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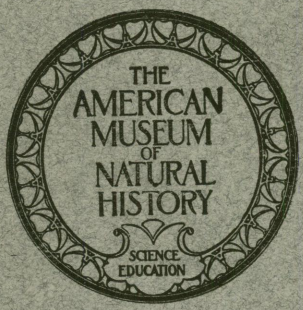

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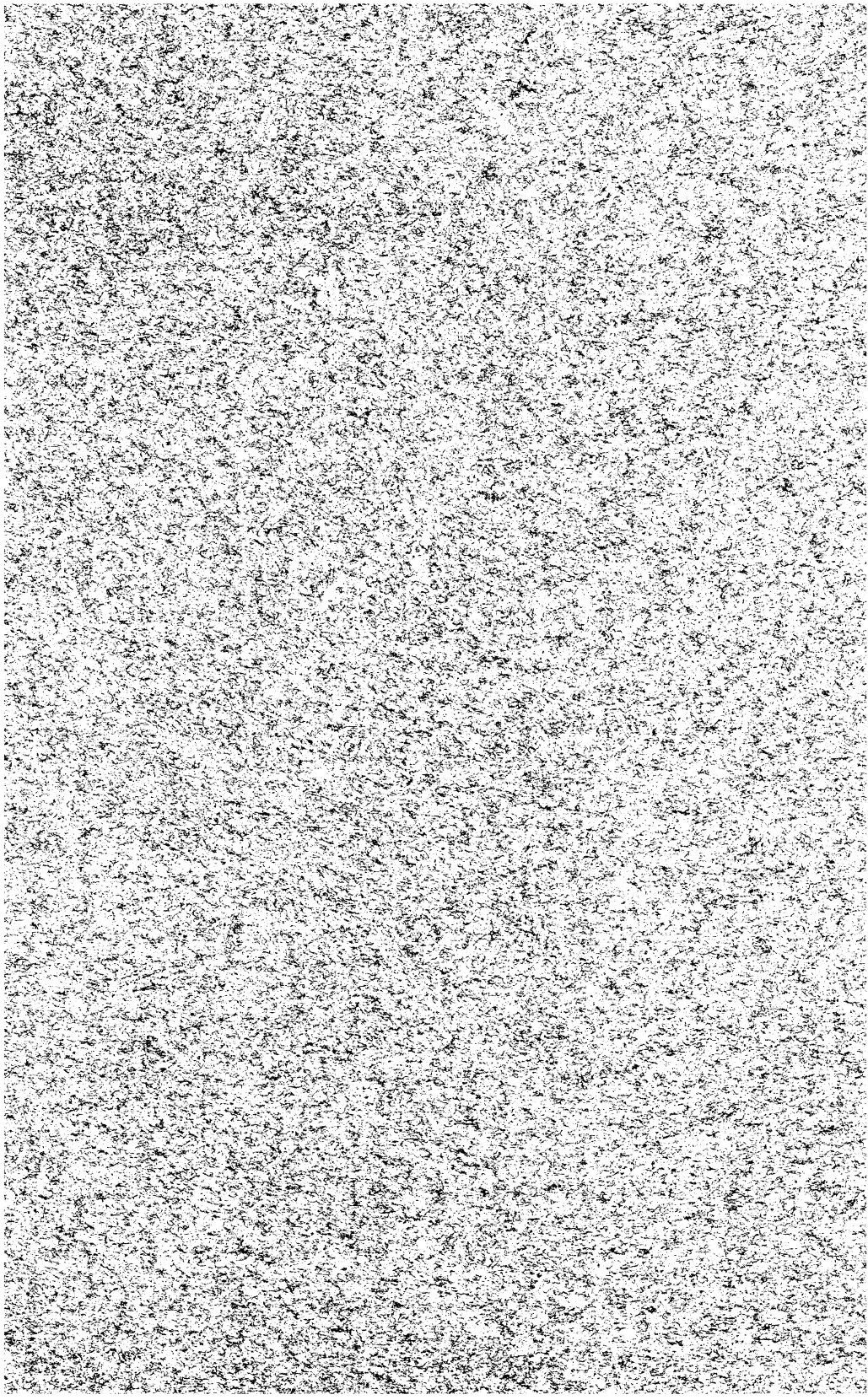

