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A STAUROTYPINE SKULL FROM THE OLIGOCENE OF SOUTH DAKOTA

(*Testudinata, Chelydridae*)

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INTRODUCTION

The modern representatives of the Staurotypinae (two genera, *Staurotypus* and *Claudius*, and three described species) are restricted to Southern Mexico and Central America. No fossils belonging to these living genera are known. A form known only from a single perfect shell from the Oligocene (Chadron) of South Dakota, *Xenochelys formosa* Hay, seems to be the only previously described fossil record of this subfamily.

Recognition of a staurotypine from shell material as good as that of the unique type of *Xenochelys* (A.M.N.H. No. 1097) is quite easy. Staurotypines differ from chelydrines in having only 23 instead of 25 marginals and 21 rather than 23 peripherals. The same feature distinguishes them from dermatemydids. They differ from kinosternines in possessing an entoplastron. In these characters *Xenochelys* is clearly staurotypine. In the elongation of the first vertebral scute and in its precise shape *Xenochelys* closely resembles *Staurotypus*. The neural series is much as in *Staurotypus*. The plastron of *Xenochelys* has a reduced number of shields, the pectorals and abdominals having apparently fused. This again is a staurotypine or chelydrine feature. The general form and height of the shell are very *Staurotypus*-like. There is also some suggestion of the tricarinate condition found in *Staurotypus* in the carapace of *Xenochelys*.

In other respects the shell of *Xenochelys* is more primitive (more dermatemydid-like) than any other member of the chelydrid series. The plastron is relatively large (although the bridge is quite narrow as in chelydrids, not as in dermatemydids). There is a xiphiplastral notch. The nuchal scute is small. There is a trace of nuchal indentation.¹

In shell characters, therefore, *Xenochelys* is a good structural intermediate between *Dermatemys* and *Staurotypus*, and it is also a temporal and phylogenetic intermediate between the complex of fossil forms called dermatemydid and the staurotypine section of the Recent Chelydridae.

It should be noted that Hay was not under any misapprehensions as to the affinities of *Xenochelys*. He quite explicitly cited *Staurotypus* and *Claudius* as "the nearest living relatives of *Xenochelys*" (1908, p. 282), and in his assignment of the form to the Dermatemydidae he merely followed Boulenger's 1889 catalog of the Recent turtles in which the Staurotypinae were associated with the Dermatemydidae. When he published his 1908 monograph he had probably not seen Siebenrock's 1907 monograph of the "Cinosternidae" in which the close affinities of the Staurotypinae and Kinosterninae were for the first time made clear; he thus missed an opportunity to point up more clearly the apparent ancestral position of the South Dakota genus.

In my 1950 classification of the testudinate order I united the chelydrines, staurotypines and kinosternines in the family Chelydridae as understood in a broad sense. To do so somewhat obscures the extreme closeness of relationship of staurotypines and kinosternines, which differ in the simultaneous loss of an entoplastron and acquisition of more or less of a box turtle habitus by the latter. The chelydrid series is surely a natural group, but within that group the staurotypines and kinosternines stand very much closer to one another than to the chelydrines.

In the Oligocene this specialized section of the Chelydridae *sensu lato* was evidently fully distinct in shell characters, if still somewhat primitive in a few features. It has, however, not previously been known to what extent the skull had evolved concomitantly with the shell.

In the collection of the Department of Geology, Princeton University, I have now found a skull (No. 13686), likewise from the Chadronian Oligocene of South Dakota, which surely belongs to a member of the staurotypine-kinosternine section of the Chelydridae. It is distinctly more specialized in a number of ways than any previ-

¹ Most of these characters might also be counted as kinosternine resemblances.

ously known staurotypine or kinosternine skull. Although incomplete it merits extended description and discussion. In the section which follows, the skull is described in detail and compared with *Claudius augustatus*, *Staurotypus salvinii*, and *Sternotherus carinatus*.

DESCRIPTION OF THE PRINCETON SKULL

The skull is complete as far as the postorbital bar. Behind this, however, only the parietals, pterygoids, basisphenoid and basioccipital are retained, all of them somewhat fragmented and incomplete. Sutures are rather difficult to make out because of fractures in critical areas.

