclined posteriorly, and comes to a point distally rather than a blunt termination as in the more posterior caudals.

The remaining caudals, four through nine in the reconstruction, may be described as a series of relatively similar vertebrae differing within the series from the more anterior to the more posterior ones. Owen figured a typical caudal of *Meiolania platyceps* (Owen, 1888, pl. 35, figs. 5, 6; the specimen has not been identified in a collection) which should be used for comparison with those illustrated here (fig. 15). The centrum of the more anterior caudals is relatively short, only slightly longer than wide but posteriorly the centrum becomes more elongate and narrower in the middle of the central body. The transverse processes, well developed on all caudals, are longer and narrower anteriorly and become shorter and broader in the more posterior caudals. The broadest but shortest transverse processes are in AM F:18706 where they closely approximate the interior diameter of the tail ring of AM F:50635. The position of attachment of the transverse processes moves from the center of the centrum more posteriorly in the posterior caudals. The neural spines are tall and have an acuminate ter-

mination in the anterior caudals while posteriorly the spines become short and blunt. The zygapophyses are closer together posteriorly. The haemal spines change slightly along the column, they are straight anteriorly but acquire a slight posteroventral bend in the posterior caudals.

PHYLOGENETIC SIGNIFICANCE OF CAUDAL CHARACTERS

Table 3

Determination of the systematic significance of caudal morphology in *Meiolania platyceps* is made difficult by the absence of comparative literature on turtle caudals. Although the cervical vertebrae of turtles have been described and compared in a number of papers, caudals are rarely dealt with. Among Recent specimens, I am aware only of the following descriptions: *Emys* (Bojanus, 1819); *Dermochelys* (Gervais, 1872; Völker, 1913); *Geochelone* (Günther, 1877); *Trionyx* (Ogushi, 1911); *Carettochelys* (Walther, 1922); and *Chelydra* (Newman, 1906, see below).

In 1887, Huxley described and figured a caudal of "*Ceratochelys sthenurus*" (= *Meiolania platyceps*, specimen in BM(NH) but not identified) which he compared with *Chely-*

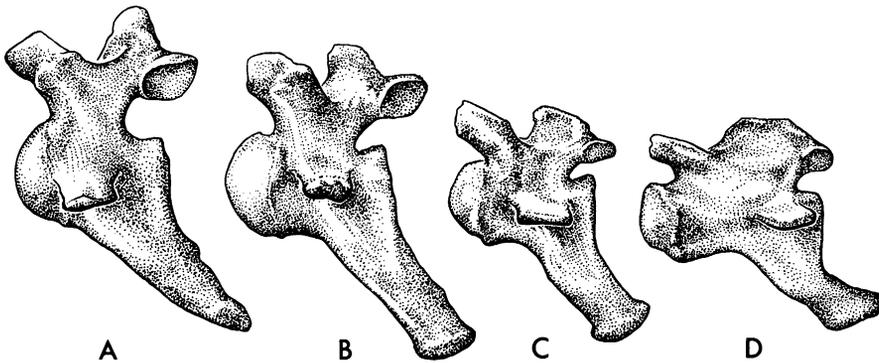


FIG. 15. *Meiolania platyceps*. Caudal vertebrae in left lateral views. A, AM F:18704 (3); B, AM F:57984 (4); C, AM F:18715 (7); D, AM F:18706 (9 and 10). Numbers in parentheses indicate position in restored tail (fig. 13).

dra. He concluded on the basis of the caudal and skull morphology (see Gaffney, 1983, for discussion and figure of skull used) that "*Ceratochelys*" was a "Chelydroid Chelonian." Specifically (Huxley, 1887, p. 237): "that the remains of crania and caudal sheaths from Australia, hitherto referred to Saurian reptiles [that is, lizards, by Owen], under the names of *Megalania* and *Meiolania* appertain to a hitherto unknown species of Chelonian, *Ceratochelys sthenurus*, closely allied to the living *Chelydra*, *Gypochelys* [= *Macroclemys*], and '*Platysternum*.'" As far as the caudal vertebrae are concerned, Huxley's argument linking *Meiolania* with the chelydrids (including *Platysternon* in the sense of Agassiz, 1857, and Gaffney, 1975) is based on the central articulation pattern and the general close agreement in morphology. Huxley referred to Baur's (1886) vertebral study in which Baur showed that the chelydrids were unusual among Recent turtles in possessing opisthocoelus caudals, all other living turtles being procoelus. This pattern has systematic significance for cryptodiran relationships. The primitive chelonian caudal pattern is platycoelus, as seen in *Proganochelys*, but the presence of opisthocoelus caudals in baenids strongly suggests that that condition is primitive for cryptodires. The procoelus cryptodires also have reduced or absent haemal arches, which are well developed in baenids and chelydrids. Therefore, it would be useful to propose a group, the Procoelocryptodira, having nearly all the caudals pro-

coelus and having very small or absent haemal arches (see also Gaffney, 1984). This group would consist of the chelonoids, trionychoids, emydids, and testudinids. The procoelus to platycoelus caudals of pleurodires would be an independent acquisition of this character. Baur (1889, p. 62) reports two specimens of *Clemmys insculpta* with opisthocoelian caudals as an individual variation.