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EDITED BY FRANK E. LUTZ

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ERRATA

Page 275, line 5 from top, for Williard G. Van Name read Willard G. Van Name.
" 295, line 12 from top (No. 8), for *Trididemnun* read *Trididemnum.*
" 446, lines 20 and 22 from top, for *rubilabia* read *rubrilabia.*
" 594, line 8 from bottom, for *magænsis* read *nagaensis.*

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Article I.—THE ANTERIOR CRANIAL ELEMENTS OF *ŒDIPUS* AND CERTAIN OTHER SALAMANDERS

BY G. K. NOBLE

PLATES I AND II

Having recently had the opportunity of examining the proof-sheets of an elaborate treatise on the lacrymal bone by Dr. W. K. Gregory, I was much impressed by the extreme difficulty experienced in determining just what has been the fate of the lacrymal in the various families of salamanders. This confusion arises in part from the fact that earlier accounts often give only meager details as to the lacrymal duct and its relation to the cranial elements. Many of the figures in the extensive accounts of Cope and Wiedersheim have no septomaxilla represented, although actually present in the species considered and of real significance. The exact structure of the skull of the salamanders is being utilized more and more to demonstrate genetic relations. My purpose in recording the following observations, mostly corrections of accepted ideas, is to facilitate future work on these relations.

THE CRANIAL STRUCTURE OF *Œdipus*

In 1869 Cope, reviewing the family Plethodontidæ, considered in detail the skull structure of the various genera but failed to find any differences between the skull of *Œdipus* and that of *Eurycea* (*Spelerpes* auct.). He (1869, p. 96) concluded that *Œdipus* differed from *Eurycea* "solely in the fœtal non-separation of the digits." This difference until very recently was not considered worthy of generic distinction by most authors. No one since the appearance of Cope's paper has hitherto questioned his observations on the skull of *Œdipus*.

Very recently the name *Œdipus* has been arbitrarily applied to those neotropical salamanders having the digits fully or partly webbed. Thus

Dunn (1918, p. 470) states: "I use *Œdipus* provisionally for the salamanders allied to *leprosus, bellii, variegatus*, etc. These do not seem to be particularly close to [t]he species of *Eurycea* or *Pseudotriton*. Still less are they allied to the European *Geotriton fuscus*."

An examination of the skulls of three of the species of this group as defined by Dunn has convinced me that Dunn is confusing at least two distinct assemblages of forms and that Cope's statement as to their uniformity of skull pattern cannot be accepted. The name *Œdipus* should be restricted to one of these assemblages, while the other I consider identical with *Eurycea*. Very marked differences in the anterior cranial elements distinguish *adspersus* and *striatulus* from *leprosus*. *Œdipus variegatus*, the type of the genus, is so closely allied to *O. striatulus* (see Noble, 1918, p. 344) that it seems probable that these cranial patterns will be shown to be the same. The following characters common to *O. striatulus* and *O. adspersus* may be considered as the distinguishing features of the genus *Œdipus* as now defined: (1) no prefrontal; (2) no septomaxilla; (3) premaxillæ ankylosed only at their extreme anterior ends.

These three points of structure are important because certain of them are shared by other genera of Plethodontidæ and the question immediately arises whether or not *Œdipus* is more closely related to these other genera than it is to *Eurycea*. Thus *Geotriton* exhibits the first two points of structure but, as regards the third point, I find that its premaxillæ are entirely separate. Still, its small nasals and half-webbed digits distinguish *Geotriton* from *Œdipus*. It is more probable that the resemblance between *Œdipus* and *Geotriton* are due to parallel modification from a common ancestral stock, rather than to any close affinity between the two genera.