The profile of the face is strikingly like that of *Staurotypus* or *Sternotherus*. The prefrontals project dorsally above the narial opening but laterally are somewhat retracted, so that in lateral view the nostril is seen as a distinct angular indentation. The premaxillae unite in the formation of a distinct median beak, while posterior to this median projection the contours of premaxilla and maxilla form a smoothly sinuous curve, which, however, is doubly incurved in the fossil in contrast to both *Staurotypus* and *Sternotherus*. The depth of the premaxilla is markedly greater than in *Staurotypus*. The orbit is relatively smaller than in *Staurotypus* and even more distinctly lateral (in contrast to dorsolateral) than in that form. The maxilla below the orbit is marked by a distinct groove running down to the second incurving of the lateral festooning of the jaw. The postorbital bar is rather wide, half the rostro-caudal length of the orbit rather than between $\frac{1}{3}$ and $\frac{1}{4}$ as in *Staurotypus*.

In lateral view the prootic is seen to project far forward about the pterygoid in a very exceptionally developed "crista praetemporalis" (Siebenrock 1897). Only a narrow channel separates these two bones. The dorsal margin of the prootic is continued also in a ridge on the parietal. A similar forward projection of prootic is seen in *Staurotypus* (and in *Graptemys*) but is far less extreme.

The "crista praetemporalis" which is the feature exaggeratedly developed in the fossil and in *Staurotypus* and *Graptemys* serves to modify and increase the leverage of the jaw muscles (Zdansky 1924, pp. 101-104). All three genera have widened alveolar surfaces of the maxilla with strong tendency to formation of a secondary palate. In the case of *Graptemys* the wide alveolar surfaces are known to be associated with a malacophagous diet. Probably in the case of the fossil a strengthening of the jaw action and a similar diet are to be inferred.

The dorsal planum of the parietal continues the remarkably flat dorsal margin of the face.

In anterior view the nostril is very small, much as in *Sternotherus*, not as in *Staurotypus*. The prefrontals are anteriorly distinctly convex, posteriorly are very flat. Behind them the frontoparietal area rises somewhat more sharply than in *Staurotypus*.

In palatal view the maxillae have united in the formation of an extensive secondary palate, complete in front with a pronounced median ridge but incomplete in the midline behind. In this secondary palate the palatines share to about the same extent as in *Staurotypus* and to a significantly greater extent than in *Sternotherus*. A striking and unique feature is the very impressive dorsomedial slope of the palatal roof. To a very slight extent this condition is prefigured in the other genera, particularly *Staurotypus*, but the difference is very considerable: in this respect no other genus is at all close. There are no ectopterygoid processes and the pterygoids also are bowed dorsally at the midline, so that their lateral flanges are very strong and high, though spreading wide apart. Anteriorly the premaxilla has the deep pit for the tip of the lower jar characteristic of chelydrids. In the specimen it breaks through into the narial region. As in *Staurotypus* and *Claudius* (differing in this from all examined kinosternines and chelydrines), foramina incisiva appear to be lacking in the fossil. At the postorbital bar the palate, and thus the whole outline of the skull, is very expanded from the side: this form must have been decidedly brachycephalic. The waist of the pterygoids, however, is only moderately broad, as in *Sternotherus*, not very broad as in *Staurotypus* or narrow as in *Claudius*. The basisphenoidal suture is not clearly distinguished from breaks in this region, but it seems probable that the exposed portion of this bone was very short and broad, not tending to be elongate craniocaudally as in *Staurotypus*. The infracondylar depression, so marked in *Staurotypus*, is less distinct in this form, as also in *Sternotherus*, but not so weak as in *Claudius*.

In dorsal view the great breadth of the skull at the postorbital bar is again evident, along with the considerable incurving of the skull contours just in front of the orbits. The origin of the supraoccipital spine is indicated by a triangular plane surface with well defined lateral margins, as in *Staurotypus* and *Sternotherus*, not as in *Claudius*.