The Chelydridae have a caudal condition that may be hypothesized as a synapomorphy for that group. Two or three of the most anterior caudals are procoelus, following them is a biconcave caudal and the remainder are opisthocoelus. In *Chelydra* and *Macroclemys* it is the third caudal that is biconcave, whereas in *Platysternon* and *Chelydropsis* (Mlynarski, 1980) it is the fourth caudal. The remaining caudals are opisthocoelus. The biconvex caudal is a rare situation, there is no evidence of it (or of any procoelus caudals) in *Meiolania* or baenids, and it has not been reported in the remaining living cryptodires or pleurodires.

It would appear that Huxley's use of opisthocoelus caudals to link *Meiolania* and chelydrids is unsatisfactory because that feature is plesiomorphic for cryptodires. Procoelus caudals do seem to define a natural group, however, which excludes chelydrids and *Meiolania* (fig. 22).

The caudals of *Meiolania platyceps* are most similar to those in the chelydrids and baenids. This similarity appears to be the result of shared primitive features for the

TABLE 3
Comparison of Caudal Vertebrae

	<i>Proganochelys</i>	<i>Meiolania</i>	Baenidae	Chelydridae	Procoelocryptodira	Pleurodira
Central articulations	Platycoelus	Opisthocoeilus	Opisthocoeilus	First 2-3 procoelus, one centrum biconvex, rest opisthocoeilus	Procoelus	Procoelus
Nueral spines	Very low to absent	Well developed	Well developed	Well developed	Usually low	Usually low
Haemal arches	Present, well developed	Present, well developed	Present, well developed	Present, well developed	Often absent, but small and rudimentary when present	Absent
Number of caudals (exclusive of tail club)	13-18	Estimated at 10 + ?	Variable, 26-43	25-30	20-25	14-22
Tail length relative to carapace	Long	Long	Long to very long	Long	Short	Short
Caudal dermal ossifications	Nodules, rings and terminal tail club	Rings and terminal tail club	None	Nodules	None	None

Cryptodira. In addition to opisthocoely as the dominant articulation pattern, *Meiolania*, chelydrids, and baenids have well-developed haemal arches on most of the caudals, relatively high and narrow centra, well-developed neural spines, and a relatively long tail; features generally lacking in Procoelocryptodira and pleurodires.

Baenid caudal morphology is known from only a few specimens. Hay (1908, p. 79) compares caudals of *Baena* with *Chelydra*, whereas Case (1939) figures disarticulated caudals of *Plesioabaena*. Russell (1934), however, has published the only figure of what appears to be a complete baenid tail, as well as figuring some individual centra. Russell's specimen is *Thescelus* (Gaffney, 1972), a genus that seems to have an unusually long tail even for baenids. *Thescelus* also has most of the caudals nearly platycoelus, although it is best described as opisthocoelus. Russell also figures a partially articulated tail of *Plesioabaena*. Case (1939) figures and describes disarticulated caudals of *Plesioabaena*. Based on re-examination of all these specimens as well as other material in the AMNH collections, I have been unable to find consistent features differentiating individual caudals of baenids, *Meiolania*, and chelydrids (except in the case of the procoelus and biconvex anterior caudals in chelydrids). Regional variation and numbers of caudals offer more possibilities but as entire tails are known in only one baenid and not at all in *Meiolania* further pursuit of this avenue must await better material.

TAIL CLUB

One of the most bizarre attributes of *Meiolania* is the prominent ossification at the end of the tail. The presence of a somewhat similar structure in the Triassic turtle, *Proganochelys*, makes the feature even more interesting.

The tail club or tail sheath of *Meiolania platyceps* (figs. 16–19) is a hollow, elongate cone of bone with vertebrae attached down its center by the transverse processes, neural spines, and haemal arches. The external surface is very rugose, with numerous pits and foramina for nutrient vessels, suggesting that the bone was covered in life by a horny scale or scales. There is a regular pattern of spines

and ridges on the tail club that has variable development among the available specimens.