Œdipina, which on external features one would consider nothing but an elongate *Œdipus*, differs radically from that genus in its fused premaxillæ. From the statements of Cope (1869, p. 101) as to the reduced nature of its parietals one would then expect that *Œdipina* possessed a cranial composition very similar to *Batrachoseps*. In fact, *Batrachoseps*, with its almost boletoid tongue, might be imagined to be a side branch of the *Œdipina* stock. Unfortunately, the specimen of *Œdipina uniformis* which I dissected does not bear out Cope's statement. The frontal and parietal elements are but slightly reduced. This condition, together with the absence of the septomaxilla in *Œdipina*, readily distinguishes it from *Batrachoseps*.

The closest relatives of *Œdipus* cannot be determined at this time because of the lack of material. It is interesting to compare, however,

figures of the skulls of *Œdipus adspersus* and *Eurycea leprosus* respectively. One is tempted to say at once that the cranial pattern of *Œdipus* has been derived directly from that of *Eurycea* by three modifications: the fusion of prefrontals and nasals on each side; the loss of the septomaxilla; and the greater union of the premaxillæ. Such is probably the correct view. A glance at the salamanders as a whole will show that parallel fusions and losses have occurred independently in many different genera and are not indicative of genetic relations. This was recognized long ago by Cope but Fowler and Dunn (1917) and Dunn (1918) have recently reviewed the subject and added many valuable suggestions.

The Anterior Cranial Elements of other Salamanders

The question of whether a fusion of parts has actually occurred in *Œdipus* or whether both prefrontal and septomaxilla have simply dropped out involves the all-important question of homology. A comparison of Dunn's (1920, Fig. 1) figure of *Rhyacotriton* with my figure of *Œdipus* (Pl. II, fig. 2) will show an element having nearly the same relative position labeled prefrontal in Dunn's and nasal in my sketch. Four skulls of *Rhyacotriton* in The American Museum of Natural History have the element labeled prefrontal by Dunn much more extensive than he has indicated, in fact covering the area a nasal might be expected to cover.

The question of homology arises again in regard to the lacrymal. When present as a definitive bone, the lacrymal is characterized by the lacrymal duct. But such a definitive bone is commonly absent in the salamanders, the lacrymal duct not piercing any bone. In most plethodontids the lacrymal duct passes ventral and medial to the ascending ramus of the maxilla or ventral to a portion of the prefrontal and nasal. In *Plethodon cinereus* it passes entirely dorsal to the prefrontal. In *Ambystoma* it pierces the prefrontal.

It may be argued that the presence of the lacrymal duct marks the position of a potential lacrymal in *Ambystoma*. Ontogeny does not support such a view. In *A. opacum* up to 41 mm. total length, the anlagen of the prefrontal is without the lacrymal duct perforation. At 65 mm. the extreme ventral edge splits longitudinally and forms along its ventral margin a hollow tube. At this stage the septomaxilla is indicated by two splints of bony tissue less than a millimeter in length, lying along the anterior end of the lacrymal duct. The nasals are at this stage entirely unossified. Later growth carries the lacrymal duct farther toward the

center of the prefrontal. The nasals very soon make their appearance. It is evident from the series of larvæ before me that at no stage of growth is there a definitive lacrymal.

In my opinion, the only method by which we are going to arrive at any sound conclusion in regard to the fusion or the dropping out of the cranial elements is by a careful comparison of the crania of forms which both zoögeographical and morphological evidence show to be closely related. Thus it may be easily demonstrated that in the Plethodontidæ the prefrontal tends to diminish in size and may reasonably be assumed to drop out at the end stages of specialization. But the affinities of *Rhyacotriton* are not yet clear enough for us to state definitely with Dunn that the nasals and not the prefrontals have been lost. Its affinities with *Dicamptodon* are shown as much in its fourth toe having but three phalanges (not mentioned by Dunn) as it is by its distinctly different hyoid and skull structure. Until the skull structure of the short-toed species at present grouped under *Ambystoma* has been investigated we cannot be certain of the homology of the anterior cranial elements of *Rhyacotriton*.