The sutures bounding the frontals are somewhat obscured by breaks, but it is extremely probable that as in other Chelydridae the frontals occupy a very small area and do not enter the orbits.

SKULL CHARACTERS IN THE CHELYDRIDAE AND THE ALLOCATION OF THE FOSSIL

For the comparisons made in the course of the description just given I have had available the skeletal collections of the Museum of Comparative Zoology and of the American Museum of Natural History. Included in the M.C.Z. collection are a young and an adult skull of *Staurotypus* (the young specimen, M.C.Z. No. 4989, is figured), while the A.M.N.H. collection has furnished for study a skull of *Claudius* (A.M.N.H. No. 65865).¹

Because the fossil is a fragment only, comparisons must remain incomplete and portions of the skull which might be diagnostically significant are unavailable. In this circumstance and in the absence of more complete knowledge of variation and difference within the genera *Kinosternon* and *Sternotherus* (valuable information which we may hope to learn in the forthcoming revision of these genera by Dr. Norman Hartweg) I do not attempt to discriminate too finely the affinities of the fossil.

However some rather general discussion is possible. We may first consider what characters define a skull as chelydrid in the broad sense, then what features are chelydrine, staurotypine, or kinosternine, and finally what provisional allocation of the fossil skull is possible and expedient.

There are six genera of living chelydrids (*Chelydra*, *Macrolemys*, *Staurotypus*, *Claudius*, *Kinosternon*, *Sternotherus*), and of these *Sternotherus* might quite properly be relegated to the synonymy of *Kinosternon*. The fossil record adds a few more (*Acherontemys*, *Chelydrops*, *Chelydropsis*, *Xenochelys*). In contrast the Testudinidae has about 30 living genera while the fossil record brings the count up to about 50. It is not surprising, therefore, that the Chelydridae seem a more closely knit group than do the Testudinidae, even if the rather isolated *Platysternon* is omitted from the latter assemblage.

If the skulls of chelydrids (all living forms North America, a few Tertiary fossils European) are compared only with the skulls of North American or European testudinids very clear distinctions are evident. If, however, the comparison is extended to the very rich testudinid fauna of Southeast Asia where, so far as known, chelydrids have never occurred, some of the forms to be found there bridge over the differences which were thought to be significant. Even so astute an observer as Baur, and one so familiar with the testudinate order, found it possible

¹ A discussion of the anatomy of *Claudius* is in preparation.

to refer *Adelochelys* (= *Orlitia*) to the "Chelydroidea" when he had the skull only, though the shell would have placed the genus without question in the Emydinae.

The distinctions between the Chelydridae and Testudinidae are wide enough, when all parts of their anatomy are taken into account and the trends within them are considered, that there is no doubt that, although related, they have long been separated, perhaps since the Cretaceous, certainly since earliest Tertiary. Thus there are differences in cervical formula (Williams 1950), in the form of the eighth cervical vertebra, in degree of development of the costiform processes of the nuchal, in the presence versus absence of inframarginals, in the characteristic reduction of the plastron or its elements in the Chelydridae, in the proximal end of the femur, and in the absence in chelydrids of gaudy or bright patterns.

However, in a way which seems very characteristic of turtles, few of these features hold good with complete fidelity in all cases. In cervical formula there is a striking difference between the two families in that the eighth cervical is biconvex in the Testudinidae, procoelous in the Chelydridae. A few individuals of the Testudinidae (mostly advanced tortoises) vary in the direction of the condition of the Chelydridae, but no chelydrids are known to vary in the direction of the testudinid condition. The eighth cervical vertebra tends to differ in the two families, the Testudinidae generally showing three ventral crests on the centrum, though the lateral ones may be barely indicated, the Chelydridae showing a single median crest which may divide into two (some *Chelydra*, kinosternines).

