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VIII.—The systematic position of Meiloania, Owen

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exaggeration of that found in the existing American genus *Dermatemys*; and since the general contour of the neural shields is the same as in the latter, it appears probable, although the evidence is not conclusive, that *Trachyaspis* is an allied form.

Trachyaspis hantoniensis, sp. nov.

A marginal in the Natural-History Museum (no. R. 1443) indicates the occurrence in the Upper Eocene of Hordwell of a species of *Trachyaspis*, which, from its much lower geological horizon, is probably specifically distinct from the type form; while its distance in space may be an argument for its distinctness from the Egyptian species.

Anostira anglica, sp. nov.

An anterior marginal and a xiphiplastral from Hordwell preserved in the Museum (nos. 33198, *x*, *y*) appear to indicate a Chelonian which cannot be generically distinguished from the genus *Anostira*, Leidy, of which the type species is from the Upper Eocene of the United States. The larger size of the present specimens and the absence of distinct radiation in the sculpture afford a specific diagnosis from the type.

VIII.—*The Systematic Position of Meiolania, Owen.*

By Dr. G. BAUR, New Haven, Conn.

THERE are at present three different views about the systematic position of *Meiolania*. According to Sir Richard Owen* *Meiolania*, together with *Megalania*, belongs to a suborder Ceratosauria, with affinities with both the "orders Chelonia and Sauria."

Prof. Huxley† considers the animal most nearly allied to the Chelydridæ and Platysternidæ.

Mr. Boulenger‡ comes to the conclusion that, far from

* Owen, R., "On parts of the Skeleton of *Meiolania platyceps* (Owen)," Phil. Trans. 1888, pp. 181-191, pls. xxxi.-xxxvii.

† Huxley, Thomas H., "Preliminary Note on the Fossil Remains of a Chelonian Reptile, *Ceratochelys sthenurus*, from Lord Howe's Island, Australia," Proc. Roy. Soc. London, vol. xlii. 1887, pp. 232-238.

‡ Boulenger, G. A., "On the Systematic Position of the Genus *Mio-lania*, Owen," Proc. Zool. Soc. 1887, pp. 554-555.

bearing any affinity to the Chelydridæ or Platysternidæ, the extinct Chelonian belongs, like the recent forms of the Australian region, to the group Pleurodira.

I am indebted to Dr. H. Woodward for permission to examine the material of *Meiolania* in the British Museum.

There can be no doubt whatever that *Meiolania* is a Chelonian; and the only question is, does it belong to the Cryptodira (the opinion held by Prof. Huxley) or to the Pleurodira (the view of Mr. Boulenger)?

Mr. Boulenger's reasons for the Pleurodiran nature of *Meiolania* are the following:—

"1. The pterygoids are very broad, not narrowed posteriorly; their outer palatal borders, instead of being emarginate, form wing-like expansions.

"2. The tympanic cavity is completely surrounded by the bony 'roof,' whilst in all known Cryptodira, however great the development of the roof, the tympanic disk is free behind.

"3. The mandible articulates with the skull by a condyle fitting into an articular concavity of the quadrate—a character by which the Pleurodiran Chelonians differ from all other Reptilia, so far as I am aware.

"4. The cervical vertebræ are those of a Pleurodiran; a strong and long transverse process is present, and the posterior borders of the odontoid bone and of the second centrum are deeply emarginate inferiorly, terminating in two diverging processes exactly as in *Chelys*."

Now let us consider the principal characters of the skull of the Pleurodira, and see how far we find these in *Meiolania*.

The principal characters in the skull in the living Pleurodira are:—

1. The quadrate is connected with the basisphenoid, sometimes with the basioccipital also (Podocnemididæ); in all the Cryptodira and the Trionychoidea the pterygoids extend between these elements.

2. The prefrontals are without descending processes joining the vomer (Cope).

3. The pterygoids are turned up at the anterior outer ends.

4. The front of the brain-case, between quadrate and petrosal (prootic), is not produced, but smooth. (The only exception among the Cryptodira, which all show this production, is found in *Dermochelys*.)

5. There is no free epipterygoid (columella).

6. The tympanic cavity is more or less surrounded by the extension of the quadrate.

7. The condyle of the lower jaw is more or less convex and fits into a concavity of the quadrate*.

If *Meiolania* belongs to the Pleurodira we ought to find the above characters.

1. The sutures between the pterygoids and the adjacent elements cannot be distinguished in *Meiolania*; a comparison, however, of the skull of *Meiolania* with the skulls of representatives of the different families of the Pleurodira proves that the pterygoids extend between the quadrate and basisphenoid. This view is also suggested by the position of the foramen pterygoideum.