Dunn (1920, Fig. 1) in figuring the anterior cranial region of *Rhyacotriton* has omitted the septomaxilla, or, rather, has drawn it as part of the lacrymal. The septomaxilla is a very distinct element, not only in *Rhyacotriton* but also in many salamanders which have been represented as lacking it. Its presence or absence should have as much morphogenetic significance as the presence of absence of the prefrontal. The structure and function of the septomaxilla in the salamanders has been recognized by many. Gaupp (1905, p. 746) has reviewed the subject briefly. There still remains to be pointed out the wide occurrence of this element in the salamanders, and the possible significance of its occasional absence. Material does not permit me at this time to go into the subject fully or do more than to indicate corrections to certain accepted figures.

The septomaxilla when present in the salamanders always tends to wrap around the anterior end of the lacrymal duct (Pl. II, fig. 1). It may be very small (Pl. I, fig. 1), a mere splinter, or it may have an expanded portion covering and supporting part of the nasal capsule. It is sometimes absent, apparently due to a crowding out by the ascending ramus of the maxilla or the nasal which have apparently shifted forward in some forms as in *Œdipus* (Pl. I, fig. 2 and Pl. II, fig. 2) and in *Geotriton*.

The majority of plethodontids possess a septomaxilla, although such an element has been often overlooked. It is not represented in the figure

of Wiedersheim (1877, Pl. xxv, figs. 104 and 105) of *Aneides lugubris* nor in those of Cope (1889, Pl. xxvii, figs. 1 and 2) of the same species. Still, in a specimen (A. M. N. H. No. 5350) in the American Museum there is a distinct septomaxilla lying in the usual position.

The elaborate figure of *Batrachoseps attenuatus* given by Wiedersheim (1877, Pl. xxv, fig. 94) is totally incorrect as regards the anterior part of the cranium. The old figure of Eschscholtz (1829, Pl. xxi, fig. 4) is a much better representation of the actual conditions. But Eschscholtz does not indicate the presence of a septomaxilla. It is a very large element in both *B. attenuatus* and *B. major*.

It has not hitherto been pointed out that in *Hemidactylium* the septomaxilla is a very large element, nearly as wide as the ascending ramus of the maxilla. It is in contact with the nasal, a rather unusual condition.

Cope (1889, Pl. xix, figs. 4 and 5) has omitted the septomaxilla from his figure of *Plethodon cinereus*. In all the species of the genus which I have examined it is present. The position of the lacrymal duct varies in the different species and, in correlation with this, the septomaxilla varies its position and contacts. Even in such closely related forms as *P. metcalfi*, *P. yonahlossee*, and *P. glutinosus* the septomaxilla does not have a constant relation to the surrounding elements.

All of the ambystomids which I have examined possessed a septomaxilla. Cope (1889, Pl. xvi) does not represent such an element in *A. maculatum*. Parker (1877) includes it in some of his figures of *Ambystoma* but not in others. Wiedersheim (1877) does not indicate it in his figure of the axolotl. I have found it present in *A. tigrinum*, *A. opacum*, *A. jeffersonianum*, and *A. microstomum*. In *A. opacum* and *A. tigrinum* it is present in an early stage. It seems to me that the septomaxilla will be found to be a constant feature of the genus *Ambystoma*.

In conclusion, it is important to emphasize that the skull of salamanders, being largely cartilaginous, cannot be studied with complete success by the ordinary methods of dissection. Clearing the skulls *in toto* and using differential stains are not only advantageous but often necessary. Conclusions based on material studied by the older methods must be accepted with caution, for not only are sutures overlooked but often well-defined elements such as the septomaxilla are missed entirely. Then the thin bony elements are subject to fracture in life. "Jugals" which I have found in *Rhyacotriton* proved on further study to be fractured portions of the maxillæ. "The "jugals" figured by Parker (1877, Pl. xxvii, fig. 6) in *Ambystoma opacum* are of similar character. The