The costiform processes of the nuchal are typically much developed in the Chelydridae, relatively little developed in adult testudinids, but the kinosternine section of the chelydrids approaches the condition of the testudinids, and young emydines have this process rather strongly developed. Inframarginals are never normally present in most testudinids, but there is an exception in the case of *Platysternon*, and inframarginals do occur as individual variations in *Chrysemys picta* (A.M.N.H. specimens to be reported on by Samuel McDowell). The plastron is never reduced in testudinids; it is strikingly reduced in protective efficiency in chelydrines and staurotypines; in some species of the kinosternines it regains its complete coverage of the ventral surface, but prior to this redevelopment it had lost one of the bones normally present in unreduced plastrata. In the testudinid femur a fusion of the trochanters tends to limit the intertrochanteric fossa to a shallow dorsal pit, though a number of emydines (and *Platysternon*)

have the juncture barely suggested. In chelydrids as in most turtles the intertrochanteric fossa is a widely open groove. The lack of bright patterns in the Chelydridae, while characteristic enough of the relatively few genera and species involved, is not consistently contrasted with the presence of such patterns in the testudinids (see, for example, the uniform pigmentation of Galapagos tortoises and of some of the Asiatic emydines.)

Nevertheless, in spite of these exceptions, these postcranial characters, external and internal, permit in combination a clear discrimination of the two families.

Several characters distinguish the skulls of chelydrids and testudinids, but here even more than in postcranial characters exceptions reduce the utility of single characters.

Chelydrids usually possess at least traces or indications of a sharp median beak or "tooth" on the upper jaw. But this is absent in some kinosternines, and while many testudinids have a notch here, a few (e.g., *Terrapene*, *Cuora*) have a beak quite similar to that of chelydrids. Most testudinids (but not *Malayemys*) have the temporal bar deeply emarginate from below; the chelydrids have this bar at most shallowly emarginate. Chelydrids have the nostril, orbits, and otic opening somewhat smaller than is frequently the case in testudinids. The supraoccipital crest is higher or more steeply arched, the premaxillary pit is usually deeper, and in staurotypines and kinosternines there is a more marked festooning of the contours of the upper jaw than occurs in testudinids. The frontals are always small and excluded from the orbit in chelydrids; this feature is variable in testudinids.

A combination of most of the characters mentioned defines a chelydrid skull. The absence of all but one or two, most often of all, defines a testudinid as contrasted with a chelydrid skull.

Within the Chelydridae determination of chelydrine skulls from staurotypine and kinosternine skulls is at once possible on one key character which offers no difficulty. All chelydrines have the temporal region more fully covered than do any of the more advanced genera.

Discrimination of staurotypine as against kinosternine skulls is more difficult on the basis of any characters which have the smallest probability of holding good if more genera are discovered. Perhaps the premaxillary beak is always more strongly developed in staurotypines and the temporal bar narrower vertically in the same group.

This difficulty in finding differences in the skulls of these two groups is akin to the difficulty in distinguishing dorsal shells. The shells of both subfamilies differ from those of chelydrines in the loss of one pair

of marginal scutes and one pair of peripheral plates. Shape and height of the shells and scute shape are essentially the same. Keeling is variable. Only in the plastron is a key difference at once apparent in the absence of an entoplastron. The mobility of anterior and posterior plastral lobes in kinosternines is another differentiating feature.

In which of these groups does the fragmentary Oligocene skull find its natural place?

It is clearly chelydrid *sensu lato*. It has the sharp premaxillary beak and deep premaxillary pit of a chelydrid. The temporal bar is broken but there is no suggestion of ventral emargination. The nostrils and the orbits are quite small. The supraoccipital crest is only partially preserved but its root gives evidence of a high arch as in typical chelydrids.

The skull is, however, clearly not chelydrine, since the temporal region is fully exposed by posterior emargination as in the two advanced subfamilies, not as in chelydrines. But the postorbital bar is wider than in any staurotypine or kinosternine; this may be a primitive feature.

Is it staurotypine or kinosternine?

It has resemblances to both groups. The premaxillary beak is very strong as in staurotypines, but the temporal bar is very stout in vertical depth as in kinosternines. The pterygoid waist is moderately broad as in kinosternines, not very broad as in *Staurotypus* or very narrow as in *Claudius*. The nostril is very small as in kinosternines and in contrast to the condition in staurotypines. Foramina incisiva are lacking as in staurotypines.

