
Crossochelys, Eocene Horned Turtle from Patagonia

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Article V.—*CROSSOCHELYS*, EOCENE HORNED TURTLE FROM PATAGONIA¹

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In a preliminary note (Simpson, 1937) the name *Crossochelys corniger* was applied to a new horned turtle from the Casamayor Eocene of central Patagonia. In the present paper a detailed description of this peculiar and important reptile is given, with a discussion of its affinities and of those of the family Meiolaniidae to which it is referred. The only known specimen was collected in 1931 by Coleman S. Williams and me. It has been prepared by Albert Thomson and the drawings made by John C. Germann.

In the task of interpreting the intricate osteological details visible in this specimen, whole, sectioned, and disarticulated skulls of several recent genera (from the Department of Comparative Anatomy of this Museum) have been used as well as the extensive literature on the osteology of recent chelonians. The fairly complete bibliography by Nopcsa (1926, 1931) makes it unnecessary to list all the papers consulted, but the most important for the present purpose are cited: Siebenrock's basic work (1897) on recent Chelonia in general, Kesteven (1910) and Fuchs (1915) on the genus *Chelonia*, Nick (1912) on *Dermochelys*, and Shaner (1926) on *Chrysemys*. *Niolamia* and *Meiolania* were compared by a good series of casts and by the literature, especially Smith Woodward (1901) for *Niolamia* and Anderson (1925) for *Meiolania*. Many fossil skulls of other chelonian families were available in the American Museum, and of these the baënid material, mostly summarized by Hay (1908), was most useful. Other literature on fossil Chelonia is cited by Hay or by Nopcsa. Except for the meiolaniids, pleurosteronids, and baënid, most fossil forms in which the skull is known are so unlike *Crossochelys* as to have little bearing on the present subject.

¹ Publications of the Searrith Expeditions, No. 29. (This paper has been unavoidably delayed in the press and Pub. No. 30, Amer. Mus. Novitates No. 965, has already been issued.)

TAXONOMY

ORDER CHELONIA

SUBORDER AMPHICHELYDIA

Family **Meiolaniidae****CROSSOCHELYS**¹ SIMPSON, 1937

TYPE.—*Crossochelys corniger*.

DISTRIBUTION.—Casamayor Formation, Eocene, Chubut, Argentina.

DIAGNOSIS.—Meiolaniid turtles with superior nasal recess extending well onto frontal; no orbitosphenoid crest; temporal openings bounded by parietals, squamosals, and supraoccipital; cavum tympani shallow and simple, columellar notch not closed posteriorly; entocarotid canal between pterygoid, basioccipital, and basisphenoid, nowhere enclosed in pterygoid; pterygoid slender with sagittal suture only anterior to and below pterygoid slit, this slit less prominent than in *Niolamia* or *Meiolania* and with a pit on pterygoid immediately posterolateral to the slit, basisphenoid well exposed ventrally. Squamosal horns much shorter and relatively stouter than in *Niolamia* and frill relatively stouter and less expanded. Scute and boss pattern about as in *Niolamia*, not *Meiolania*, except for differences of proportion.

Crossochelys corniger² Simpson, 1937

TYPE.—Amer. Mus. No. 3161, disarticulated skull including most of the cranial elements as listed below.

HORIZON AND LOCALITY.—Casamayor Formation, in green bentonite with *Sebecus*, birds, etc., Cañadón Hondo near Paso Niemann south of the Río Chico del Chubut, southern Chubut Territory (central Patagonia), Argentina.

DIAGNOSIS.—Sole known species of the genus as diagnosed above.

DESCRIPTION OF CRANIUM

The cranial elements known include the frontal, parietal, exoccipital, and quadrate of the left side and the squamosal, quadrate, exoccipital, proötic, opisthotic, and pterygoid of the left side, as well as the median supraoccipital. The left quadrate is fragmentary, but the right quadrate is well preserved. Both exoccipitals are in fair preservation but the left, nearly perfect, is better. The sole preserved opisthotic is only a fragment of that bone and the squamosal is not quite complete. The other elements are excellently preserved. In every case, even for the less complete bones, there is no crushing and the surface details, foramina, etc. are readily visible in full detail.

No two of these bones were found together. The sutures are all open and the bones were scattered through several blocks of matrix.

¹ κροσσώω, fringe, χελυς, tortoise, in allusion to the neck frill or fringe.

² Corniger, horn-bearing.

Nevertheless they certainly belong to one individual, for on careful cleaning they all articulate with each other with no question. In the same matrix there were a premaxilla and several other chelonian bones not definitely placed. These may also belong to *Crossochelys*, but they do not articulate with the cranial parts. Other chelonians were present, as shown by small bits of carapace improbably of this genus, so that it cannot be assumed that these other elements are really of *Crossochelys* and they are omitted from the description. The face, palate, and arches are thus unknown, but in the cranial region, proper, only the postorbital, basioccipital, basisphenoid, and, if one existed, epipterygoid are unknown and even as regards these much information can be derived from their sutures with preserved elements.

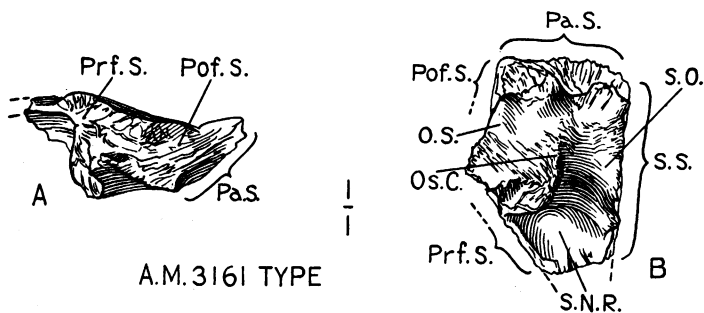


Fig. 1. *Crossochelys corniger* Simpson. Left frontal bone of type, Amer. Mus. No. 3161. A, lateral view. B, inferior view. Natural size.

O. S., orbital surface. Os. C., orbitosphenoid crest. Pa. S., parietal suture. Pof. S., postfrontal suture. Prf. S., prefrontal suture. S. N. R., superior nasal recess. S. O., olfactory sulcus. S. S., sagittal suture.

FRONTAL.—The frontal has a deep, strong sagittal suture and a still stronger, almost directly transverse parietal suture, overlapping the parietal dorsally. The lateral suture is complex. Presumably it is for the postorbital posteriorly and the prefrontal anteriorly but the boundary is not surely discernible. The great depth of this suture in its most lateral part as well as the nature of the dorsal scale pattern show that the frontal was widely excluded from the orbital rim. This is a variable feature in some recent chelonians but is so decisive in *Crossochelys* as probably to be constant. It is a common character in the Amphichelydia and occurs in various Cryptodira but in the Pleurodira the frontal normally reaches the rim of the orbit. On the lower surface, the sulcus olfactorius is wide but poorly delimited and only a small part

of the superior orbital surface is on this bone. The orbitosphenoid crest, between these two surfaces, is only faintly indicated and the orbit was widely open into the olfactory sulcus and thence into the nasal recess, a marked distinction from almost all forms to which *Crossochelys* might be related. Another peculiarity is that the posterior part of the superior nasal recess is roofed by the frontal and that the frontal forms the base of the lamina between this recess and the orbit, although the partition itself was evidently formed by the prefrontal, as is more normal.

PARIETAL.—Aside from the straight sagittal border, the edge of the parietal is separated by distinct points into five parts of unequal size. The smallest is posteromedian and overlaps the supraoccipital, for which there is the usual type of elevation and long fan-like suture on the ventral surface. Lateral to this is a larger, concave border with a free, somewhat feathered edge, not in contact with any other bone but forming the anterior border of a temporal opening. Lateral and anterior to this, extending to the most lateral part of the bone, is a sutural edge of nearly equal size and also concave in outline, for contact with the squamosal. Extending from the most lateral point almost in a straight line anteromedially is the long suture for the postorbital and between the anterior end of this and the mid-line is the straight frontal suture. On the lower side, the temporal surface is simple and gently concave. A complete, wall-like alisphenoid lamina extends from the elevated supraoccipital suture to the anterior end of the bone, where it ends abruptly, leaving no place for an orbitosphenoid crest. The lower edge of this lamina is not perfectly preserved, but from apparent traces of sutures it seems to have been remarkably shallow and poorly fitted to articulate with the pterygoid, so that an epipterygoid probably intervened, possibly one of unusual size.

SQUAMOSAL.—The squamosal is a very heavy, unusual bone, largely because of the presence on it of the horns and bosses described elsewhere. Posteromedially it has a nearly vertical, triangular suture for the supraoccipital. Along the medial side between this suture and that for the parietal there is a space with a rounded edge where a definite temporal opening, unique among Chelonia, occurs. The most external part of this opening, bordered by the squamosal, is pointed and notched as if for a blood-vessel. The most inferior and external part of the bone, where it was applied to the quadrate, is not adequately preserved.¹

¹ The lateral squamosal horn has on its anterior face a funnel-shaped pit, cut into the bone as if with a pick but full of undisturbed matrix as found. The most probable explanation is that it was made by a tooth of some other animal before burial. It shows no signs of suppuration or healing and was probably made at or after death.

