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ON THE SKELETON
OF
TOXOCHELYS LATIREMIS

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FREDERICK J. V. SKIFF,
Director.

ON THE SKELETON OF TOXOCHELYS LATIREMIS.

O. P. HAY. PH. D.

The genus *Toxochelys*, having as its type *T. latiremis*, was originally described by Professor E. D. Cope in the Proceedings of the Academy of Natural Sciences of Philadelphia for 1873, page 10. In the year 1875 the same author, in his Cretaceous Vertebrata, p. 98, pl. viii. figs. 1 and 2, vol. 11, U. S. Geol. Survey, further described the original species and (op. cit. p. 299) a new one under the name of *T. serrifer*. Of *T. latiremis* Professor Cope possessed only a portion of a lower jaw and the coracoid, which he figured, and some of the phalanges. Of *T. serrifer* the materials were somewhat ampler, consisting of some skull bones and two marginals; but none of these were figured. In the Proceedings of the American Philosophical Society for 1877, p. 176, Professor Cope gave descriptions of two skulls of *T. latiremis* which had by this time come into his hands. From these, Professor Cope came to the conclusion that the general form of the skull was much like that of some of the *Trionychidæ*, but that from this family *Toxochelys* was separated by the possession of marginal bones and the character of the extremities. Before this, however, in his description of *T. serrifer*, Professor Cope had regarded the genus as having relationships with the *Cheloniidæ* and the *Chelydridæ*. In his description of *T. latiremis* in the same work he had spoken of the phalanges as being flattened, as in *Protostega*. As will be observed during the discussion of the skeleton of this genus, I conclude that it is related to *Cheloniidæ* and *Chelydridæ*, and not at all to the *Trionychidæ*.

The materials in my hands consist of a single skull of *T. latiremis*, whose length from the snout to the occipital condyle is close to 115 mm. The distance from the alveolar border to the condyle of the quadrate is about 105 mm. The length of the lower jaw described and figured by Professor Cope was 157 mm; so that it must have belonged to a skull having a length from snout to condyle of about 170 mm.

The skull in my hands has been broken across the middle, and some parts of the roof of the mouth are missing; but nothing essential for our understanding of the structure. The damage to the upper por-

tion of the skull is more serious, since the frontals are wholly gone, as well as the postfrontals, the squamosals, the quadratojugals, and most of the parietals and of the jugals. A study of the parts remaining yields me the following results:

1. As already observed by Professor Cope, the choanæ are located far forward in the roof of the mouth, as they are in *Chelydra*; that is, immediately below the union of the prefrontals with the vomer. It will be seen from the figure on Plate xv that the descending processes of the prefrontals have been forced by pressure into the choanæ. In the *Cheloniidæ*, through the development of horizontal laminæ from the vomer, the maxillaries, and the palatines, the choanæ are thrown farther back in the roof of the mouth.

2. A vacuity, the palatine foramen, is present on each side of the roof of the mouth, lying in the point of meeting of the palatine, the maxillary and the pterygoid. This foramen is present in the *Chelydridæ* and most other turtles, but is absent in the *Cheloniidæ* and the *Dermochelyidæ*. Dr. G. Baur (*Zool. Anzeiger*, vol. 12, p. 45) states that this foramen is placed between the palatine and the maxillary and is present in all turtles except the two families last named. However, in many, possibly all, of the *Pleurodira* the foramen is located in the hinder border of the palatine, out of contact with the maxillary.

3. The cutting edge of the maxillary is very narrow, as we find it in *Chelydra*. In the *Cheloniidæ* and especially in *Chelonia* the alveolar wall is proportionally much deeper, as shown by the distance of its lower border from the roof of the mouth and from the lower rim of the orbit.

4. The width of the horizontal alveolar surface, in proportion to the width of the roof of the mouth, much more closely resembles that of *Chelydra* than it does that of any of the *Cheloniidæ*. The width of the effective crushing surface in *Toxochelys* is increased by the participation of the palatine. The outer edge of this bone extends from the outer anterior border of the palatine foramen to a point somewhat in front of the choana, nearly reaching the premaxillaries, an arrangement whereby the maxillary is excluded from the latter opening. Parallel with and close to the outer border of the palatine is a moderate, but distinct, roughened ridge, corresponding with which there was probably a rough triturating ridge on the horny beak. In *Chelydra* and *Macrochelys* the palato-maxillary suture passes directly between the choana and the palatine foramen; but mesiad of the suture there is a slight roughened ridge, as in *Toxochelys*. In the structure of these parts we have a combination of the characters found in both of the families referred to.