Some features, however, are extremely specialized. The degree of development of the secondary palate is greater than in any presently recognized chelydrid species, significantly greater than in *Staurotypus*. Quite unique (unique in the order) is the extreme obliquity and dorsal arching of the secondary palate.

All in all, the skull seems more specialized than that of any living staurotypine, but at the same time more primitive in at least one respect (the strong premaxillary beak) than any living kinosternine, and perhaps more primitive in the width of the postorbital bar than either modern staurotypines or modern kinosternines.

The skull is Oligocene in age. The only known shell to which it might belong is *Xenochelys*, of the same age and not distant in locality. But the shell of *Xenochelys* is quite primitive for its group. Can so specialized a skull be assigned with any probability of correctness to so primitive a shell?

Such an association is by no means impossible. Indeed, in the Princeton skull a few features like the very strong premaxillary beak and the wide postorbital bar may point to a stage of differentiation not very different from that of the *Xenochelys* shell: advanced in some respects, primitive in others. For the present it seems expedient to refer the Princeton skull — with doubt — to *Xenochelys formosa* Hay.

THE GEOLOGIC RANGE OF THE CHELYDRIDAE

The Princeton skull and the American Museum shell of *Xenochelys formosa* are the oldest known representatives of the Chelydridae (Chadronian Oligocene). An older fossil from the Eocene of Tunis was indeed referred to the family by De Stefano (1903), but his description was based on a few bone fragments associated with the mold of three pleurals. The generic and species names, *Gafsachelys phosphatica*, erected on this very insufficient basis may be disregarded as a *nomen vanum* and need no longer be considered as part of the fossil history of the Chelydridae.

It is, of course, surprising that the oldest representatives of the family should be staurotypine rather than chelydrine. It is, however, possible that future more complete knowledge may connect some of the other forms called dermatemydine by Hay (1908) with the Chelydridae. The type species of *Hoplochelys* Hay was first called *Chelydra crassa* by Cope, and this genus, though possessed of a full complement of marginals and peripherals was regarded as possibly related to *Staurotypus* by Hay himself. Both this genus (Paleocene of North America) and *Baptemys* (Lower and Middle Eocene of North America) have the plastron considerably reduced, the bridge narrowed and the posterior lobe pointed, and an arrangement of plastral scutes like that of Recent *Chelydra* (pectorals meeting femorals). The shape of the shell in both genera is quite like that of staurotypines and kinosternines, and in *Hoplochelys* the shell is tricarinate, as it is also in one species of *Baptemys*. The humerus of *Baptemys tricarinata* is very like that of *Chelydra*. However, the first vertebral is never elongate as in staurotypines and kinosternines. The other vertebrae are never as wide as in chelydrines, though wider in later (Torrejon) than in earlier (Puerco) *Hoplochelys*. The costiform process of the nuchal is said to be short in *Baptemys* (Hay, 1908). The skull of *Baptemys wyomingensis* is known and is quite un-chelydrid in its major characters: the temporal bar is deeply emarginate from below, and the temporal region widely open above, there being a much greater caudal emargination than in

chelydrines. The postorbital bar is in consequence relatively narrow. The orbit also is rather large.

None of the conditions just mentioned in which *Baptemys* and *Hoplochelys* differ from chelydrids positively debars them from ancestry. For the present, however, and until they are better known and transitional forms are discovered, it seems convenient to retain them in the Dermatemydidae, merely calling attention to their possible special relation to the Chelydridae.

Unless these forms, perfectly suitable in age, are ancestral chelydrids, there is no record of the family until the early Oligocene, and it is then first represented, as the shell and the referred skull of *Xenochelys formosa* show, by an advanced subfamily.