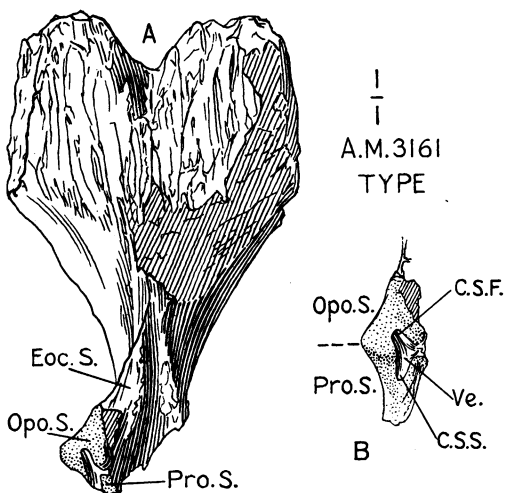


Fig. 2. *Crossochelys corniger* Simpson. Supraoccipital bone of type, Amer. Mus. No. 3161. A, inferior view. B, oblique inferior view of end of epiotic process. Natural size.

C. S. F., notch for frontal semicircular canal. C. S. S., notch for sagittal semicircular canal. Eoc. S., exoccipital suture. Opo. S., opisthotic synchondrosis. Pro. S., proötic synchondrosis. Ve., dorsal wall of vestibule.

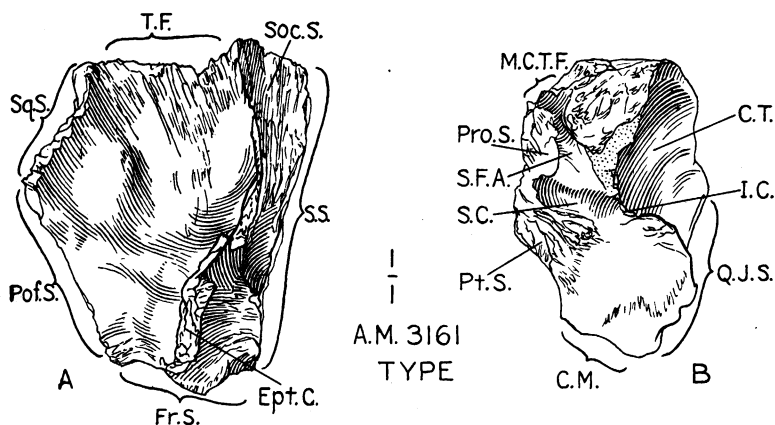


Fig. 3. *Crossochelys corniger* Simpson. A, left parietal bone, inferior view. B, right quadrate bone, posterior view. Type, Amer. Mus. No. 3161. Natural size.

C. M., condyle for mandible. C. T., tympanic cavity. Ept. C., epipterygoid crest. Fr. S., frontal suture. I. C., columellar incisure. M. C. T. F., margin of carotico-temporal foramen. Pof. S., postfrontal suture. Pro. S., proötic suture. Pt. S., pterygoid suture. Q. J. S., quadratojugal suture. S. C., sulcus cavernosus. S. F. A., sulcus for facial artery. Soc. S., supraoccipital suture. Sq. S., squamosal suture. S. S., sagittal suture. T. F., free edge against temporal fenestra.

SUPRAOCCIPITAL.—The supraoccipital is characterized by the enormous and, except for *Niolamia* and perhaps *Meiolania*, altogether unique development of its crest. Unlike the spine-like projection of other chelonians this is here a great, heavy, blunt, bifid process. Anteriorly there is a triangular surface for the parietals, but the greater part of the dorsal surface is exposed. The ventral surface of this part is very rugose and ridged anteroposteriorly as if it were a suture, which, however, is impossible. The exoccipitals almost met above the foramen magnum, but apparently the supraoccipital did reach the rim of the latter. The descending epiotic processes are developed normally, more or less as in *Chelonia*, and have the usual nearly flat, triangular surfaces for proëtic and opisthotic, meeting each other at an obtuse angle. The epiotic recess in these surfaces is single and has its simplest form, about as in *Emys* or *Testudo*, with the semicircular canals both entering merely the ends of a single groove and neither bridged to form a foramen.

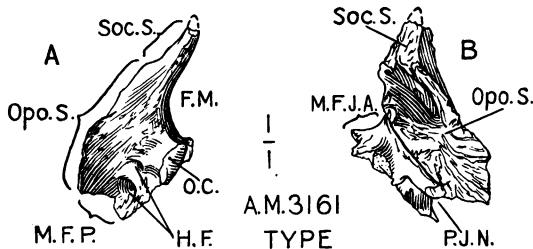


Fig. 4. *Crossoschelys corniger* Simpson. Left exoccipital bone of type, Amer. Mus. No. 3161. A, posterior view. B, anterolateral view. Natural size.

F. M., foramen magnum. H. F., hypoglossal foramina. M. F. J. A., margin of anterior jugular foramen. M. F. P., margin of postotic foramen. O. C., occipital condyle. Opo. S., opisthotic suture. P. J. N., posterior jugular notch. Soc. S., supraoccipital suture.

EXOCCIPITAL.—The exoccipital is rather like that of *Chelonia* but with some differences most of which are baënid-like. In most recent chelonians (excepting *Dermochelys* and perhaps one or two others) the basioccipital is excluded from the foramen magnum and the condyle is formed mostly by the exoccipitals. In *Crossoschelys* each exoccipital forms only a small part of the condyle and the basioccipital must have entered widely into the rim of the foramen magnum, an amphichelydian character. As in *Chelonia* and still more exactly as in the Baënidæ but unlike most cryptodires and all pleurodires, the posterior jugular opening

is not a foramen but is only a notch on the exoccipital rim of a large fenestra postotica. The notch is small and the lamina above it large and produced downward in *Crossochelys*, which evidently had a strong exoccipital-opisthotic-quadrate bridge as in *Niolamia* and *Meiolania* with the postotic fenestra opening almost entirely ventrally as in the former of those two genera. The opisthotic suture is otherwise about as in *Chelonia*, as is that for the supraoccipital. The surface for the basioccipital is also about as in *Chelonia*, sharing with that genus the peculiarity that the condylar part and a channel running forward from it have flat surfaces for synchondrosis while above and below the channel are elevated and rugged sutures. There are two hypoglossal canals, the more posterior with a double internal opening, at least on the left side (broken on the right side). Possible union of the exoccipital with the pterygoid is not clear; it was small if present.

QUADRATE.—In the common chelonian way, the quadrate has a large smooth, involute superior and superoposterior surface applied against the squamosal and a rugged anteroinferior suture for the quadratojugal, the external rim along these surfaces sharp and elevated and bounding a large tympanic cavity. In *Crossochelys*, unlike *Niolamia*, *Meiolania*, and the Pleurodira, this is open posteriorly and the columella left the cavity through an open and unusually shallow notch. The cavity extends downward and forward from this notch much more than in *Chelonia*. The posterosuperior part of the cavity is deepest, as always, but does not form a more or less separate cavity or extension, sometimes (but I think inappropriately) called an antrum mastoideum, a structure present in most chelonians, including the Baenidae, and peculiarly specialized in Pleurodira but absent in *Chelonia* as in *Crossochelys* and also *Meiolania* (doubtful in *Niolamia* but probably absent). On the posterointernal surface the columellar notch is seen to lead into a depression from which three grooves (closed to form canals by the articulation of adjacent bones) depart. The upper of these is for the facial artery (Nick; external carotid according to Siebenrock). Its canal, completed by a corresponding groove on the proötic, runs upward into the temporal fossa where it opens at the carotico-temporal foramen. A lower groove, not reaching the edge of the quadrate, ends at the junction of the proötic and pterygoid sutures and passes into the canalis cavernosus formed by those bones. Between these two grooves, here hardly distinguishable on the quadrate itself but plain on the proötic, is the columellar groove, leading to the fenestra vestibuli. The quadrate does not seem to have reached the sphenoidal fissure although

this may be due to slight breakage; in some baënid it barely reaches or does not reach this opening. The rim is slightly broken in the region of the epipterygoid process, but from the suture on the pterygoid a small process was probably present, unlike the *Pleurodira*. As in all chelonians, the quadrate is produced downward into a condyle for the mandible. The articular surface is transversely extended with the external part convex and the internal concave.

PROÏTIC.—In anteroexternal view the outline of the proötic is roughly quadrate and the smooth, saddle-shaped temporal surface is seen. At the posteroexternal corner of this is the carotico-temporal foramen, half formed by the proötic and half by the quadrate as already described. In most chelonians these two elements form in this region a strong, transverse pretemporal crest but in *Crossochelys* this is ab-

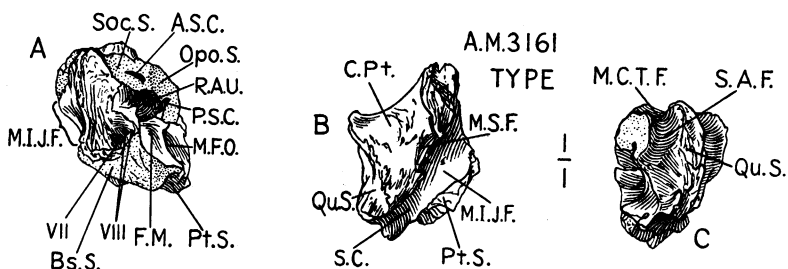


Fig. 5. *Crossochelys corniger* Simpson. Right proötic bone of type, Amer. Mus. No. 3161. A, posteromedial view. B, anterior view. C, posterolateral view. Natural size.