5. The structure and the connections of the anterior ends of the pterygoids are greatly like those of the *Chelydridæ*. The ectopterygoid processes are prominent, their postero-external angle directed backward, and their outer border broad for muscular attachment, just as in *Chelydra*.

6. The orbits are of moderate size, being intermediate between those of *Chelydra* and *Chelonia*. The plane of the rim has been directed, as in *Chelydra*, outward and upward. In this respect the orbits resemble those of *Chelydra*, but not those of *Macrochelys*. In this genus the orbits appear to have been given a perpendicular rim through the excessive narrowing of the snout, just as is also the case with *Eretmochelys*.

7. The external border of the pterygoid bone runs backward as a sharp keel terminating on the mesial side of the pedicel of the quadrate. In this arrangement *Toxochelys* resembles *Chelydra*, *Thalassochelys*, *Lepidochelys*, and *Eretmochelys*, but not *Chelonia*. In the last genus the external border of the palatal portion of the pterygoid ceases abruptly on the under side of that portion of the bone which lies between the quadrates, thus leaving a broad notch in the pterygoid.

8. That portion of each pterygoid which lies between the quadratic pedicels is furnished with a broad groove which terminates posteriorly behind the inner border of the pedicel. This groove does not appear to have had any considerable depth, but some allowance must be made for the effects of pressure. In *Chelydra* this region is flat and smooth; in *Chelonia* it is also nearly flat, while the border is notched.

9. Between the posterior ends of the pterygoidean grooves, on the basisphenoid and the basioccipital, is found an elevated triangular rough surface for the attachment of muscles. A similar surface is found here in all the *Cheloniidæ*, but not in the *Chelydridæ*.

10. In *Chelonia*, there is found below and behind each jugular foramen a strong process into which enter the basioccipital, the exoccipital, and the pterygoid. This process is wanting in the *Chelydridæ* and most other turtles, but is present in the *Cheloniidæ*. It was well developed in *Toxychelys*. In the *Chelydridæ* the exoccipital contribution to this process is well developed and its outer extremity extending across the jugular foramen joins the paroccipital, thus cutting off a portion of the jugular foramen as a special pneumogastric foramen. In *Toxochelys* the arrangement of the parts is as in *Chelonia*.

11. The tympanic cavity closely resembles that of *Chelonia*. It has, however, been extended downward further on the pedicel of the quadrate, since this is distinctly concave nearly to the articulate

surface for the lower jaw. Furthermore, there has been a deep notch in the upper and posterior part of the quadrate. This suggests that the tympanic cavity has been supplemented by a cavity in the squamosal. In *Chelonia* there is no such notch, but the quadrate is deeply scooped out in that direction. In *Chelydra* the squamosal is much enlarged backward and excavated to a thin shell of bone and forms a large bulla, into which the cavity in the quadrate freely opens. Most living turtles, outside of the *Dermochelyidæ* and *Cheloniidæ*, possess more or less developed squamosal bullæ. While that of *Toxochelys* was probably not greatly developed, there was a beginning of the structure.

12. The quadrate bears an open stapedial notch, as it does in the *Cheloniidæ* but not in the *Chelydridæ*.

13. The parietals are mostly wanting in my specimen. On the left side there is a portion of the bone which entered into the side wall of the brain-case. From the upper outer edge of this piece there jutted out the plate which helped to roof over the temporal fossa. How far backward this roof extended, and whether or not there was produced a parieto-squamosal arch, cannot be determined; but, at any rate, at the hinder end of the piece which remains, the horizontal plate is quite thick. Professor Cope (Proc. Amer. Phil. Soc. 1877, p. 176) states that the temporal fossæ, as shown in his skulls, were extensively roofed over. We are therefore justified in concluding that the arrangement was quite like that in the *Cheloniidæ*.

In front of the piece of the parietal referred to, there are seen on each side the lower ends of the descending processes of the parietals.

14. The frontals of my specimen are wholly missing. Professor Cope in describing *T. serrifer* (Cret. Vert., p. 300) indicates that they entered into the rim of the orbits. This is most probable, judging from the shortness of the prefrontals of my specimen. In the *Chelydridæ* the frontals are widely excluded from the orbital rims.