The first occurrence of apparent Chelydrinae is in Europe and later in the Oligocene. Fragments of doubtful value from the middle Oligocene of Germany have been assigned to "*Chelydra* sp." by Reinach (1900), and in the later Oligocene of Germany rather good remains are found of an undoubted chelydrine, "*Chelydra*" *decheni* v. Meyer. Reference of the latter form to the Recent genus *Chelydra* is, as Zangerl (1945) has already pointed out, extremely doubtful: though the shell shape is that of a chelydrine, there are curious resemblances to *Staurotypus* and to *Macrolemys* rather than to *Chelydra*. Indeed, H. v. Meyer himself in 1852 expressly admitted that the inclusion of this form in *Chelydra* depended upon a very wide generic concept, and his idea of the genus was very definitely much wider than that current today.

In the Miocene of both Europe and North America there is a flowering out — real or apparent — of chelydrine types. In Europe "*Chelydra*" *murchisoni* Bell and four other named species of "*Chelydra*" and *Chelydropsis carinata* Peters record the rather widespread occurrence of the subfamily. The remarks above for "*C.*" *decheni* apply also to "*C.*" *murchisoni* and the other European forms referred to "*Chelydra*."

The carapace of *Chelydropsis carinata* has been excellently figured by Peters (1869). Unfortunately it does not seem possible to verify in his figure the features upon which Peters relied in distinguishing this form generically. I am unable to interpret the plate as showing the presence of supramarginals, and while a division of the nuchal bone into two parts is clearly shown, I (as also Boulenger in 1889) doubt that this reflects the normal condition of the animal. Nevertheless, I consider it probable, if only on the grounds of zoogeography and age, that the genus will stand, though requiring redefinition. It

may at least be pointed out that if the eventual much needed restudy of the European chelydrines should reveal that they all belong to one genus, the name *Chelydropsis* is available.

From the Miocene of North America three chelydrines have been described. Two are known from skulls only: *Chelydrops stricta* Matthew and *Macrolemys schmidtii* Zangerl. Both of these are from Nebraska, *M. schmidtii* from the Middle Miocene, *Chelydrops stricta* from the Upper Miocene. Both are certainly related to Recent *M. temminckii*, but they are distinct from that form and from one another. *Chelydrops* is unique among known chelydrids in having a ridged alveolar surface of the maxilla.¹ *M. schmidtii* differs from *Chelydrops* and from *M. temminckii* by the considerably shorter antorbital portion of the face.

The other Miocene North American form (from the Roslyn Miocene of Washington) is known from the carapace only, no portion of the plastron nor any skeletal parts having been recovered. Hay described this form as a new genus and species, *Acherontemys heckmani*, because of the close articulation of pleurals and peripherals and because the vertebrae were even broader than in living chelydrines. This shell may belong to either or neither of the forms represented by the skulls before mentioned.

Zangerl (1945) has described a skull fragment from the Pliocene (Clarendonian) of South Dakota, which is indistinguishable from Recent *M. temminckii*. Gilmore (1923) has described from the San Pedro Valley of Arizona, either Pliocene or Pleistocene, a *Kinosternon* which is said to differ from Recent *K. flavescens* mostly in size.

Two species of *Chelydra* and one of *Macrolemys* have been described by Hay from the Pleistocene of Florida. The value of these forms, based on fragmentary material, will be difficult to determine. There are also scattered Pleistocene records for the Recent species *Chelydra serpentina* and *Macrolemys temminckii*.

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¹ The type and figured adult skull fragment has this ridge. The young specimen referred by Matthew to this form lacks the ridge.

TABLE 1. FOSSIL SPECIES OF THE CHELYDRIDAE

OLIGOCENE:

- Xenochelys formosa* Hay
 Chadronian Oligocene (S. Dakota) North America
"Chelydra" decheni v. Meyer
 Upper Oligocene (Siebengebirge) Europe

MIOCENE:

- "Chelydra" murchisoni* Bell
 Miocene (Oeningen) Europe
Chelydropsis carinata Peters
 Miocene (Eibiswald) Europe
"Chelydra" meilheuratiae Pomel
 Miocene (Allier) Europe
"Chelydra" lorettana (v. Meyer) Glaessner
 Miocene (Leithagebirge) Europe
"Chelydra" argillarum Laube
 Miocene (Preschen) Europe
"Chelydra" allinghensis E. Fuchs
 Miocene (Viehhausen) Europe
Macrolemys schmidtii Zangerl
 Middle Miocene (Nebraska) North America
Chelydrops stricta Matthew
 Upper Miocene (Nebraska) North America
Acherontemys heckmani Hay
 Miocene (Washington) North America
 and additional European records for *"Chelydra sp."* and
"Macrolemys sp."