For the purposes of description, the spines may be grouped in pairs aligned as a series of segments along the length of the tail club. Each segment consists of a dorsolateral pair of spines and a lateral pair. The spines begin as a low ridge anteriorly and increase in size posteriorly, becoming acuminate to end in a projection that points posteriorly and away from the main axis of the tail club. The dorsolateral spines are distinctly smaller. These spine pairs are arranged in four segments. The spines vary in size and shape among the available specimens of tail clubs (about two dozen, not counting small fragments). In AM F:18721 (fig. 17) the spines are particularly acuminate, more so than in many specimens such as MM F:13831a (figured in Owen, 1888, pl. 37). Rounded, blunt spines are seen in AM F:64435 and AM F:61404. Other types of tail club variation also exist. In AM F:61404 the dorsolateral spines are closer together at the midline than in the other specimens and the lateral spines are comparatively large in contrast to tail clubs such as AM F:18721. In all complete tail clubs the dorsolateral and lateral spines are arranged in four segments along the length of the tail. In some, such as MM F:13831a (Owen, 1888, pl. 37) the spines decrease in size posteriorly but in others, such as in AM F:18721 and a club in the Lord Howe Island Museum, the second spine pair is the largest, with the first, third, and fourth being smaller.

The ventral surface of the tail club lacks spines and has a pattern of elongate hexagonal scales down the midline. There are four of these scales corresponding to the segments formed by the spine sets, but some clubs (AM F:18721, for example), show indications of a fifth scale at the very end. In most tail clubs, such as AM F:64435, the scale sets are clear and well defined and the rugose bone surface preserves all the details of the pits and foramina. But in some tail clubs, such as AM F:18721 (fig. 17) the ventral surface shows signs of mechanical erosion and abrasion, particularly anteriorly, that has resulted in thinning of the bone and perforation in some areas. This erosion does not seem to have been postmortem and may have occurred

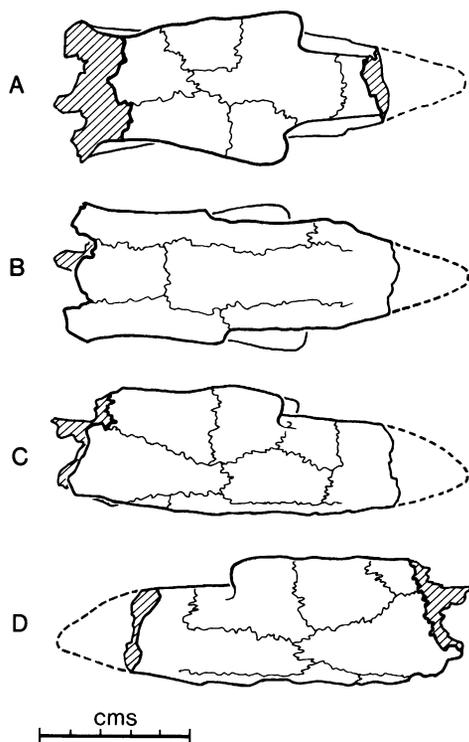


FIG. 16. *Meiolania platyceps*. Partial tail club, AM F:18863. This tail club is one of the few showing sutures.

during life when dragging the tail abraded through the scale covering. There are no other indications in any specimens of tail club damage during life. The tail clubs are not precisely symmetrical, they may curve slightly to one side, and the development of the spines may not be precisely symmetrical in extent or position.

The terminal portion of the tail club varies from acuminate in AM F:18721 to blunt in AM F:64435. The terminal segment may be rugose and featureless as in AM F:64435 but it often has a variably developed midline ridge that is particularly apparent in AM F:18724 and AM F:18720.

The internal morphology of the tail club (figs. 18, 19) is determinable by examination of damaged specimens in which the outer bone layers have been removed. Owen (1886, pl. 31, fig. 3—BMNH R679, fig. 4—BMNH R680; error in figure references in Gaffney,