In the Pleurodira this foramen is situated free on the base of the skull between the pterygoids and the basisphenoid; in *Meiolania* it is placed far back as in the Cryptodira.

2. *Meiolania* has very strong descending processes to join the well-developed vomer, a character of the Cryptodira.

3. The pterygoids in *Meiolania* are not turned up at the anterior end, as in all Pleurodira. Mr. Boulenger states that their outer palatal borders, instead of "being emarginate, form wing-like expansions."

The same character we find in the Trionyichidæ and very often in the Testudinidæ among the Cryptodira. The want of this emargination therefore is not unique for the Pleurodira.

4. The front of the brain-case, between quadrate and petrosal, is produced as in the Cryptodira.

5. In regard to the epipterygoid I cannot give a definite opinion, but I suppose that it was present.

6. There is a thin bony layer extending behind over the tympanic cavity; but this layer is not a part of the quadrate as in all the Pleurodira, but it represents only an extension of the dermal ossifications so highly developed in the skull of *Meiolania*. This dermal ossification reaches *behind* the quadrate, and just this condition proves its dermal origin; in no other Chelonian do we find a posterior process of the quadrate.

7. The condyle of the lower jaw is not visible, the latter being not separate from the skull. The articular face of the quadrate, however, is very distinctly shown in some of the remains. I cannot find any essential difference between this face and that in some of the Testudinidæ; besides, I do not give much value to this character, only well developed in the Podocnemididæ among the Pleurodira.

* The condyle is well developed in the Podocnemididæ and Sternotheridæ, but not distinct in the Chelydridæ.

We see there is not a single definite character in the skull of Meiolania which could prove its Pleurodiran nature.

The cervical vertebræ form another evidence for the systematic position of *Meiolania* among the Pleurodira, according to Mr. Boulenger.

Only the first two vertebræ being present in *Meiolania*, we may at first examine what are the principal characters of the first two cervical vertebræ in the Pleurodira.

1. The centrum of the first vertebra (the so-called odontoid process) is absolutely free from the second, with which it articulates freely.

2. It is the centrum which supports the neuroids of the atlas; the first intercentrum (hypapophysis) is very small, free or coossified with the atlas-centrum. The atlas therefore looks very much like the other cervical vertebræ, especially in the Sternotheridæ and Chelydridæ. The Podocnemididæ show the same character; but the atlas-centrum is not so elongate and the neuroids are not ossified as in the other Pleurodira. The first intercentrum is very small, free, and slightly connected with the neuroids; but there is never an "atlas-ring."

3. In all the Pleurodira well-developed diapophyses are present, in the second and all the following cervicals they are placed in the middle of the vertebræ.

4. In none of the Pleurodira does the diapophysis of the first vertebra form a foramen with the first intercentrum.

Now what do we find in *Meiolania*?

1. The centrum of the first vertebra is not absolutely free from the second, but more or less connected, as in the Cryptodira.

2. The first intercentrum is very large and supports the neuroids of the atlas, forming an atlas-ring, exactly as in the Cryptodira.

3. There is a very well-developed diapophysis on the second vertebra, not placed in the middle, but on the anterior part of the vertebra, exactly as in *Staurotypus* and especially in *Testudo polyphemus* and other Cryptodira.

4. The diapophysis of the neuroids of the atlas forms a foramen with the first intercentrum exactly as in *Staurotypus*, *Testudo polyphemus*, and other Cryptodira.

We see that the cervical vertebræ are not at all Pleurodiran, but truly Cryptodiran.

How Mr. Boulenger could compare the cervicals of *Meiolania* with those of *Chelys* I do not understand. There could not be a greater fundamental difference.

The so-called Pleurodiran characters of Mr. Boulenger do

not exist in *Meiolania*, and there can be no doubt whatever that *Meiolania* is a true *Cryptodiran* *.

The question now arises, to which group of the *Cryptodira* does *Meiolania* belong? Prof. Huxley says that it is "closely allied to the living *Chelydra*, *Gypochelys*, and *Platysternum*."

But the *Platysternidæ* have nothing in common with the *Chelydridæ*; they belong to quite a different group together with the *Testudinidæ* and *Emydidæ*. Therefore *Meiolania* cannot be genetically allied to both.

The only similarity between the *Platysternidæ* and *Chelydridæ* consists in the appearance of the skull and the opisthocœlian nature of a part of the caudal vertebræ. Both these similarities, however, are the result of parallelism only.

The opisthocœlian caudal vertebræ are of secondary nature.