PLIOCENE:

- Macrolemys temminckii* (Holbrook) Zangerl
 Early Pliocene (S. Dakota) North America

PLEISTOCENE:

- Macrolemys floridana* Hay
 Pleistocene (Florida) North America
Chelydra laticarinata Hay
 Pleistocene (Florida) North America
Chelydra sculpta Hay
 Pleistocene (Florida) North America
Kinosternon arizonense Gilmore
 Pleistocene (Arizona) North America
 and additional North American records for *M. temminckii* and
C. serpentina

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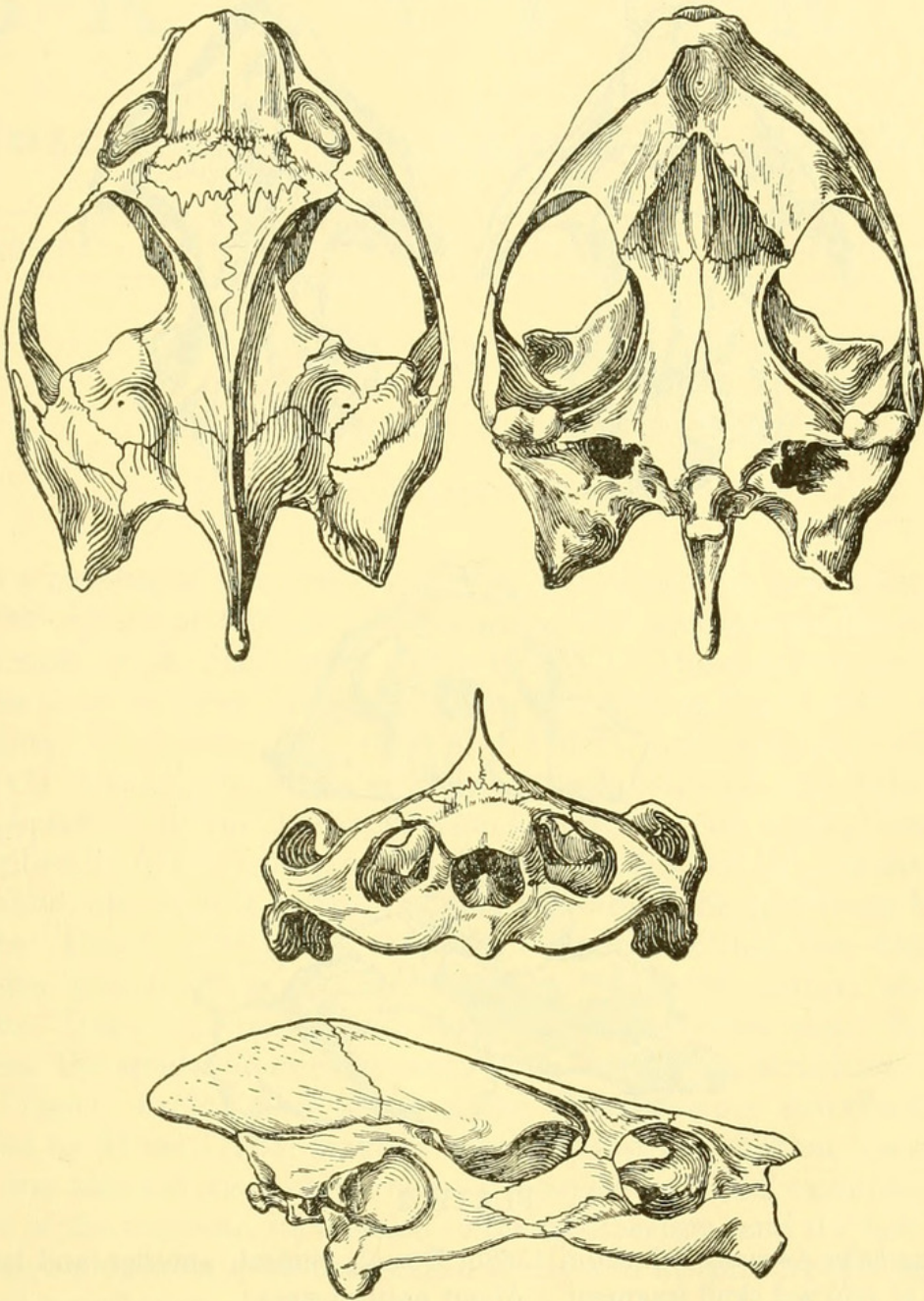