A. S. C., anterior semicircular canal. Bs. S., basisphenoid synchondrosis. C. Pt., region of the pretemporal crest. M. C. T. F., margin of carotico-temporal foramen. M. F. O., margin of fenestra ovalis. M. I. J. F., margin of internal jugular foramen. M. S. F., margin of sphenoidal foramen. Opo. S., opisthotic synchondrosis. P. S. C., posterior semicircular canal. Qu. S., quadrate suture. R. A. U., recess for utricle and ampullae of anterior and horizontal semicircular canals. S. A. F., sulcus for facial artery. S. C., sulcus cavernosus. Soc. S., supra-occipital synchondrosis. VII, inner end of canal for seventh nerve. VIII, inner ends of canals for branches of eighth nerve.

sent as such, as it is in baënid, *Chelonia*, and *Dermochelys*. On the anterosuperointernal projection is a suture for the parietal and along the lower surface sutures for the pterygoid. The gap between these two sutural areas near the anterointernal edge of the bone forms part of the edge of the sphenoidal foramen and of the foramen cavernosum (the two here in communication with each other). From the latter,

along the lower surface of the bone, runs a strong sulcus, the roof of the canalis cavernosus. The external face of the proötic is occupied for the most part by the quadrate suture, with the sulcus arteriae facialis. The endocranial face is bounded anteriorly by the smooth notch bordering the cavernous foramen. The face itself is marked by a peculiar, wrinkled pattern of small, sharp ridges, irregular but vertical in direction for the most part. At the posteroinferior corner of this face is a shallow pit, homologue of the internal auditory meatus although here hardly a meatus. At the anteroinferior edge of this is the relatively large foramen for the exit of the facial nerve (VII) from the brain cavity. Above and slightly posterior to this is a smaller foramen and posterior to the latter a still smaller, minute foramen, these two being for the auditory nerve (VIII). Below this face, seen on the disarticulated bone, is the surface for contact with the basisphenoid, a large smooth one for union by synchondrosis, directed inferomedially, a small, rough sutural area above the anterior part of this, and a small triangular area for synchondrosis posterior and at a slight angle to it. In the posterior, or slightly posteromedial, aspect of the proötic the principal feature is a large cavity lodging much of the inner and a small part of the middle ear. The more internal part of this is the fovea major, part of the vestibular wall. In its upper part is a deep pit, directed anteroexternally, which lodged the utriculus and the ampullae of the anterior and horizontal semicircular canals. The horizontal semicircular canal left this pit by an open notch in the superoexternal border, at the edge of the flat surface for synchondrosis with the opisthotic, not by a closed foramen as in *Pleurodira*. The anterior semicircular canal leaves the ampullar pit by a canal from near the bottom of the pit and is seen again as a foramen on the surface for the supraoccipital. This surface, at an open angle to that for the opisthotic, is triangular, flat in general but with both sides of the anterior acute angle bounded by elevated flanges of bone that clasped the anteroinferior angle of the supraoccipital between them. In the posterior wall of the ampullar recess, in the groove from the notch of the horizontal canal, is a small foramen, as noted by Nick in *Dermochelys*. The external part of the fovea vestibuli is open but is delimited by a semicircular rounded ridge, roughly in a vertical plane, external to which is a large groove leading outward and downward onto the posterior face of the quadrate when the bones are articulated. I take this groove to be for the columella and the ridge between it and the fovea to be the anterior rim of the fenestra vestibuli (ovalis), although it is unusual for

this to be so far from the outer edge of the proötic. In the inferolateral part of the columellar groove is a foramen that was probably the exit of the (principal branch of the) facial nerve, approximately homologous with the apertura tympanica canalis facialis of mammals. The inferior face of the proötic is occupied largely by a broad groove, roof of the canalis cavernosus, bounded anteroexternally by a suture with the pterygoid and anterointernally by the superoposterior rim of the sphenoidal foramen, as already mentioned. Posterior or posterointernal to the sulcus cavernosus is a large and complex suture for the pterygoid, its anterointernal part a more or less vertical surface facing the sulcus and its larger posterointernal part an inverted V in section, clasping an ascending process of the pterygoid. At the apex of the inverted V is a

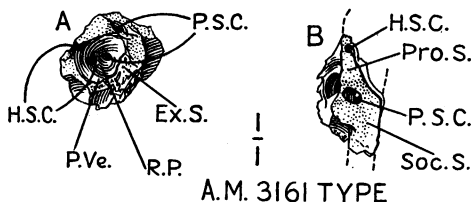


Fig. 6. *Crossochelys corniger* Simpson. Incomplete right opisthotic bone of type, Amer. Mus. No. 3161. A, anteromedial view. B, superior view. Natural size.

Ex. S., exoccipital suture. H. S. C., horizontal semicircular canal. Pro. S., proötic synchondrosis. P. S. C., posterior semicircular canal. P. Ve., posterior wall of vestibule. R. P., recess for ampulla of posterior semicircular canal. Soc. S., supraoccipital synchondrosis.

small foramen from which a groove, closed to a canal by the pterygoid, runs almost straight ventrally reaching the entocarotid canal beyond the proötic as will be seen later. This is evidently for the ramus palatinus of the nervus facialis (or the nervus vidiani), which thus does not appear in the sulcus cavernosus, an arrangement consistent with primitive cryptodiran or, presumably, amphichelydian affinities but distinctive from the Pleurodira.

OPISTHOTIC.—The available opisthotic is incomplete, probably about half missing, but it preserves the most important features of this bone. Its anterointernal face shows the posterior wall of the vestibule, with a deep fossa for the ampulla of the posterior semicircular canal, into which fossa the horizontal semicircular canal also opens. Unlike *Testudo* and similar forms, both these canals have closed foramina on the upper su-

tural surfaces of the opisthotic. These surfaces, at an open angle to each other, are for synchondrosis with the proötic and supraoccipital. As far as preserved they fit the corresponding surfaces of the latter bones closely and suggest that little cartilage was intercalated between these bones. Posterior to the ampullar fossa, part of the large exoccipital suture is preserved but the strong process that formed part of the bridge from exoccipital to quadrate (behind the fenestra postotica) is mostly broken off. Below the ampullar fossa part of the vestibular wall is preserved and here there is a small foramen in a position sometimes occupied by the opening of the glossopharyngeal canal but here (as may be seen on a broken surface) leading to a canal running upward posterior to the ampullar fossa and hence very unlikely to be for the glossopharyngeal nerve (IX). The borders of the fenestra cochleae and f. vestibuli are not preserved nor is the true foramen for IX. From adjacent elements and analogy with the most similar other genera, the latter almost surely had the relationships seen in the *Amphichelydia*, some *cryptodires*, and *Meiolania*, quite unlike the *pleurodire* condition.

PTERYGOID.—The pterygoid appears to be the most characteristic single bone in the *Chelonia* and in most cases it is possible on this bone alone not only to diagnose a genus but also to determine its affinities accurately, as is shown by the correlation of its structures with all the others on a balance of which taxonomy depends. In *Crossochelys*, also, the pterygoid has unique (generic) characters and others shared with various other groups with which a consensus of all known characters shows the genus to be related. In inferior, palatal, aspect the pterygoid generally and about equally resembles those of *Chelonia*, *Dermochelys*, and the *Baënidæ*. The margin of the infraorbital fenestra has no marked differences from those forms. The posterior margin differs from *Chelonia*, less from *Dermochelys*, and least from the *Baënidæ* in the presence of an unperforated, smoothly rounded margin, part of the posterior or inferior rim of the fenestra postotica, here still more expanded than in the *Baënidæ*. This is correlated with the great development of the quadrate process which is much better developed in *Crossochelys* than in *Chelonia*, more comparable to the *Baënidæ* but even longer and extending still farther posteriorly than in that family. The pterygoid here very widely separates the basicranial elements from the quadrate, showing an extreme of a tendency exactly opposite to that of the *pleurodires*, of which such a connection is highly typical. Although the basioccipital and basisphenoid are not preserved, it is clear that they must both have been well exposed ventrally, as in the *baënid*s,

the opposite pterygoids being widely separated posteriorly with only a relatively short and anterior sagittal suture. At about the middle of the length of the pterygoid, near its medial margin where this must have abutted against the basisphenoid, is a prominent, irregular pit, not a foramen but with two small slit-like foramina on its medial wall and a large notch (foramen with the participation of the basisphenoid) at its posteromedial edge. Anterior to this pit, the pterygoid extends an-

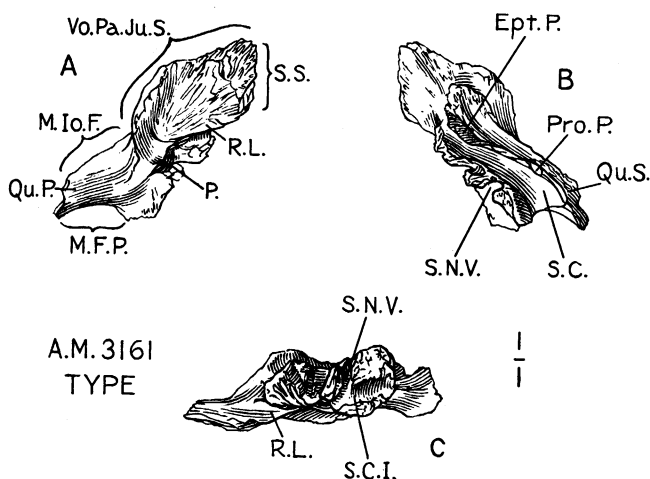


Fig. 7. *Crossoschelys corniger* Simpson. Right pterygoid of type, Amer. Mus. No. 3161. A, inferior view. B, superior view. C, posteromedial view. Natural size.