All *Testudinata* have the second sacral vertebra convex behind. There is no exception whatever. Prof. Leidy †, it is true, states that "the posterior articular surface of the second [sacral] centrum is concave" in *Bæna*. But this is not correct: what Prof. Leidy describes as the posterior articular surface of the second is the anterior of the first sacral vertebra. The second sacral vertebra of *Bæna* is convex behind, as in all other *Testudinata*. Therefore the first caudal vertebra must be either concave-convex (procœlous) or biconcave, never convex-concave (opisthocœlous) or biconvex. In fact it is always procœlous, and so are the next following vertebræ. Now if opisthocœlian vertebræ are found in the caudals of some Chelonians, it can only be produced by the interference of an amphicœlian vertebra; and this is the case in *Chelydra*, *Macrochelys*, *Platysternum*, and must also be in *Bæna* and *Meiolania*.

In *Platysternum* (one specimen) the fourth caudal vertebra is biconcave, in *Chelydra* and *Macrochelys* the third or fourth. Prof. Huxley thinks that perhaps *Staurotypus* may also have opisthocœlian vertebræ; but this is not the case.

That the opisthocœlian caudal vertebræ of Chelonians are of secondary nature is also proved by palæontology. In *Toxochelys*, Cope, an indubitable Chelydroid ‡ from the Cretaceous, the caudal vertebræ are procœlous.

* Another support of this view is given by the caudal vertebræ; there are well-developed paradiapophyses in the caudals of the *Pleurodira*; in *Meiolania* we have well-developed caudal ribs (as in *Cryptodira*) coossified with the centrum.

† Leidy, Jos., 'Contributions to the Extinct Vertebrate Fauna of the Western Territories,' Washington, V., 1873, p. 108.

‡ I may notice here that *Anosteira*, Leidy, placed by Cope among the *Chelydridæ* and by Boulenger among the "*Pseudotrionychidæ*," belongs

Opisthocœlian vertebræ are present in those Chelonians which have long free tails.

There are Testudinata with nearly as many caudal vertebræ as *Chelydra* and the others, but in all these the tail is not free, but covered for the greater part by the carapace, and we never find opisthocœlian vertebræ.

Together with the opisthocœlian vertebræ we always find well-developed intercentra (chevron bones). They may be present in rudimentary condition in long tails without opisthocœlian vertebræ, as in *Emys europæa* and *Blandingii*, in *Chelymys victoriæ* at the posterior end of the tail, and in others. In *Toxochelys*, Cope, they are even well developed.

It was especially the caudal vertebræ of *Meiolania* which led Prof. Huxley to the conclusion of its affinity with the Chelydridæ; but I think that this character is not conclusive. I imagine that opisthocœlian caudal vertebræ could be developed in any group of the Chelonians. These characters are adaptive and cannot be used for the genetic relations of groups.

But how can we determine the systematic position of *Meiolania* among the Cryptodira?

That *Meiolania* is a terrestrial herbivorous Cryptodiran there is no doubt. The only true terrestrial herbivorous Cryptodira we know are the Testudinidæ; some more or less terrestrial forms we find also among the Emydidæ.

We know that the true Testudinidæ originated from Emydidæ. Why is not *Meiolania* also a true Testudinid? Or did it take its origin from one of the other families of the Cryptodira, the Chelydridæ, or Staurotypidæ, the Cinosternidæ, or another family?

I am inclined to consider Meiolania as a highly specialized branch of the true land-tortoises, the Testudinidæ, the true Testudinid characters of which are only obscured by the enormous development of dermal ossifications, especially on the skull, which gave to it quite an extraordinary appearance.

My reasons are the following:—

The lower face of the skull resembles most the Testudinidæ among the Cryptodira.

The long vomer has the strong characteristic keel. The situation and form of the foramina palatina are just as in this family, and so are the pterygoids.

either to the Staurotypidæ or to the Cinosternidæ. There are only ten peripheralia (marginal bones), and the dermal plates are not entirely absent.

It is only in the Testudinidæ among the Cryptodira that we find forms with pterygoids not emarginate in front. *Testudo tabulata* and some of the gigantic tortoises show it especially.

I cannot give much value to the apparent expansion at the posterior half of the pterygoids; it may be that it is produced by crushing of the edges, and even if it were natural, it would not be of great importance; the Trionychoidea show all stages of these expansions; in some we have no trace, in others they are very well developed.

The hyoid bones of *Meiolania* are of the same form as in the Testudinidæ.

The anterior nasal opening in *Meiolania platyceps* is divided by a process connecting the premaxillaries with the prefrontals.

In *Meiolania Oweni* this process is interrupted in the middle.

Indications of such processes showing a tendency to divide the anterior nasal openings we find *only* in the Testudinidæ. In most of these a sharp ascending process is developed from the premaxillaries, and also one descending from the anterior end of the prefrontals.