15. A portion of the jugal is still present, bounding the left orbit. It has been deeply excavated on the lower border, while the bone between this excavation and the rim of the orbit is very narrow.

16. From the above examination of the skull of *Toxochelys* it is seen that in general the anterior portion resembles more or less closely that of *Chelydra*, the posterior portion that of the *Cheloniidæ*. In the anterior portion the most important deviation from the Chelydrine pattern consists in the extension of the palatine around the outside of the choanæ. In the hinder portion there is no essential deviation from the Chelonian type, unless it shall prove to be in the

lack of a parieto-squamosal arch and in the occurrence of a well developed squamosal bulla, neither of which things is probable.

In its general form the skull of *Toxochelys* is more like that of the *Cheloniidae* than it is like that of the *Chelydridæ*. As to the hinder part, there is no question. Anteriorly the snout is broad and rounded, not acuminate, as it is in the *Chelydridæ*. The large orbits also remind us of the sea-turtles. The skull appears to have been rather depressed, as in *Thalassocheilus*; not high, as in *Chelonia*. The lower jaw figured by Professor Cope resembles that of *Chelydra*; but is not hooked, and has no decided cutting edge.

Professor Cope has figured the coracoid of his specimen. In form and proportions it closely resembles that of *Chelonia*. Its length was 250 mm. The coracoid of a specimen of *Chelonia*, whose shell is 1 metre long, is 300 mm. in length and the ramus of the lower jaw is 150 mm. Since the proportional lengths of the coracoids in *Chelydra* and *Chelonia* are about the same, the shell which belonged to Professor Cope's specimen was probably about 825 mm. long, and the head was somewhat larger than that of *Chelonia*.

Dr. Joseph Leidy, in his "Contributions to the Extinct Vertebrate Fauna of the Western Territories," page 269, plate 36, 1873, has described and figured some turtle bones. These he refers with some doubt to Professor Cope's genus *Cynocercus*. A comparison of Dr. Leidy's figures 20 and 21 with Professor Cope's figures of the coracoid of *Toxochelys* convinces me that they belong to the same animal. Beside the portions of the two coracoids, Dr. Leidy possessed a portion of the scapula, a complete femur, and the proximal end of the humerus. Notwithstanding that these bones are somewhat fragmentary and more or less flattened by pressure, we may learn something from a comparison of them with the corresponding bones of the *Chelydridæ* and the *Cheloniidæ*.

One character which as much as any other distinguishes the sea-turtles from other turtles is the great development of the anterior limbs. In most turtles the humerus has about the same length as the femur. This is true of the *Chelydridæ* and such habitual swimmers as the *Trionychidæ*. But in *Chelonia* the femur is only two-thirds the length of the humerus. Now, it is not wholly certain that the humerus and the femur in Dr. Leidy's hands belonged to the same skeleton, but he supposed that they did. If so, then the humerus of that animal must, on proper estimate, have been nearly as much longer than the femur as that bone is in *Chelonia*. This deduction, taken in connection with Professor Cope's statement that the phalanges are flattened, compels us to regard *Toxochelys* as a true sea-turtle, as does also the fact that it is found so abundantly in the Cretaceous deposits of Kansas.

Professor Cope has himself suspected that his genus *Cynocercus* is identical with *Toxochelys*. If this is true the latter name becomes a synonym of *Cynocercus*. This genus was founded on a metapodial bone and some caudal vertebræ. As Professor Cope has observed these vertebræ differ from those of the *Chelydridæ* in being procœlous. If the two genera referred to are identical, we have in these caudal vertebræ an additional evidence of the relationship of our fossil to the *Cheloniidæ*.