1983, p. 474) described and figured two such specimens and Etheridge (1889, pl. 25, fig. 1 and pl. 26, fig. 1) also figured a broken tail club. Further study of the Australian Museum collection resulted in the discovery of another piece belonging to the tail club figured by Etheridge so that the specimen now consists of the figured portion (AM F:16867) and a terminal portion (AM F:228, but this is a group number containing other specimens). The newly discovered piece allows all four spine segments to be identified on this specimen expediting comparisons. This tail club has also been acid prepared and now serves as an illustration of the internal morphology of a *Meiolania platyceps* tail club (fig. 18; see also sections of a tail club, AM F:18725, fig. 19). The cone of bone forming the external part of the club or sheath has a string of vertebrae that run down its center all the way to the tip. At least three centra are recognizable anteriorly and these correspond to the first three segments formed by the spine pairs. Each vertebra is recognizable as a posterior caudal because they have an elongate centrum, broad transverse processes, and a haemal arch positioned at the posterior end of the centrum. The most anterior vertebra to be attached within the tail club has a centrum with a convex articulation on its anterior surface and a platycoelus synchondrosis posteriorly that is open in most specimens but is fused in some, such as AM F:61404. All the other centra in the tail club articulate by means of a platycoelus synchondrosis but the contact is tighter posteriorly to become virtually indistinguishable between the third and fourth centrum. The centra are constricted in the middle giving them an hourglass shape. The neural spine attaches to the tail sheath distally for most of its length and the neural canal retains its integrity, at least anteriorly (fig. 19; Owen, 1888, pl. 37, fig. 3). Each transverse process also attaches to the bony cone of the tail club at its distal termination, as does the haemal arch of each centrum so that the centra are suspended down the middle of the tail club. Posteriorly, however, as the cone of the tail club narrows, the centra do not narrow and the relatively large space enclosed by the tail club anteriorly (fig. 19, left) becomes greatly reduced posteriorly, as can be seen in AM F:

18725 (fig. 19, right) and AM F:18361. In these specimens it can be seen that the terminal portion of the club is nearly solid bone with only a thin space separating centrum and external bone.

The positioning of the centra within the club corresponds with the segmental arrangement of the spikes. The centra tend to overlap the segments slightly so that the anterior third of the centrum extends into the posterior part of the preceding spike segment. This characterization is a bit subjective because the separation between spike segments would appear to be on a transverse plane that is tilted posteriorly at the top of the club and anteriorly at the bottom.

The tail clubs vary in size but because only a few are complete enough to measure the range is difficult to determine. The smallest complete club (AM F:18721) is about 60 percent the size of the largest complete club (MM F:13831a). As most clubs lack sutures it is difficult to see how these could represent growth stages. There are no tail clubs found associated with shells, skulls, or other major skeletal elements and AM F:18721 was chosen for the AMNH skeletal reconstruction because AM F:57984, the specimen that provided about 40 percent of the reconstruction, is one of the smaller *Meiolania platyceps* specimens.

Owen (1888, p. 188) suggested, on the basis of MM F:13831a, that the tail club in *Meiolania* consisted of "five anchylosed segments" comparable to the tail rings. He included the four spike sets plus the terminal cone. The close similarity between the tail rings and the tail club in the position of the spike sets and the vertebrae support Owen's contention that the tail club may be interpreted as serially homologous with at least four fused tail rings. It is, therefore, surprising to find that the only tail club with sutures (fig. 16) is inconsistent with this hypothesis. This specimen, AM F:18863, is a partial tail club consisting of the last set of spikes but lacking the terminal tip. Although sutures are present, AM F:18863 is larger than AM F:18721 and seems to be comparable in size to MM F:13831a. The sutures preserved on AM F:18863 do not appear to be related to its supposed serial homology with the tail rings. The preserved portion consists of at least 12

separate ossifications, and as some of these are partially fused, it is possible that additional ossifications were present earlier in development. The three ventral ossifications seem to be symmetrical on the midline but the others are not. The pair of dorsal spikes are each made of two ossifications, the right one, at the tip of the spike, extends over the midline but the left one does not. The anterior margin of the tail club segment is a sutural surface that is in the correct position for a tail ring anterior margin and it is possible that the terminal segment of a tail club does ossify in numerous centers of growth, whereas the more anterior portions are more like tail rings. It is also possible that this specimen is anomalous and does not represent the usual ossification pattern.

A tail club is also known in "*Meiolania oweni*" from the Pleistocene of Queensland, described and figured by Owen (1882). This tail club is very similar to the one in *Meiolania platyceps*, differing primarily in size and the number of spike segments. The "*Meiolania oweni*" club is about four times the diameter and much more massive in proportions than *Meiolania platyceps*. *Meiolania platyceps* has four spike segments consisting of two spike pairs, whereas "*Meiolania oweni*" has only two spike segments with the spike projections being more obtuse and thicker but the orientation, relative size, and position of the spikes being the same in both species (see Owen, 1882, pl. 65).