Ept. P., epipterygoid process. M. F. P., margin of postotic fenestra. M. Io. F., margin of infraorbital fenestra. P., pit in pterygoid. Pro. P., proötic process. Qu. P., quadrate process. Qu. S., quadrate suture. R. L., reflected lamina flooring a choanae-like slit. S. C., sulcus cavernosus. S. C. I., sulcus caroticus internus. S. N. V., sulcus nervi vidiani (ramus facialis). S. S., sagittal suture. Vo. Pa. Ju. S., sutures for vomer, palatine, and jugal, not clearly separable.

teromedially to the sagittal suture as a thin lamina with a narrow slit roofed by this lamina and floored laterally by the body of the pterygoid and medially by the basisphenoid. Although considerably less developed than in those genera, this is evidently the pterygoid slit so characteristic of *Meiolania* and *Niolania* and not present as such in other chelonians. This general region in *Crossoschelys* is decidedly more specialized than and is aberrant with respect to the Baënidæ (or Amphichelydia generally) but the latter do suggest a more primitive stage from which *Crossoschelys*

might have evolved. At about the position of the pit in the *Crossochelys* pterygoid, the baënid has a pit¹ between pterygoid and basisphenoid from which a canal runs posteriorly between these two bones, another, very small, upward into the pterygoid, and a much larger canal anteriorly between pterygoid and basisphenoid. The further separation and expansion of these features could readily give exactly the condition found in *Crossochelys*, which in turn could give rise to the peculiarities of *Nirolamia* and *Meiolania*, despite the fact that the latter are here so different from the baënid that a possible derivation is suggested only by *Crossochelys* as a middle term. The anterior and anterolateral edges of the pterygoid have sutural edges presumably for palatine and jugal, but these connections cannot be positively delimited. There is no distinct ectopterygoid process, one of a few characters in which *Crossochelys* is more like *Chelonia* and, in this case, especially *Dermochelys* than like the Amphichelydia. There is no trace of the peculiar and very typical upturned postorbital process of the Pleurodira.

The median surface of the body of the pterygoid is occupied by a suture divided into three unequal parts by two grooves. The largest of these grooves is longitudinal and runs from the posterior edge to the rim of the ventral pit described above. At this rim it narrows, and probably a branch from it passed into the basisphenoid just before reaching this point. This groove is surely the sulcus caroticus internus and was closed by the basioccipital and probably anteriorly in part by the basisphenoid to form the internal carotid canal, a peculiar arrangement but probably as in some baënid, since in the latter the opening of this canal on the occiput is sometimes on the basioccipital-ptyergoid suture as in *Crossochelys*. The other groove is smaller, shorter, and runs vertically downward into the carotid groove reaching the latter near and posterior to its opening into the ventral pit. This groove is for the palatine ramus of the facial nerve, running from the proötic as mentioned in describing that bone. The upper parts of the two large articular surfaces anterior and posterior to this groove were overlapped by the proötic while the lower parts, the whole anterior end of the anterior surface, and the smaller surface below the carotid groove must have been in contact with the basisphenoid anteriorly and the basioccipital posteriorly; the division point between these is not known.

The upper surface of the pterygoid is marked by the large, long,

¹ Noticed by Hay (1900) as a presumably vascular foramen. I have not had sufficient good baënid material to warrant sectioning or dissection so that the internal connections remain uncertain, but by external preparation of a specimen of *Chisternon* the structure given in this text was determined.

simple sulcus cavernosus bounded by prominent ridges on each side. The relations of these parts have been sufficiently suggested in describing adjacent bones. There are several small foramina that I have not definitely identified. One is seen on the upper surface just external to the anterior end of the epipterygoid crest. Another is anterior to this on the suborbital surface and from its direction it may communicate with one in the lateral side of the pterygoid slit. Many chelonians have such small vascular or nervous foramina, usually individually variable,

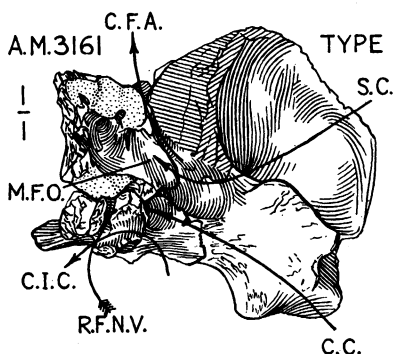


Fig. 8. *Crossochelys corniger* Simpson. Right proötic, pterygoid, and quadrate of type, Amer. Mus. No. 3161, in articulation with surrounding bones removed. Approximately posterior view. Natural size.

C. C., arrow leading into cavernous canal. C. F. A., arrow through facial artery canal. C. I. C., arrow through internal carotid canal (here a groove). M. F. O., anterior margin of fenestra ovalis. R. F. N. V., arrow leading into canal for facial ramus of vidian nerve. S. C., sulcus for columella.

but I have not found one sufficiently close to *Crossochelys* to identify these with certainty. Their significance is doubtful and perhaps slight.

POSTOTIC FENESTRA.—From a description of the separate bones it is difficult to visualize all the relations of the various foramina in and near the postotic fenestra. These are usually characteristic and important so they are here summarized as far as known. On the exoccipital lateral to the condyle is a hypoglossal foramen and posterolateral to this another. More or less ventral to this, perhaps also lateral to it, at the occipital junction of pterygoid and basioccipital and near or at the lower end of the exoccipital is the posterior end of the entocarotid canal. The fenestra postotica itself was a large opening with the exoccipital forming its medial, mediodorsal, and medioventral rim. The rest of the dorsal rim was probably formed by the opisthotic, here

broken, while the rest of the ventral rim is formed by the pterygoid and the external rim, broken by the columellar notch, by the quadrate. The most ventral part of the fenestra is occupied by the large posterior end of the canalis cavernosus above which is the fenestra vestibuli, of about equal size. Slightly above and external to the latter is the tympanic end of the canal for the facial artery (carotico-temporal canal). The most medial part of the fenestra postotica was occupied by the jugular notch and between this and the fenestra vestibuli must have been the glossopharyngeal foramen, although this is not preserved. This general arrangement is not essentially unlike the Baënidæ, *Dermochelys*, *Chelonia*, or *Meiolania*. It is essentially unlike most other chelonians.

TEMPORAL REGION AND FRILL

Crossochelys is the only known chelonian in which an enclosed temporal fenestra occurs and, together with *Niolamia*, it adds an unexpected and peculiar chapter to the history of this region in the Chelonia.

From the work of many students, well summarized and significantly supplemented by Versluys (1919) and by Zdansky (1924) the general history of the chelonian temporal region is known with great probability. Primitively the skull roof was complete as in the Cotylosauria, a primary condition seen in *Triassochelys*. In most chelonians this roof is reduced and it is sometimes entirely lost. This reduction is by emargination and not, as in most other reptiles, by the appearance and enlargement of true temporal openings originally surrounded by bone. The chelonian emarginations are in two regions, on the upper surface at the posterior edge and on the lateral surface at the lower edge (between orbit and ear). Extreme development of the upper notch eliminates the temporal roof, generally leaving a lower arch of bone, jugal-quadratojugal, in the position of the infratemporal arch of diapsidan reptiles, as seen in *Trionyx*. The extreme development of the lower notch also results in loss of the temporal roof and may leave an arch, parietal-squamosal, in the position of the posttemporal arch of diapsidans, as seen in *Rhinemys*. Sometimes both notches develop and the arch occupies a more or less intermediate position, cf. *Emys*, *Testudo*, although in these cases it usually seems homologous with the lower arch, the dorsal squamoso-parietal contact being lost with any marked development of the posterosuperior notch. The arch may be lost altogether (e.g., *Chelodina*, in which the lower notch has reached the posterior edge, or *Terrapene*, in which the two notches have met and coalesced). While the reptiles with true temporal perforations have a

posttemporal arch and one or two lateral arches, the *Chelonia* never have two or three arches (except *Crossochelys*) but only one or, in specialized extreme forms, none.¹

The function of the temporal roofing is evidently that of armor; it protects the cranium as the carapace does the trunk. The reduction of this roofing is correlated in a general way with the power to withdraw the head into the carapace, so that the latter takes over the protective function. If this type of protection is reduced or lost, as by the reduction of retractility of neck and head, the temporal roof tends to expand secondarily and may even become complete, as it was originally, but with some evidence that this is not the primitive condition retained. All marine turtles have well-developed temporal roofs and this seems to be not directly an aquatic adaptation but rather concomitant with lesser retractility conditioned by this habitus. Varying degrees of this secondary roofing are seen in forms like *Chelonia* or numerous Mesozoic marine turtles such as *Archelon*. Even in such a form as *Podocnemis* the carapace fails to protect the cranium completely and there is probably some secondary expansion of the temporal roof.

The meiolaniids are of exceptional interest in the light of these general tendencies in chelonian evolution. They have in *Niolamia* and to less degree in the other two known genera the most complete temporal protection known in this order, even exceeding the primitive condition of *Triassochelys*. The roof is complete (except *Crossochelys* and this is an apparent but not essential exception as will appear), its protection is supplemented by heavy bosses and horns, and especially in *Niolamia* this armor is even extended as a frill protecting the neck. This extreme development is in itself sufficient evidence that the head could not be drawn back into the shell and that it had to carry its own protection. The full retraction of these expanded, horned heads is almost inconceivable in any case and in *Meiolania*, in which alone the neck is known, the neck was short and certainly did not permit retraction of the head into the carapace. *Crossochelys* shows the unique process by which the temporal armor has arisen in this group.