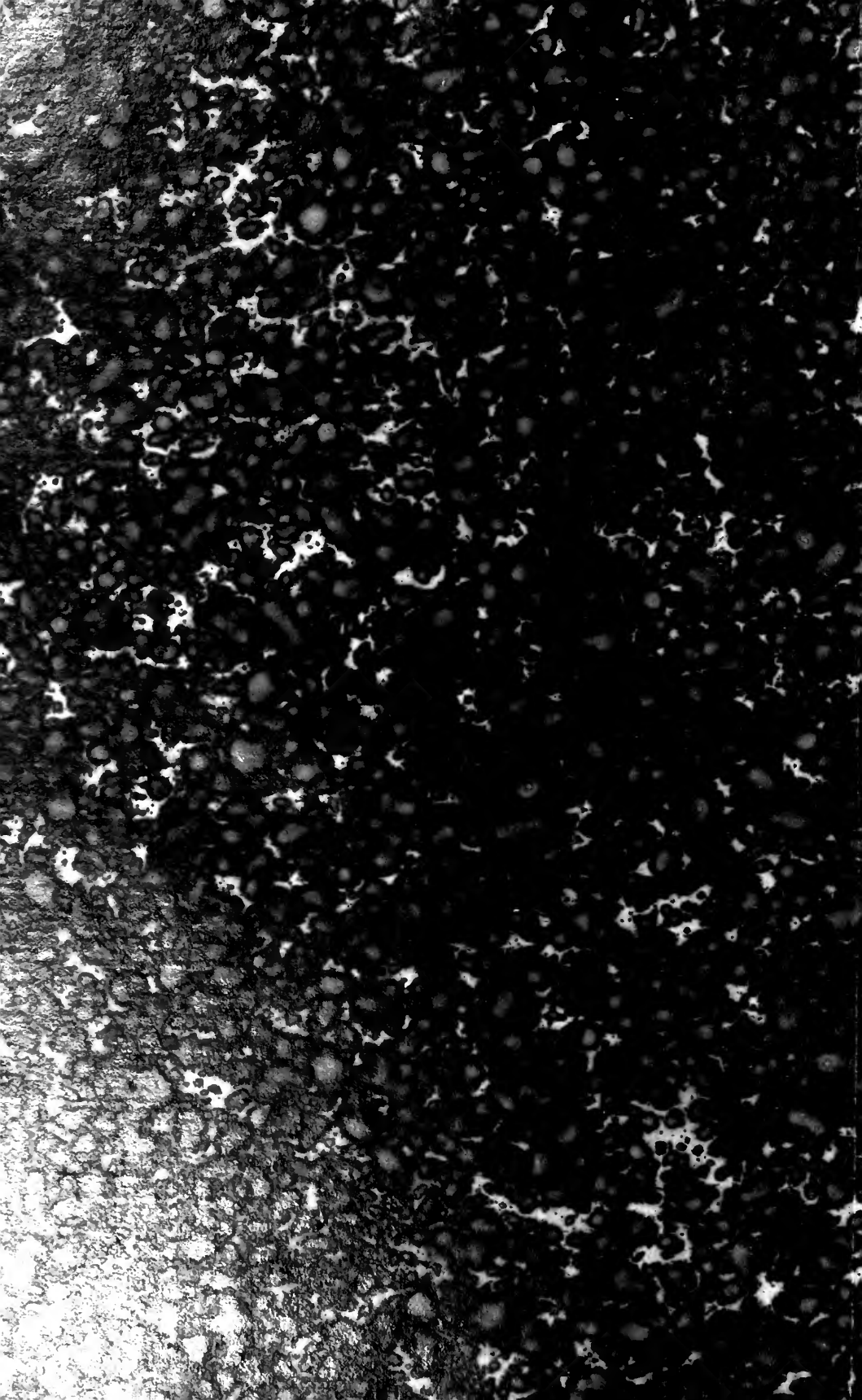
In short, I conclude that *Toxochelys* is related both to the *Chelydridæ* and the *Cheloniidæ*, but that the relationship is much closer to the last named family, and with the carnivorous division of this family, *Thalassochelys*, etc.

As to its systematic position, I agree with Dr. G. Baur's recent statement that it should form the type of a new family.

As to its phylogenetic relations, *Toxochelys* is probably an offshoot from the line which led to the *Cheloniidæ*, an offshoot after the latter family had disengaged itself from forms like the *Chelydridæ*. The skull of *Toxochelys* is too much modified in the direction of the sea-turtles ever to be transformed into that of the modern snappers; and the same remark will apply to the flattened phalanges, the probably greatly developed anterior limbs, and procœlous caudal vertebræ. While there appears to be no special reason why *Toxochelys* might not develop into a modern sea-turtle, we must remember that true *Cheloniidæ* had already made their appearance at the time when *Toxochelys* left its remains in the upper Cretaceous deposits of Kansas.









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