The only other turtle to have a tail club fully enclosing caudal vertebrae is *Proganochelys* (fig. 12). The club in *Proganochelys* is similar to that in *Meiolania* in consisting of a series of spikes fused together. The three *Proganochelys* tail clubs available show some variation indicating some asymmetry rather than the strict bilateral symmetry seen in meiolaniids. The *Proganochelys* club has spike sets that are arranged in triads with a median spike on the midline in contrast to the spike pairs of meiolaniids. The ventral and lateral parts of the *Proganochelys* are covered by short, wide plates with no indication of hexagonal scales in meiolaniids. In *Proganochelys*, as in *Meiolania platyceps* and "*Meiolania oweni*", the morphology of the tail club is comparable to the dermal ossifications found more anteriorly on the tail.

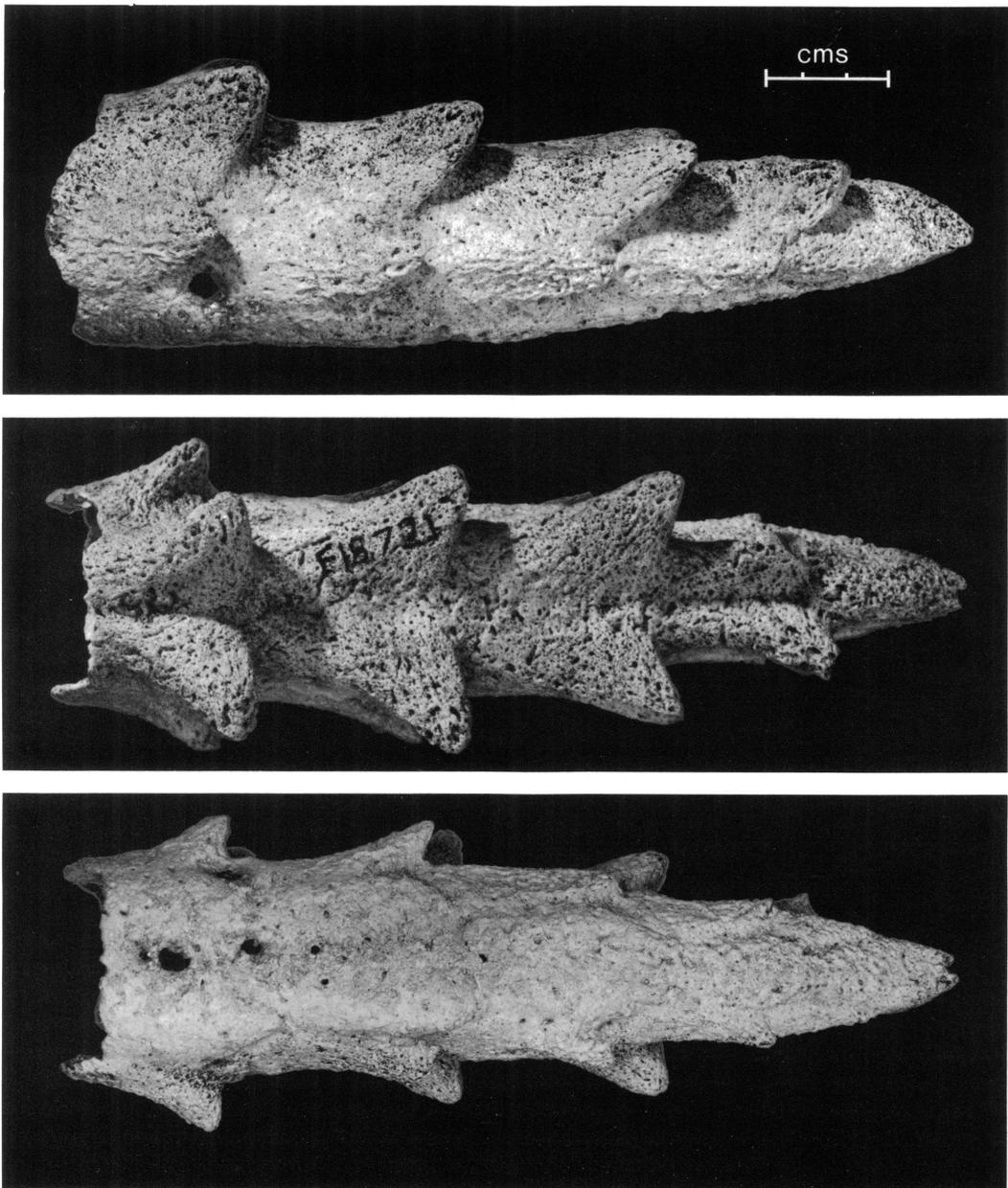


FIG. 17. *Meiolania platyceps*. Tail club, AM F:18721. Top, left lateral view; middle, dorsal view; bottom, ventral view. Anterior to left.