PLATE 1

Staurotypus salvinii M.C.Z. 4989: Dorsal, ventral, anterior and lateral views of skull. X about $1\frac{1}{4}$.

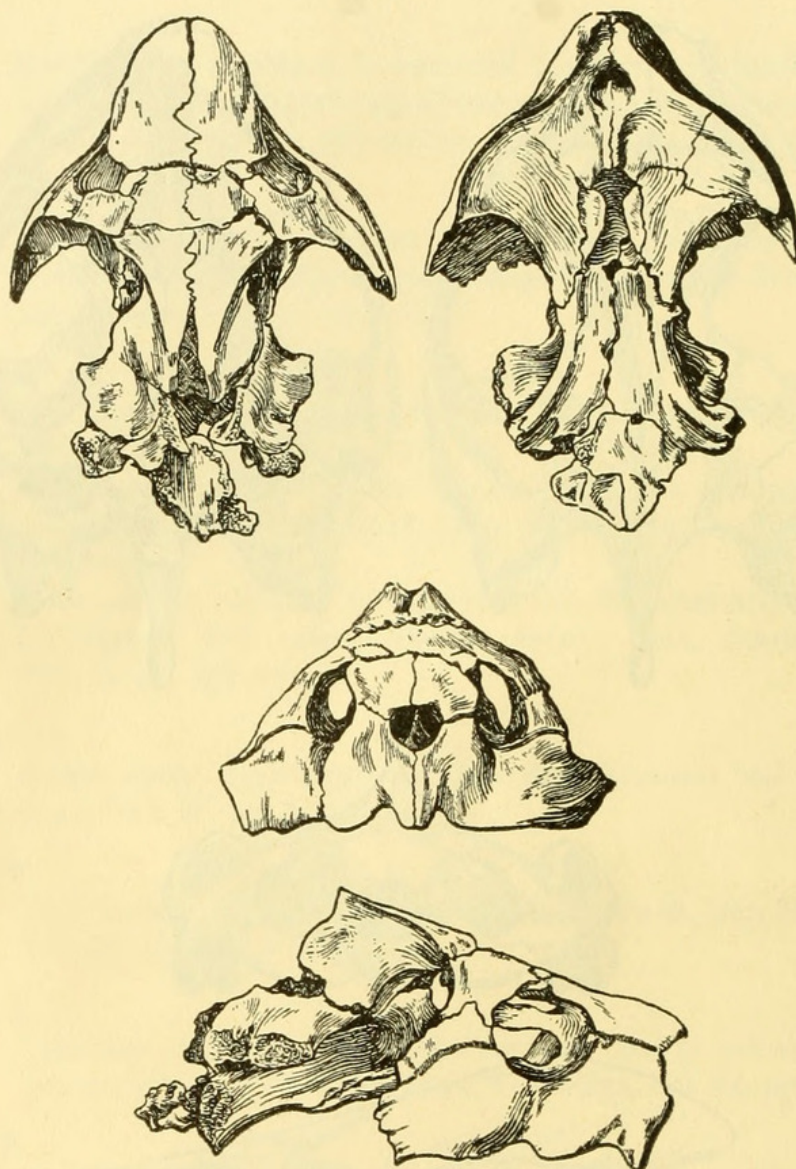


PLATE 2

Xenochelys formosa Princeton 13686: Dorsal, ventral, anterior and lateral views of referred skull fragment. About natural size.



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