The temporal fenestra of *Crossochelys* has the superficial aspect of the normal supratemporal opening of other reptiles (except Anapsida),

¹ It has, indeed, been suggested by Broom and others that the *Chelonia* did originally have a true temporal perforation lost by the disappearance of one of the arches or by secondary covering of the opening by the surrounding bones. The evidence for this view is indirect and the direct evidence favors the more orthodox theory summed up above. As will appear, *Crossochelys* does not suggest the presence of a temporal opening in the chelonian ancestry in spite of the fact that it has such an opening itself. Its immediate ancestry almost surely had but one broad arch and the question as to the possible presence of two in a still more remote and at present hypothetical ancestry does not arise in this connection.

that is, of the single parapsidan opening or the upper of the two diapsidan openings, but this is certainly not a homology. The posttemporal bar in *Crossochelys* is not, as in other reptiles, formed by dorsal elements, usually parietal, squamosal, or both, but by the supraoccipital and the squamosal. Evidently it has arisen from a form with a superoposterior notch and supraoccipital produced into a dorsoposterior spine, a normal and widespread chelonian condition, by the lateral expansion of the posterior part of the supraoccipital and the medial expansion of the posterior part of the squamosal. These processes have met, cutting off

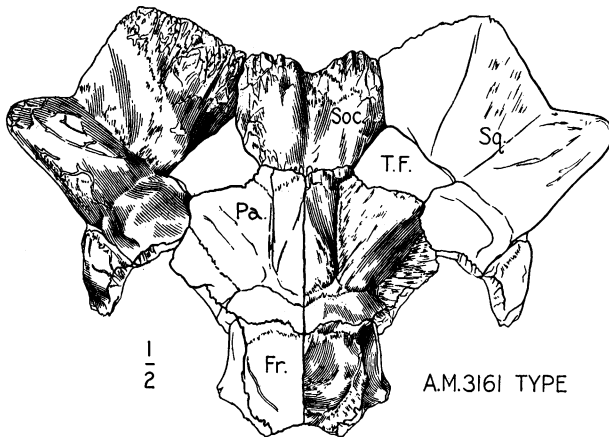


Fig. 9. *Crossochelys corniger* Simpson. Dorsal view of posterior part of skull of type, Amer. Mus. No. 3161. The fully shaded bones are preserved and the others are mirror images of these. One-half natural size.

Fr., frontal. Pa., parietal. Soc., supraoccipital. Sq., squamosal. T. F., temporal fenestra.

the anterior part of the notch and leaving it as an enclosed fenestra which thus is not a perforation in origin and has nothing to do with the normal reptilian supratemporal opening. In *Niolamia* further expansion of the surrounding elements has closed the fenestra and produced a secondarily complete roof.¹ There is some probability that the ancestry of *Meiolania* went through the same history, but this is uncertain and will remain so until it is known what elements form the frill in that genus or whether it is really a descendant or close relative of *Niolamia*.

¹ As elsewhere noted, it is possible that the opening is a juvenile character in *Crossochelys* and that the adult had a complete roof, but even in this case the evidence as to the historical origin of this roof is valid.

The analogy between the horned, frilled meiolaniid turtles and the horned, frilled ceratopsian dinosaurs is interesting. The horns and frills are not formed by the same bones in the two groups and in any case would hardly be supposed homologous, but they arise in a similar way and must have had similar functions. The only important functional difference seems to be that the principal horns of ceratopsians are essentially offensive weapons and are far better adapted for this purpose than are the horns of meiolaniids, which are more analogous to the spikes on the frill of *Styracosaurus* or on the jugals of *Pentaceratops* than to the brow and nose-horns of *Triceratops* and others. In most ceratopsians, including all the more primitive forms, the frill surrounds an opening on each side that is not one of the normal reptilian temporal perforations, in full analogy with *Crossochelys*. In such a form as *Protoceratops* it is still more obvious than in *Crossochelys* that this opening is secondary, for this ceratopsian clearly has the full complement of archæosaur openings, infratemporal, supratemporal, and posttemporal, in addition to the opening in the frill. In the later *Triceratops* the frill opening has secondarily closed, just as, I believe, the frill opening seen in *Crossochelys* has secondarily closed in *Niolamia*.¹

HORNS AND SCALE AREAS

Since the skull of *Crossochelys* is not completely known, its cranial scale system may be studied by comparison with *Niolamia*. In the latter, there are large, definitely horn-like posterolateral processes, pointing outward, upward, and backward. These are triangular, but are compressed and flattened on the dorsal, or strictly dorso-latero-anterior, faces. The homologues of these in *Niolamia* are obvious but are much shorter, not compressed, all faces gently convex and a section almost an equilateral triangle. They are wholly on the squamosal. Between these in *Niolamia* is a great posterior frill, well analogous to that of ceratopsians, extending backward and upward, divided by a median notch into two broad, flat, thin plates or horns. Each of these has a lesser notch in the rim so that it is double but with the lateral part much larger than the medial. In *Crossochelys* this frill is considerably less expanded and is less flattened and compressed, being much thicker dorsoventrally. The open sutures in our specimen show that these projections are really compound. The major, more lateral parts are on the squamosals but the lesser, more median lobe of each pro-

¹ The analogy of the ceratopsians and other considerations show that the possibility that *Niolamia* is the older genus and the possibility that the opening in *Crossochelys* is juvenile do not seriously oppose this interpretation of the history of the frill.

jection is formed by the supraoccipital. The vaguely double nature of each lobe in *Niolamia*, although so inconspicuous that it has been thought of no importance, leaves little doubt that it is composed of the same elements as in *Crossochelys*. This general area extends slightly onto the parietals near the mid-line in *Crossochelys*, but the whole frill is practically formed by squamosals and supraoccipital.

Anterior to each of the main posterolateral horns in *Niolamia* is a much smaller lateral horn, posterior to the upper rim of the orbit. This is apparently represented in *Crossochelys* by a more dorsal, less projecting and not horn-like boss the posterolateral part of which is on the squamosal with a smaller anteromedian part on the parietal and an anterolateral part, missing on our specimen, probably on the postorbital. Below this, between the lower part of the orbit and the quadrate opening, *Niolamia* has another, smaller and less projecting paired boss or small horn. In *Crossochelys* this is also well developed, the posterior half on the squamosal and the anterior half, missing on the specimen, probably on the postorbital, quadratojugal, or both.

On the dorsal surface in *Niolamia*, on the posterolateral parts of the cranial roof proper and medial to the bases of the principal horns, there is a pair of large, strongly convex bosses. This is evidently homologous with the main parietal scale area of *Crossochelys*, although the latter is relatively smaller, has a different form and is separated from the horn base. These differences would be reduced if the parietal in *Crossochelys* grew out over the temporal opening and perhaps overlapped the squamosal.

Between these bosses in *Niolamia* is a large median area, delimited by grooves as are the other areas and with a raised rim but with the center depressed. A similar but relatively much smaller area occurs on the parietals in *Crossochelys*. Anterior to this, anteromedian to the largest dorsal bosses, is a pair of smaller, transversely elongate bosses. Their obvious homologues, closely similar in all respects, occur in *Crossochelys* at the anterior ends of the parietals, overlapping slightly onto the frontals. Between and anterior to these in *Niolamia* is a single, median boss similar to one of these paired bosses in size and shape. This unpaired area also occurs in *Crossochelys* but is there relatively larger, less transverse, and with the posterior half or two thirds flattened or even concave. This is wholly on the frontals.

Niolamia also has an elongated boss along and above each dorsal orbital rim. This is not preserved as a whole in our specimen of *Crossochelys* but its most medial part laps onto the frontal and is seen on this

specimen. The anterior end of the dorsal surface in *Niolamia*, on the prefrontals (and the nasals if the latter occurred), is relatively smooth and not distinctly boss-like. This region is not known in *Crossochelys*.

Thus every known scute and horn in *Crossochelys* can be homologized with *Niolamia* and despite many differences of proportion or details the structure in this respect is basically the same in the two genera. Al-

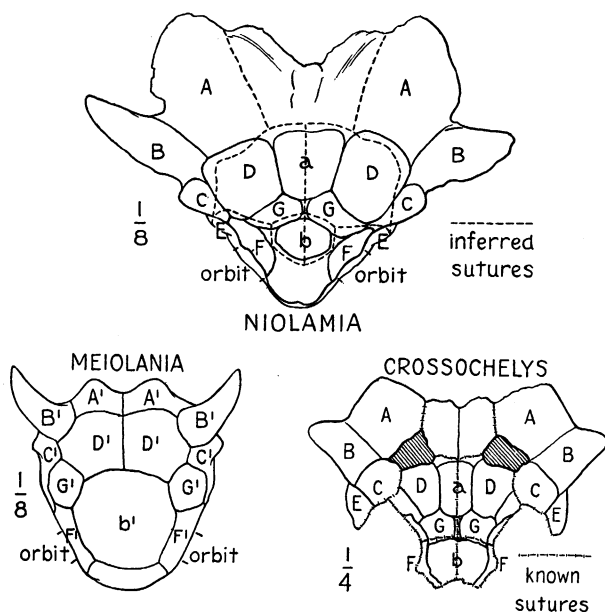


Fig. 10. Comparison of dorsal surfaces of skulls of the three genera of Meiolaniidae. *Niolamia*, one-eighth natural size, drawn from cast of skull in the La Plata Museum. *Meiolania*, one-eighth natural size, from casts of partial skulls and restoration by Anderson. *Crossochelys*, one-fourth natural size, from data in this paper. The lettering on the skulls of *Niolamia* and *Crossochelys* shows the evident homologies of the bosses or scale areas in these two genera. *Meiolania* cannot be surely homologized with these two and the lettering given shows one of several possibilities. The skull of *Crossochelys* is incomplete and not restored anteriorly.

though superficial, these characters are so complex and so peculiar that this correspondence alone testifies to rather close relationship.