Is the tail club of meiolaniids and *Proganochelys* strictly homologous or is it a synapomorphy for meiolaniids which was independently present in *Proganochelys*? Examination of the preferred hypothesis of

meiolaniid relationships (fig. 22) indicates that the tail club would have to have been lost at least three times (pleurodires, pleurosternids, baenids) if this hypothesis is correct and if the tail clubs are homologous. The tail clubs

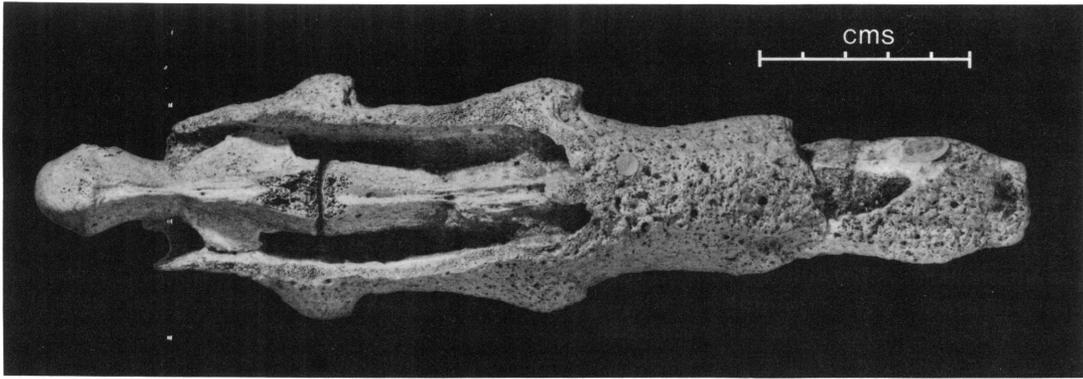


FIG. 18. *Meiolania platyceps*. Tail club, AM F:16867 and AM F:228 (in part). Ventral view of damaged specimen showing internal features.

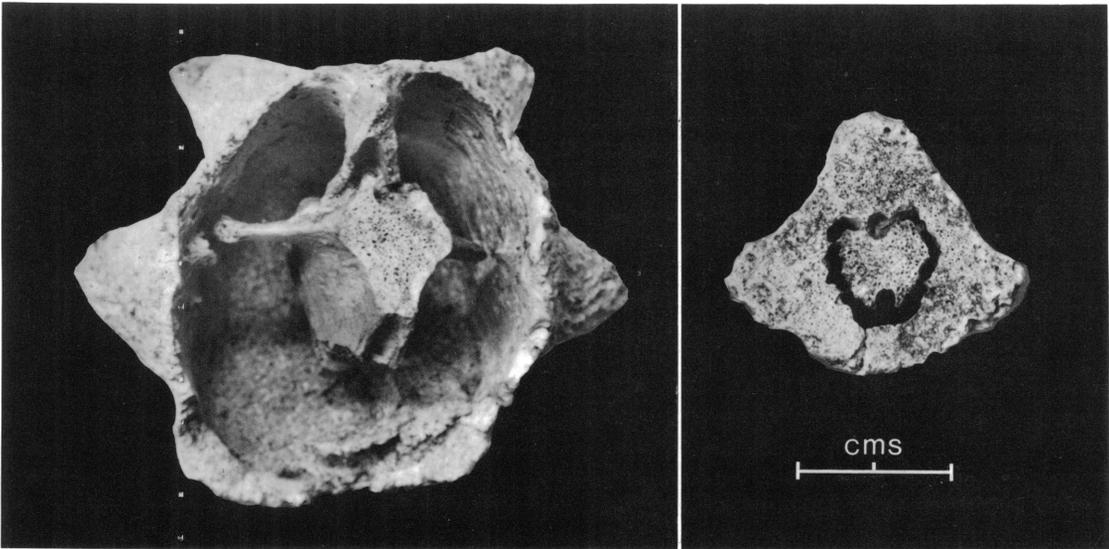


FIG. 19. *Meiolania platyceps*. Tail club, AM F:18725. Left, anterior view of anterior (natural) end of tail club; right, posterior view of broken posterior end of tail club.

are similar but not identical so the alternative hypothesis of independent origin is quite possible. Nonetheless, I think that the degree of similarity is close enough to require the structures to be homologous in spite of the multiple loss made necessary by accepting this hypothesis.