lacrymal figured by Cope (1889, Pl. XI, fig. 2) in *Amphiuma means* is apparently also a fractured splinter. Stains, such as alizarin, which bring out sutures will, I believe, solve the mystery of the various azygous cranial elements which have been reported in salamanders. The questions of homology indicated above cannot be determined until many more forms have been examined and studied with regard to their mutual relations. This work needs the support from the field of zoögeography as well as from that of comparative anatomy. Still, one conclusion may be certainly reached at this time from the above observations. The cranial elements even within the single order Caudata cannot be homologized at random. Contacts do not always determine homology. An understanding of relationships is essential.

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PLATE I

Plate I

Dorsal surface of the cranium.

Fig. 1. *Eurycea leprosus.*

Fig. 2. *Œdipus adspersus.*

Fr.—frontal; *1.*—foramen of lacrymal duct; *Mx.*—maxilla; *Na.*—nasal; *Pa.*—palatine; *Per.*—periotic; *P.mx.*—premaxilla; *Pr.f.*—prefrontal; *Q.*—quadrate; *S.mx.*—septomaxilla; *Sq.*—squamosal; *Vo.*—prevomer.

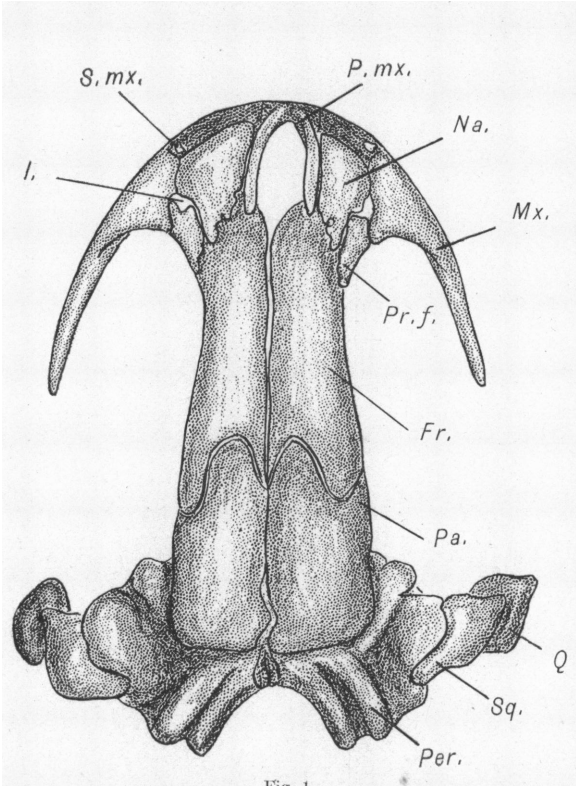

Fig. 1

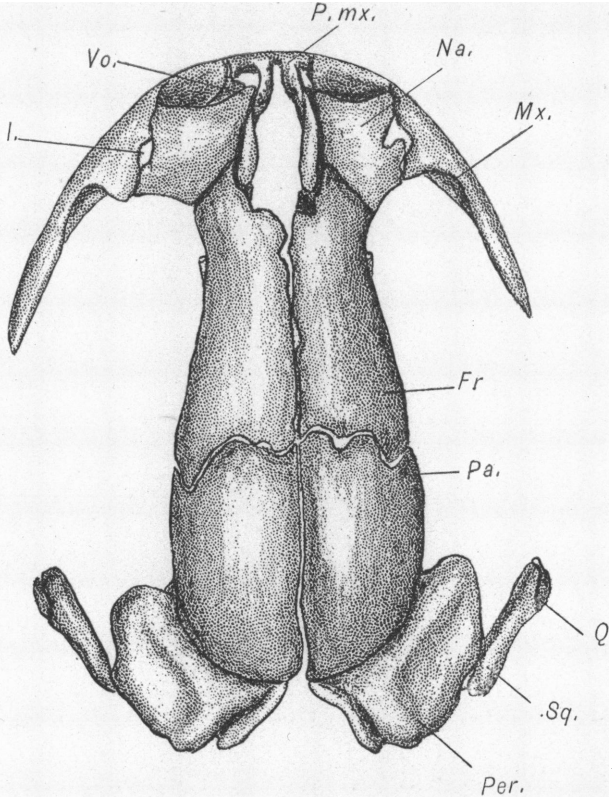

Fig. 2

PLATE II

Plate II

Lateral aspect of anterior portion of the cranium; cartilaginous elements omitted.