Crossochelys shows that these bosses and horns are not separate dermal elements fused with the skull bones, as has sometimes been assumed for *Niolamia* and *Meiolania*, but are outgrowths of the normal cranial elements. Although the usual sutures are all widely open in our

specimen, there is no trace of any suture between a boss and the underlying bone and the continuity of texture and fine bony structure is such that origin by fusion is practically out of the question.

Comparison of the skull roof in *Crossochelys* and *Niolamia* with that of *Meiolania* shows less agreement than would be assumed from the common placing of *Niolamia* in the synonymy of *Meiolania*. A frill is hardly developed in the latter. The crest seen in the occipital view of *Niolamia*, beyond which the frill projects, is posterior in *Meiolania* and the projection is only in the form of two small bosses, even smaller than in *Crossochelys*. These have no clear sign of double origin in *Meiolania*. They may be wholly on the supraoccipital or on the squamosals—in any case, it is probable that the structure here is not exactly homologous with that of *Crossochelys*. The posterolateral horn cores are of characteristic shape in each genus, but occupy about the same position in all and appear to be either homologous or “homoplastic.” There is also in *Meiolania* a small boss anterior to each of these, analogous or homologous with that of *Crossochelys* and *Niolamia* but relatively smaller than in the latter. There is also a very vague convexity in *Meiolania* that may represent the boss between eye and ear in *Crossochelys* and *Niolamia*, but as far as I have seen on casts or in the literature this is too indefinite in *Meiolania* to have any clear significance. The dorsal pattern in *Meiolania* is unlike the two South American genera, as shown in the diagram (Fig. 10). It might possibly be derived from the latter with homologies more or less as suggested in the diagram, but the fact remains that it is distinctive and could be of independent origin. A minor but also distinctive feature is that in *Meiolania* the scale areas are bounded by ridges, in *Crossochelys* and *Niolamia* by grooves.

NIOLAMIA, MEIOLANIA, AND CROSSOCHELYS

Ameghino (1899, p. 10) stated that the family Meiolaniidae is represented in Patagonia “por *Niolamia argentina* n. gen. n. sp. de la que se acaban de encontrar trozos de escudos óseos dérmicos, casi planos, que indican una coraza muy deprimida, de superficie externa lisa pero con surcos divisorios de los escudos córneos epidérmicos. Los trozos de cráneo que acompañan estos restos indican claramente un género muy cercano de *Miolania* Ow., con las mismas protuberancias óseas periféricas de las que se puede determinar la existencia del par posterior o parietal, del par mediano que divergen lateralmente en forma de grandes cuernos y probablemente existía también el par anterior. Talla gigantesca, comparable a la de *Miolania Oweni* Smith-Wd. del cuaternario de

Australia (Queensland). Formación guaranítica del Sehuen y del Chubut."

Smith Woodward (1901) described a complete skull and some other parts found by Roth in Patagonia. He assumed that this was the same as Ameghino's *Niolamia argentina*, but considered it to belong in *Meiolania*,¹ thus making *Niolamia* a synonym of that genus. Ameghino accepted both of Smith Woodward's equations, for he subsequently (1906, Figs. 14–15) reproduced the figures of this skull as "*Miolania argentina* (Amgh.)." Smith Woodward said the skull was from the same locality as a caudal ring previously found which in turn was from "the red sandstone of Chubut." In an earlier note Moreno (1899) was even less explicit, but Ameghino (1906, p. 80) said that these remains were found "à peu près à trois kilomètres au Nord de la partie occidentale du lac Colhué-Huapí, mêlés . . . aux débris de la faune du *Notostylops*," adding in a footnote that he could not understand why the Cretaceous age of the South American *Meiolania* was considered doubtful since he had material from four localities in all of which it was mixed with remains of the *Notostylops* fauna.

There are several difficult problems involved in this history.

1.—Is the referred skull described by Smith Woodward really referable to *Niolamia argentina* Ameghino?

2.—Is this skull really referable to *Meiolania* Owen?

3.—What are the true geological horizons of these various remains?

4.—Do any of them belong rather to *Crossochelys*?

The type of *Niolamia argentina* has not been fixed, the original diagnosis mentioning various specimens from widely different localities. This material has not been described more fully than in the passage quoted above and it has not been figured. The description is consistent with the material described by Smith Woodward and Ameghino himself accepted this reference. It seems justifiable to accept this and to fix the usage by designating the skull described by Smith Woodward, now in the La Plata Museum, as neotype of *Niolamia argentina* Ameghino.

It will be shown on a later page that the species thus fixed does not belong to *Meiolania*.

Ameghino's data "formación guaranítica del Sehuen y del Chubut" are not conclusive. He included in the Guaranitic his marine or semi-marine Salamanquén, Rocanéen, Sehuenéen, and Luisaén, and his terrestrial Péhuenchéen, Notostylopéen, Astraponotéen, and Pyrotheréen.

¹ Like most other writers on this genus he spelled it *Miolania*, but *Meiolania* was the original and is therefore the correct spelling.

These marine beds are now generally considered to be of late Cretaceous age, although it is quite possible that the most recent of them are Paleocene. The Pehuenchéen of Ameghino included both true Cretaceous and Paleocene strata in different places. The last three terrestrial formations mentioned, now called Casamayor, Musters, and Deseado, are surely Tertiary, probably Eocene to Oligocene. Specification of Sehuen as one of the *Niolamia* localities suggests the Sehuen beds, probably (but not surely) Cretaceous in age. Ameghino's later statement that all his material was associated with the *Notostylops* fauna is flatly contradictory, since this fauna had not and has not been found on the Río Sehuen whence he earlier said some of his material came. Yet I would credit his statement to the extent of believing that some of his material was from the *Notostylops* beds, that is, the Casamayor, since his brother and collector Carlos Ameghino is very unlikely to have been mistaken in such an observation. But now that two genera are known to occur in Patagonia at about this time, the question arises whether all his fragmentary material was *Niolamia* and none *Crossochelys*. His original description of skull parts applies to the former rather than the latter, but the locality of these is not well specified.

"Red sandstone of Chubut" usually implies the Chubut Formation, which is Cretaceous in age, but this is not at all certain, since material with similar field data in early collections varies from Cretaceous to Oligocene. The more exact data for Roth's find given by Ameghino are not thoroughly dependable. Carlos Ameghino's explicit field associations are almost invariably correct but data given by Florentino Ameghino as from other field workers are frequently wrong. In this same work (Ameghino, 1906) another closely similar datum given as if supplied by Roth (relative to deposits near Gaiman) was certainly incorrect and is widely different from what Roth himself said when he later published his observations. The locality mentioned, 3 kilometers north of the western part of Lake Colhué-Huapí, is more likely to be correct than the horizon. As far as I know, only the Chubut Formation, Cretaceous, is exposed in this exact locality, yet Casamayor and other Tertiary beds occur in this same region and no positive conclusion is possible.

In fact it is still unknown whether *Niolamia* really is from the Cretaceous, Eocene, or both.¹ Moreover, while it is highly probable that some, at least, of Ameghino's type material and practically certain that

¹ Aside from the persisting doubt as to whether it is from the Casamayor ("*Notostylops* beds"), Ameghino's statement that it is surely Cretaceous because from those beds has a different meaning now that all agree that the Casamayor is Tertiary.

the neotype of *Niolamia argentina* are distinct from *Crossochelys*, it is quite possible that some of the fragmentary material referred to *Niolamia* (or *Meiolania*) really belongs to this latter genus and tends to confuse the record. *Crossochelys* is definitely of Casamayor age, Eocene. *Niolamia* is either from the same beds or from the Cretaceous—it is unlikely to be from the Paleocene, and almost surely not post-Eocene. Although *Niolamia* appears to be the more specialized genus of the two, it is apparently no younger than *Crossochelys* and may well be older.

The external form of the skull of *Niolamia* is well known from the neotype skull, as described and figured by Smith Woodward. The details of its cranial structure, however, are almost unknown.

The discovery, occurrence, and characters of the Australian genus *Meiolania* are so well summarized by Anderson (1925) that they need not be repeated here. Thanks largely to Anderson, the cranial structure is almost completely known, except that most of the boundaries between the various cranial bones have not been determined.

Many of the most important points of comparison between *Crossochelys*, *Niolamia*, and *Meiolania* have been mentioned in the course of the description of *Crossochelys*. It has been shown that the horn and scute patterns and frill structure, in general the external appearance of the skull, suggest fundamental similarity between *Crossochelys* and *Niolamia* despite their superficial differences and also suggest that *Meiolania* differs considerably from *Niolamia*, despite a greater superficial resemblance, and still more from *Crossochelys*. A few internal details require more explicit or extended consideration.

Smith Woodward (1901) says that the nasal cavity is completely separated from the orbit in *Niolamia*. In *Meiolania* the separation is incomplete and in *Crossochelys* there is open communication by way of the nasal sulcus. The orbitosphenoid crest is very strong in *Meiolania*, probably present in *Niolamia*, practically absent in *Crossochelys*. All have a descending septum, probably on the prefrontal. In *Crossochelys* the base of this is on the frontal and this and the superior nasal recess are probably more posterior than in the other two genera, although this is uncertain as the sutures are unknown in the latter. *Meiolania* has a maxillary pocket from the nasal recess probably absent, surely not in the same position, in *Crossochelys*.