There may be an objection; the fissure for the stapes in the quadrate is open in *Meiolania*, closed in all the known Testudinidæ, so far as I am aware. An open fissure of course is the original condition. But if we have in one family—the Chelydridæ—both conditions, we cannot lay very much stress upon that. *Chelydra* and *Macrochelys* have the fissure closed, *Toxochelys* has it open.

Another objection may be that there is not a single form of the Testudinidæ with the temporal fossæ completely arched over and with the quadratojugal region so much developed as in *Meiolania*.

Of course there is none! But in *Meiolania* we have to distinguish between true ossifications of the skull and dermal ossifications!

I believe that the whole posterior half of the skull of Meiolania is modified by the enormous development and extension of dermal ossifications, in the same way as the skull of Phrynosoma.

In some of the Lacertilia we have only horny scales, without any ossifications; in *Phrynosoma*, however, we find ossified horn-cores not separable from the bones of the skull.

I think that the dermal ossifications in the skull of *Meiolania* have originated in the same way as I have indicated

for the same ossifications in the skin of the limbs in the Testudinidæ.

There were at first horny scales, which developed more and more; on some of these ossifications appeared which were entirely free from the bones of the skull. By the extension of these ossifications they were at first suturally connected with each other, forming a solid layer over the bones of the skull; the sutures disappeared and the dermal ossifications united with the bones of the skull, forming one continuous mass.

I think therefore that the peculiar appearance of the skull of *Meiolania* is no objection against its Testudinid nature.

The pelvis and especially the cervical vertebræ also compel me to consider *Meiolania* allied to the Testudinidæ.

The two cervical vertebræ preserved are essentially identical in form with those of *Testudo polyphemus*.

I at first thought that these parts were very much like the corresponding ones in *Staurotypus*, a fine skeleton of which I was able to examine through the kindness of Prof. von Krauss, of Stuttgart.

In *Staurotypus* the neuroids of the atlas and the second vertebra have very strong diapophyses, more developed than in any other Cryptodiran I know. There is likewise a foramen between the diapophysis and the first intercentrum of the atlas.

But in *Staurotypus* I find, just as in the Chelydridæ, a very strong lamellar process on the lower part of the second vertebra, which is entirely absent in *Meiolania*.

It is also absent in *Testudo polyphemus*.

Here we have, precisely as in *Meiolania*, a well-developed diapophysis on the neuroids of the atlas. The first intercentrum is very well developed, and there is the foramen between it and the diapophysis.

The posterior part of the atlas-centrum and that of the axis is deeply emarginate, as in *Meiolania**, and the second vertebra has a very well-developed diapophysis of the same form and the same position as in *Meiolania*.

More could be said, especially with regard to the geographical distribution of the Testudinidæ and the peculiar evolution of this family in some islands; but the consideration of these points would take me beyond the limits of this communication.

Further discoveries will prove whether the opinion on the

* These emarginations are formed by the union of the corresponding intercentra with the posterior part of the vertebræ.

systematic position of *Meiolania* brought forward here is true or not, and I hope that the decision may be given soon.

Nov. 11, 1888.

Note.—Since the above was written I have examined the caudal vertebræ of two specimens of *Clemmys insculpta*, Ler., one of the Emydidæ, with a pretty well-developed tail.

In one I found *opisthocælian vertebræ*, in the other true opisthocælian vertebræ were not present, but the tendency was there to form such vertebræ.

First specimen.—Caud. 1-7 concave-convex; caud. 8 biconcave; caud. 9 and the next following *convex-concave*.

Second specimen.—Caud. 1-7 concave-convex; caud. 8 concave-plane; caud. 9 biconcave; caud. 10 biconcave; caud. 11 plane-concave; caud. 12 biplane; caud. 13-15 concave-plane; caud. 16 biconcave, also the following.

Between the vertebræ well-developed cartilaginous intercentra are found, like those in *Sphenodon*, only between the 8th and about the 15th caudal they are ossified and represent chevrons.

The question of course is whether the Platysternidæ, characterized by the opisthocælian caudal vertebræ, can now be considered as a distinct family. *Platysternum* comes nearest to the ancestors of Emydidæ, which still had the inframarginals well developed. I think it best to consider it as belonging to a subfamily—the Platysterninæ.

BIBLIOGRAPHICAL NOTICE.

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ATTENTION was particularly called to the occurrence of marine forms of life in fresh waters by Dr. E. von Martens some thirty years ago, and since then the investigations of naturalists have demonstrated the presence of such types in nearly all parts of the world. Among the earliest researches were those upon the Swedish lakes, which revealed phenomena of great interest, especially in connexion with the geographical features of the region, and in Finland Malmgren and others noticed the presence in the fresh waters of species of *Mysis*, *Pallasea*, *Gammaracanthus*, and *Pontoporeia*. Little, however, was done with respect to the Entomostraca of Finland.