Fig. 1. *Rhyacotriton olympicus.*

Fig. 2. *Œdipus adspersus.*

Fr.—frontal; *L.*—lacrymal bone; *l.*—foramen of lacrymal duct; *Mx.*—maxilla; *Na.?*—nasal?; *P.mx.*—premaxilla; *S.mx.*—septomaxilla; *Vo.*—prevomer.

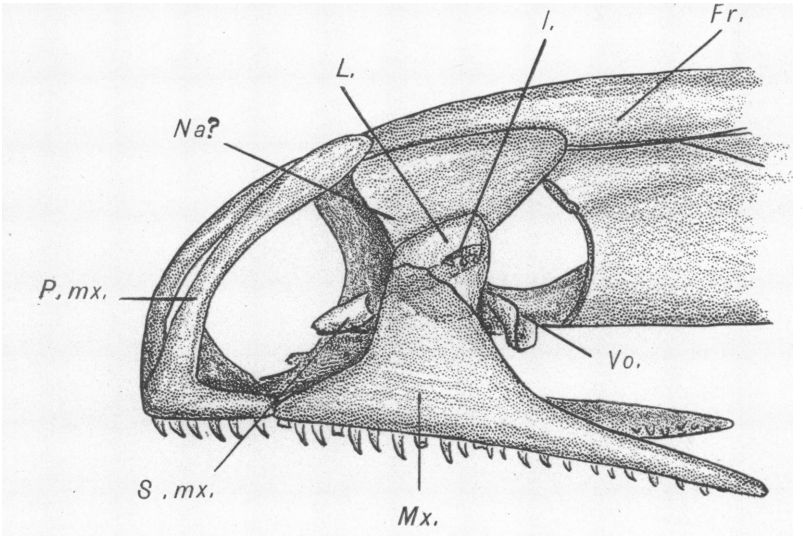

Fig. 1

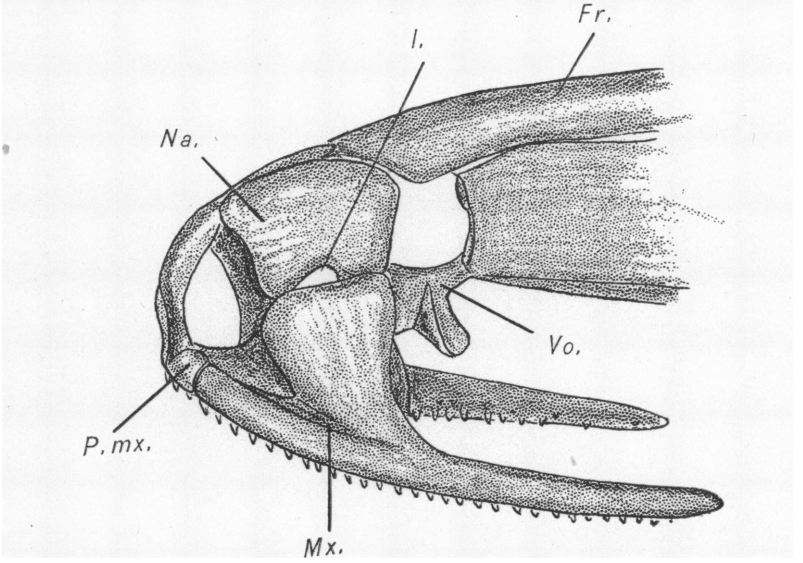

Fig. 2