The roofs of the orbit and of the temporal fossa are separated by a sharp crest in *Meiolania*, while in *Niolamia* this crest is feeble and rounded and in *Crossochelys* it is practically absent, at least on the fronto-parietal part.

In *Meiolania* the pterygoids have a long sagittal suture extending posterior to the pterygoid slit and the basisphenoid is not exposed ventrally. In *Crossochelys* the suture is short, wholly anterior to the transverse slit, and the basisphenoid must have been well exposed. The sutures are not known in *Niolamia*, which superficially, at least, rather more resembles *Meiolania* in this region. There is, however, a pronounced basisphenoid—basioccipital flexure in *Meiolania* that is less pronounced in *Niolamia*. Correlated with this is the fact that in *Meiolania*, oriented on a palatal plane, the postotic fenestra faces more posteriorly than ventrally and in *Niolamia* more ventrally. This point is uncertain in *Crossochelys* but probably was more as in *Niolamia*.

In *Crossochelys* the tympanic chamber is open posteriorly and even the notch for the columella is unusually shallow, while in both *Niolamia* and *Meiolania* the chamber is completely circled by bone and the columella passes through a foramen. The difference may not have been quite as great as appears, for *Crossochelys* probably had a posterior descending process of the squamosal and quadrate together that nearly touched the lower border of the columellar notch, the bones of our specimen being imperfect at this point. This is the condition in the Baenidae, in some of which a very slight expansion of this process would close the chamber and make the notch a foramen. This strongly suggests that in such circumstances the mere fact that the notch is quite closed, as opposed to being nearly so, is not of any great importance, in spite of the fact that in recent chelonians this character is supposed to have basic importance. In these recent forms it is important only because it is correlated with well-marked and complex distinctions throughout the quadrate region. In the fossil genera here in question the quadrates are closely similar except for this one character. Baur (1889a) attributed the closure in *Meiolania* to fusion of extraneous dermal ossifications. The situation in the baenids and in *Crossochelys* makes it very unlikely that this is the true explanation in either *Meiolania* or *Niolamia*, but does support Baur's contention that the closure is not a basic structure indicative of pleurodire affinities.

The other structures of the ear region and of the postotic fenestra are not known in *Niolamia*, beyond the important fact that it did have a postotic fenestra and not a variety of smaller and separate external foramina in this position. There are numerous differences of detail, proportion, and the exact placing of the various elements in this region between *Crossochelys* and *Meiolania* and comparison is made imperfect by ignorance of any of the sutures here in *Meiolania*. Nevertheless, as

far as the comparison can be made the otic and postotic regions seem to be generally similar in these two genera and they suggest a basic resemblance in these important characters.

Crossochelys and *Niolamia* are probably rather closely related forms. In spite of incomplete knowledge of each, in different respects, there are many important points of comparison and all seem to favor this view, the differences between them, abundant as they are, apparently all being of minor importance and such as do occur between chelonians quite distinct generically but related sufficiently closely for reference to one family. In this connection it is necessary to consider the probability that the specimen of *Crossochelys* is juvenile and the possibility that an adult would more closely resemble *Niolamia* or perhaps even would prove to be *Niolamia*. The *Crossochelys* skull is smaller than that of *Niolamia* and all its sutures are widely open whereas those of the latter (also those of all known skulls of *Meiolania*) are mostly or entirely closed. On the other hand the sutures and the surfaces for synchondrosis in *Crossochelys* fit so closely and the soft parts (notably in the ear region) are already so extensively enclosed in bone that it seems unlikely that much more ossification would have occurred or that it would have changed the relationships in any essential way. Moreover even if, for instance, it be supposed that the temporal openings might have closed in an adult, that the frill might have been extended, etc., the resulting pattern would still have differed markedly in proportions and in details from that of *Niolamia*. Even though the unique specimen of *Crossochelys* may not be fully grown, it is probably essentially adult and synonymy with *Niolamia* seems extremely improbable.

It further seems probable that *Crossochelys* and *Niolamia* are related to *Meiolania*. *Niolamia* is, on the whole, more like *Meiolania* than is *Crossochelys* but numerous differences, some of them of considerable importance, have been shown to exist between the South American and the Australian forms. Differences are inevitable between genera of such diverse ages and geographic position, and these are mostly offset by resemblances strongly suggestive of affinity. There is a possibility that *Meiolania* is convergent toward the South American genera, a member of the same broad group but developing horns independently, but this possibility is slight and the great probability is that the relationship is closer, special to these three genera, and that a family, *Meiolaniidae*, of horned turtles is a natural unit.

On the other hand the hitherto current opinion that *Niolamia* is synonymous with *Meiolania* draws the generic definition much more

broadly than is done among other chelonians or among reptiles in general. This opinion has already been expressed by Tate Regan (1914), who gave generic value to the distinctions already noted as specific characters by Smith Woodward (1901). With the assistance of *Crossochelys*, which indirectly advances knowledge of *Niolamia*, and by further reference to the available publications and to casts, other important distinctions of *Niolamia* from *Meiolania* have been given above, and there now seems little choice but to separate the genera.

AFFINITIES OF THE MEIOLANIIDAE

The affinities of *Niolamia* have been little discussed because it has been assumed that this genus was either synonymous with or closely related to *Meiolania* and hence had the same general relationships. Attention has been focussed on *Meiolania* and on it there has been much discussion and difference of opinion.

On fragmentary material, Owen confused *Meiolania* and *Megalanania* (whence the unfortunate similarity in names) and eventually referred them to a Suborder Ceratosauria supposedly allied with both Chelonia and Sauria (Owen, 1889). Huxley (1887) recognized the purely chelonian character of *Meiolania* (his "*Ceratochelys*") and considered it as allied to the Chelydridae and Platysternidae. Boulenger (1887) referred it to the Pleurodira, the opinion still most current, principally on these grounds:

- 1.—Broad pterygoids, not narrowed posteriorly, with outer palatal borders forming wing-like expansions.
- 2.—Enclosed tympanic cavity.
- 3.—Mandibular condyle articulating with a concavity of the quadrate.
- 4.—Pleurodire-like cervicals.

Baur (1889a) strongly attacked this view. He gave the following as the principal pleurodiran skull characters:

- 1.—Quadrate meeting basisphenoid, sometimes also basioccipital.
- 2.—Prefrontals not meeting vomer.
- 3.—Pterygoids turned up at anteroexternal ends.
- 4.—Front of braincase between quadrate and proötic smooth.
- 5.—No free epipterygoid.
- 6.—Tympanic cavity more or less surrounded by quadrate.
- 7.—Mandibular condyle convex and quadrate articulation concave in Podocnemididae, less distinct in other Pleurodira.

Of these, he says that *Meiolania* does not have 1-4 or 7, that 5 is not determinable but was probably as in Cryptodira, and that as to 6 the tympanic cavity is surrounded but is probably closed by a dermal ossifi-

cation, not by the quadrate. He finds similar non-pleurodiran but cryptodiran characters in the first two vertebrae, which are not known in the South American forms and will not be reviewed here, and concludes that "*there can be no doubt whatever that Meiolania is a true Cryptodiran.*" Among the Cryptodira he finds various resemblances to the Testudinidae and supposes the great and obvious differences from *Testudo*, etc., in the skull to be due to enormous development and extension of dermal ossifications. Logical enough at the time, his argument for special relationship to *Testudo* is not supported by present knowledge of the skull structure and does not need detailed review. No other author has accepted this opinion.

Boulenger (1889) replied to Baur, reaffirming the pleurodiran nature of *Meiolania*. Rearranged for comparison with the numbered points from Baur, as abstracted above, he makes these comments:

1.—Certainty is impossible, but the quadrate probably did join the basisphenoid in *Meiolania*, and in any case it does not in *Chelys*.

2.—The prefrontal-vomer connection is variable in cryptodirans and a prefrontal-palatine contact is present in some pleurodirans; the connection in *Meiolania* may have been prefrontal-palatine.

3.—Not discussed, but the pterygoids are affirmed to be laterally expanded and generally pleurodire-like.

4.—Not discussed.

5.—Not discussed.

6.—There is a complete bony ring in *Meiolania* and Boulenger decidedly holds it to be formed by the quadrate.

7.—Not discussed. [Boulenger had previously said the articulation was especially pleurodire-like.]

In the same year, Baur (1889b) replied to Boulenger's reply to Baur's attack on Boulenger's first paper on *Meiolania*. Using the same numbering, his new arguments may be summarized:

1.—The real point is the backward extension of the pterygoid in Cryptodira, usually separating basisphenoid and quadrate; Boulenger's denial of this in *Meiolania* is not based on stated evidence. [In fact, Boulenger was wrong and Baur right on this point.]

2.—Despite variations (given in some detail) the inferior processes of the prefrontal do differ in cryptodirans and in pleurodirans and *Meiolania* is near the cryptodiran condition. [This is probably true.]

3.—Lateral expansions of the pterygoids also occur in cryptodires and have no diagnostic value. [Anderson has shown that the pterygoids are generally more cryptodire-like than pleurodire-like.]

6.—Boulenger gives no evidence that the tympanic ring was closed by the quadrate. [This is still uncertain, but Boulenger may well have been right.]