A "compromise" hypothesis is also possible making independent acquisition seem plausible. The presence of caudal ossifications is more widespread among turtles than

are tail clubs, being found in chelydrids and testudinids as well as in meiolaniids and *Proganochelys*; and it might be argued that the ossification potential exists or existed in many turtle groups, allowing the multiple evolution of tail clubs. The presence in testudinids of well-developed "anal bucklers" (Hay, 1908) is consistent with this hypothesis, which, although not favored here, should be kept in mind.

In summary, I think that the particular form

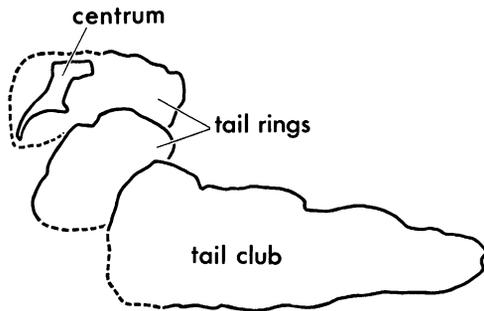
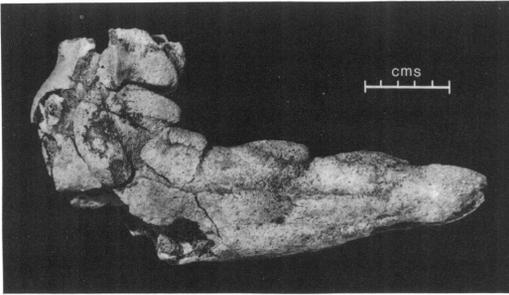


FIG. 20. *Meiolania platyceps*. Tail club with two articulated tail rings, AM F:9051.

of the tail club with two pairs of spikes is synapomorphic for meiolaniids, the presence of a caudal ossification surrounding caudal vertebrae is primitive for turtles and is a synapomorphy for the whole group.

TAIL RINGS

The tail of *Meiolania platyceps* is covered with a segmented dermal armor composed of tail rings (fig. 21). Only one specimen, AM F:9051, preserves these rings in articulation with other elements (fig. 20) and this specimen shows that, at least posteriorly, the rings articulate with one another and that there is one per vertebra. The tail rings in this specimen, which is not well preserved, are bent dorsally and lie at an angle to the tail club, a condition that is the result of postmortem disturbance. These tail rings are similar in curvature and spike morphology to the tail club. A disarticulated tail ring, AM F:50635 (fig. 21) shows this morphology more clearly. The dorsolateral spike pair extend postero-dorsolaterally, as on the tail club, and are much larger than the lateral spike pair. There

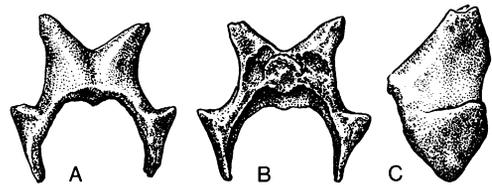


FIG. 21. *Meiolania platyceps*. Tail ring, AM F:50635. A, anterior view; B, posterior view; C, left lateral view (anterior to left).

is no sign of fusion or sutural attachment between tail ring and any vertebral element. In contrast to the tail club, the tail rings in *Meiolania platyceps* are incomplete ventrally, also in contrast to the tail rings in "*Meiolania*" *oweni* (Owen, 1882) and *Niolamia* (Woodward, 1901) in which they are complete ventrally. The anterior margin is indented for articulation with adjacent rings.

It seems likely that the tail rings, definitely known only for the posterior portion of the tail, extend anteriorly for much of the length of the tail, probably one for each caudal. Although there are no complete anterior tail rings it is likely that some fragments belong to tail rings from the anterior series. One of these (MM F:13829) was figured by Owen (1888, pl. 36, figs. 7-9) as a "sternal arch." Examination of the specimen indicates that of the three knobs or spikes seen in posterior view, the two left-hand ones are equivalent to the dorsolateral spikes on the posterior tail rings. If the circumference of this ring were restored it would have a diameter of about three times that of a tail club and might correspond to the base of the tail. Another ring of this sort is AM F:1196, but it has a smaller restored diameter and might be from a more posterior section of the tail. If this identification is correct, the anterior tail rings would differ from the posterior ones in being thinner anteroposteriorly, lacking articulation with each other, having a larger diameter, and having much lower spikes but the same pattern. There are many fragments in collections (for example, AM F:193, AM F:5754) that can be interpreted as belonging to tail ring fragments intermediate between the ones described above, but their fragmentary nature