Baur also discusses the cervical vertebrae and hyoids, apparently making out a good case for their not being diagnostically pleurodiran.

Ameghino (1899) in establishing *Niolamia* referred it to the Meiolaniidae and the Testudinata but made no subordinal reference.

Smith Woodward (1901) concluded that *Niolamia* was synonymous with *Meiolania* and that it completely established Boulenger's reference of the latter to the Pleurodira. No very explicit discussion of this point was given, but apparently he relied mainly on a carapace fragment referred to *Niolamia* (i.e., to "*Meiolania argentina*") and interpreted as showing fusion of the ilium with a costal.

Boulenger's opinion carried the day and since 1889 *Meiolania* and with it *Niolamia* have been almost universally referred to the Pleurodira, with a single highly important exception (Anderson, see below). This is, for instance, the position given it in representative recent texts such as those of Abel, Broili-Zittel, Williston, Romer, and many others.

Anderson (1925) has given far the best data on *Meiolania*. Even his material had very few skull sutures and left many points unsettled, but among the important points established by him are that the pterygoid does separate the quadrate from the basicranial bones and in general lacks special pleurodiran characters, that the ear is less complex than in Pleurodira, that the neck is neither characteristically pleurodiran nor cryptodiran, and that the pelvis is quite unlike the pleurodires and resembles the Testudinidae. In general Anderson shows that Boulenger's arguments were not well founded but that Baur's are also partly, but less, erroneous. Almost the only specifically pleurodire-like character confirmed is the closure of the tympanic fossa by encircling bone and even this is of doubtful significance. As between Pleurodira and Cryptodira, *Meiolania* more resembles the latter but it lacks some special cryptodire features and Anderson refers it to the primitive, extinct Suborder Amphichelydia.

Crossochelys gives better evidence on relationships than do either of the other two genera. They are known more completely, but in the cranial region, the most important from this point of view, they are known in less detail. The first conclusion that stands out is that *Crossochelys* is certainly not a pleurodire. This is so obvious that it requires little analysis or discussion. The Pleurodira have many unique characters and many others that are unusual and almost confined to some or to all numbers of this group. *Crossochelys* does not have even one of these many characters. This is true in almost equal degree of *Meiolania* and *Niolamia*. Boulenger was relying on only a few characters,

some of them quite superficial, and regarding even these he erred in several respects, as has been shown by Baur, Anderson, and the present study. It is surprising that so ill-founded a conclusion has been all but universally accepted. Doubtless the tempting *non sequitur* that extinct chelonians known from South America and Australia should belong to the only recent group, Pleurodira, common to the two continents has been a factor in this uncritical acceptance.

The principal evidence for pleurodiran relationships still factually acceptable is that in both *Niolamia* and *Meiolania* the tympanic rim is complete posteriorly and that in *Niolamia* the ilium was probably fused to the costals. The first point has already been mentioned and it has been shown that it is untrue of *Crossochelys*, which nevertheless appears to be related to the other two genera, that the closure was a very slight change from a common amphichelydian and not or not necessarily pleurodiran condition, and that the tympanic region in general is profoundly unlike that in the pleurodires despite this one superficial, almost verbal rather than deeply structural, resemblance. As regards fusion of ilium and costals, Anderson has shown that in *Meiolania* the pelvis was not suturally united to the carapace and that the pelvis as a whole is very unlike any pleurodire and very like some cryptodires. In primitive non-pleurodiran Mesozoic forms the ilium is buttressed against the carapace and its sutural union would be a relatively slight change, rather closely analogous to the closure of the cavum tympani, not necessarily accompanied by any other or more profound pleurodiran modifications and not valid evidence of pleurodire affinities unless accompanied by such characters.¹ It is, moreover, possible that the fragment on which Smith Woodward relied in making this observation did not really belong to *Niolamia*. Probably it did, but a mistake in association would not be unusual in view of the history and nature of the discovery and the probable field conditions.

Nor can it be supposed that the absence of conclusively pleurodiran characters is merely primitive. The meiolaniids are not generalized or synthetic types; they could not conceivably be in or very near the ancestry of any other known chelonians. *Bothremys* is known to be at least as old as the oldest of the known meiolaniids and its skull has essential, specialized pleurodiran characteristics of which there is no trace in the meiolaniids. The common ancestry of the meiolaniids and

¹ Abel (1919) defined the Pleurodira on the single character of union of pelvis and plastron and he referred to this suborder the "Amphichelyidae" (an invalid name for the Pleurosternidae in the broadest sense) because they approach the pleurodires in this one respect. Their non-pleurodiran character is otherwise so clear and so generally admitted that discussion is not necessary here.

of the pleurodires cannot have been itself pleurodiran in any acceptable sense.

While Baur was certainly right in excluding *Meiolania* from the Pleurodira, his suggestion of special testudinid affinities is not well borne out by later study of *Meiolania* or by *Crossochelys*. The very limited resemblance to *Testudo* in the skull seems largely to depend on retention of a few primitive features and is outweighed by many characters inconsistent with such relationships. Anderson (1925, 1930) has shown that *Meiolania* is similar to *Testudo* in some details of the limbs, but this seems to be because both are large, essentially terrestrial chelonians rather than to indicate any close affinity and Anderson refers the two genera to separate suborders, an arrangement strongly supported by *Crossochelys*.

Among the cryptodires, the *Crossochelys* cranium resembles that of the Cheloniodea¹ more than that of any other group. There are also many and important differences, and the comparison seems rather to mean that *Crossochelys* lacks peculiarities of the testudinoid (or emydoid) and trionychoid groups than that it is specifically a chelonoid. In *Meiolania* the skeleton (Anderson, 1925, 1930) is not chelonoid, partly because it is not that of a pelagic form but also in less obviously adaptive features opposing close relationship.

That the resemblance between *Crossochelys* and the Cheloniodea is largely explicable by the retention of primitive characters from a rather remote common Mesozoic ancestry is further supported by the fact that these characters, with some exceptions but also with the addition of some non-chelonoid characters, are likewise shared with the older and generally more primitive Pleurosternidae and Baenidae.² As far as comparable parts have been made known, these families show a grade of structure admirably suited to be ancestral to the Meiolaniidae, except for a few points noted in the preceding description. The Suborder Amphichelydia, to which the Pleurosternidae, Baenidae, and some other ancient forms are now generally referred, is an essentially horizontal division for a divergent group of early phyla, mostly Mesozoic, which are distinguished from later forms and united with each other

¹ Using the term essentially as the "Chelonicidae" of Hay (1930), Cheloniodea or similar forms of several previous writers, except that *Dermochelys*, given subordinal distinction by Hay, is included. The work of Nick (1912) and Völker (1913) seems to me to prove that *Dermochelys* is really related to *Chelonia* in approximately the grade of a superfamily and that its distinction by Hay and some others is greatly exaggerated. It is noticeable in the description above that *Crossochelys* resembles *Dermochelys* almost as much as it does *Chelonia*.

² These families are so similar that there is some question whether they should be separated. In this paper comparison has been made especially with the Baenidae because much better material was available for that group. The resemblance to the Pleurosternidae seems to have been at least as great.

by primitive characters. A strictly phyletic classification, were such possible, would reject this suborder as generally defined, but, as so often happens in practical taxonomy, it is now most convenient if not necessary to recognize it. The ancestral meiolaniids would undoubtedly belong in this group by definition and since the side-branch that they represent is not very close to any of the later major groups, it is probably best to consider them as aberrant amphichelydians.

The most probable conclusions as to the affinities of *Crossochelys* are:

- 1.—It has no characters of the Pleurodira and is not related to that group.
- 2.—It resembles the Cryptodira in general as opposed to the Pleurodira.
- 3.—Among cryptodires it most resembles the Chelonioidea in skull structure.
- 4.—The basic structure is closest to that of the Amphichelydia, from the (other) known members of which it differs chiefly in the marked specialization of the temporal region and a few other progressive characters (such as the pterygoid slit).
- 5.—It was probably derived from unknown forms amphichelydian by definition, independent of any group commonly referred to the Cryptodira or Pleurodira but perhaps not far removed from amphichelydian ancestors of the Chelonioidea.

The extent to which these conclusions apply also to *Niolamia* and *Meiolania* may be judged from preceding comparisons with those genera. I tentatively place all three in a family Meiolaniidae referred to the Suborder Amphichelydia.

MEIOLANIA AND LAND BRIDGES

From Moreno (1899) on, the presence of meiolaniids in Patagonia and in the Australian region has been frequently cited as evidence of a southern and more or less direct land connection between those two areas. This rather hasty conclusion has, however, been attacked with good reason (for instance, Tate Regan, 1914, Anderson, 1925). On the following grounds, *Meiolania* seems to me to give no evidence for (or against) such a land bridge:

- 1.—*Niolamia* and *Meiolania* are not as closely or as surely related to each other as has generally been supposed. Even if, as is probable, they are related, it is highly unlikely that *Niolamia* is the actual ancestor of *Meiolania*.
- 2.—There is no conclusive evidence as to where this common ancestry really did live; it could have been Asia or North America.
- 3.—The two genera are separated by most or all of the great span of the Tertiary; until we have some idea where the meiolaniids were during this time, it is rather futile to build bridges for them, although it is conceivable, to be sure, that the gap in knowledge is caused by their having been in Antarctica.
- 4.—It is almost certain that some or all members of the family could swim well; given some fifty or sixty million years they might have reached almost any place, under no necessity of getting there without wetting their feet.

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