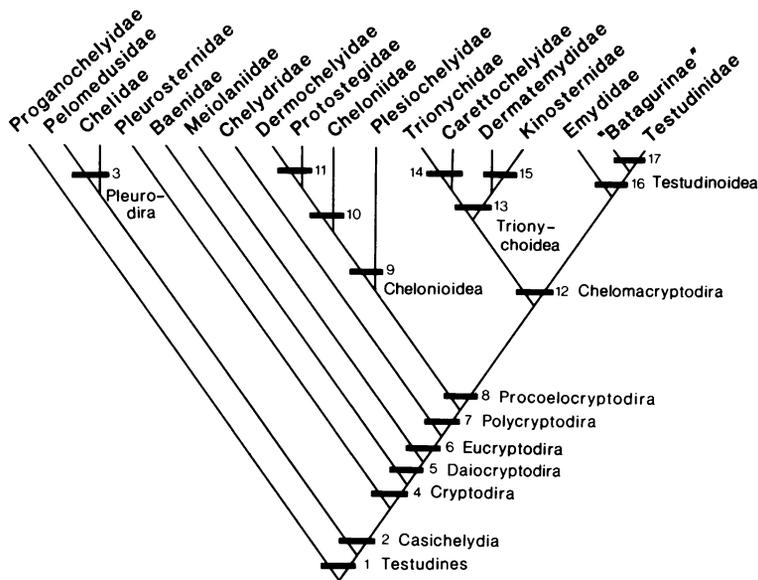


FIG. 22. Cladogram of turtles showing hypothesized position of meiolaniids. See also Gaffney, 1983, figure 65. Characters in this cladogram are described and discussed in Gaffney (1984).

precludes useful description. It might be worth mentioning here that it is difficult to distinguish fragments of tail rings from skull fragments in the supraoccipital-squamosal area of the "A" horn and scale area.

Among the presumed tail ring fragments are a few (AM F:374, AM F:61110) that are bilaterally symmetrical, seem to be from the dorsal section forming part of the dorsolateral spikes, and are limited laterally by sutures. This suggests that the tail rings may ossify from a median section and have two or more lateral ossification centers.

Tail rings occur in other meiolaniids and *Proganochelys* has caudal ossifications that may be compared with *Meiolania*. "*Meiolania*" *oweni* has a tail ring (Owen, 1882, pl. 65) that is quite similar to that of *Meiolania platyceps*, with a large dorsolateral spine pair and a smaller lateral spine pair, both with their apices trending posteriorly. Although the specimen is broken, it is likely that the ring formed a complete circle, in contrast to the known tail rings of *Meiolania platyceps*. The "*Meiolania*" *oweni* tail ring, furthermore, is tightly articulated with the tail club which consists of only two spine sets rather than four in "*Meiolania*" *oweni*. It is possible that

the tail ring of "*Meiolania*" *oweni* is homologous with a portion of the tail club in *Meiolania platyceps* rather than with the tail rings themselves.

A tail ring is known for *Niolamia argentina* (Woodward, 1901, pl. 18, fig. 2), but whether or not a tail club was also present is not known. This tail ring is similar to that in the other meiolaniids in having two spine pairs with the dorsolateral one being the largest. It differs from the other meiolaniids in having the spines relatively flat in one plane rather than circular in cross-section. As in "*Meiolania*" *oweni* but in contrast to *Meiolania platyceps*, the tail ring of *Niolamia argentina* forms a complete circle.

The only other turtles known with ossified caudal plates are some of the testudinids. Hay (1908, figs. 560, 603) describes caudal ossifications in some extinct species of *Geochelone* ("*Testudo*" *osborniana* and "*Testudo*" *orthopygia*) that consist of loose ossicles and a flat plate of fused ossicles lying on the dorsal surface of the last caudal vertebrae. Auffenberg (1963) also describes a similar ossification in a subgenus of *Geochelone* which he named *Caudocheilus*. The caudal vertebrae in these forms are short, with very wide trans-

verse processes and the plate is borne on the dorsal surface of the caudal amongst many separate dermal ossicles. Auffenberg's hypothesis that this plate, termed by him a supracaudal anal buckler, served the purpose of protecting the anus and surrounding area, seems reasonable. There are no particular similarities with meiolaniid tail rings or tail clubs.

Proganochelys has many dermal ossicles in the tail. On the dorsal surface are a series of broad ossicles (fig. 12) bearing three spikes that seem to be serially homologous with the spikes in the tail club. These ossicles are roughly comparable with tail rings in meiolaniids but do not extend down the side of the tail and do not have spikes arranged in pairs.

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