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AN INTERPRETATION OF THE SKULL OF *BUETTNERIA*, WITH SPECIAL REFERENCE TO THE CARTILAGES AND SOFT PARTS

BY

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AN INTERPRETATION OF THE SKULL OF *BUETTNERIA*, WITH SPECIAL REFERENCE TO THE CARTILAGES AND SOFT PARTS

By JOHN ANDREW WILSON

CONTENTS

INTRODUCTION

THE original plan for this paper included certain studies of *Trimerorhachis*. Among them were an examination of the process of chondrification and a comparison of it with that in Triassic Amphibia, but so many new features were discovered in *Buettneria* that it became necessary to postpone work on *Trimerorhachis*. The completion of the present investigation will greatly facilitate the interpretation of that genus.

The purpose of this study is to determine, so far as possible, the cranial anatomy of *Buettneria perfecta* Case and *Buettneria bakeri* Case. Particular attention is paid to the structure of the chondrocranium and its relation to the bones. Wherever sufficient evidence was found the soft parts were restored.

PREVIOUS WORK

Buettneria was first described by Case in 1922. He had previously (1920) assigned a thoracic shield to *Metoposaurus jonesi*, but it is now believed to belong to *Buettneria*.

The genotype, *Buettneria perfecta* No. 7475 of the collection of the Museum of Paleontology of the University of Michigan, is an almost complete specimen, and little additional work has been done on it since the original description. It has been referred to by various authors, for instance, by Branson and Mehl (1929), Kuhn (1933), and Säve-Söderbergh (1935).

The skull of *Buettneria bakeri* Case was first described in 1931 by Case. In that paper he discussed the brain case; in a later one (1932) he gave a description of the postcranial bones.

MATERIALS AND METHODS

A new skull of *Buettneria perfecta*, upon which most of the following description is based, is No. 21326 of the University of Michigan. It was collected by the author in the summer of 1939 in the badlands near the Cerita de la Cruz Creek in Potter County, north and west of Amarillo, Texas. The strata there exposed are part of the Dockum group of the Upper Triassic. Neither the lower jaws nor any of the postcranial bones were found.

This skull is larger and even more nearly complete than that of the type specimen. The points of the finest teeth were still in place, proving that the specimen could not have been washed any great distance. The skull is not crushed, and there are only one or two minor breaks. Its excellent preservation has enabled the author to study many details not shown on the type specimen.

Two bones not previously discovered in *Buettneria perfecta* were in their natural positions in the skull — the stapes and the proötic. The epipterygoids were in their proper position, and although one ascending process was found in the type specimen it was not recognized as such.

The specimen was cleaned by the use of small grinding wheels and needles. A layer of particularly hard hematite made the cleaning rather slow and difficult in certain places.

ACKNOWLEDGMENTS

The author is deeply indebted to several persons for aid received during the course of this study: to Miss Grace Orton for drawing the figures; to Dr. Norman E. Hartweg for helpful criticism and suggestions; and to Dr. E. C. Case, under whose direction the work was undertaken and who has been an unfailing source of inspiration during numerous discussions and conferences.

DISCUSSION OF *BUETTNERIA PERFECTA*

Description of Bones not Previously Found in This Species

The epipterygoid in No. 21326 (Figs. 1–2) is a rather large bone and is not broken or disturbed. It is located a little anteromedial to the anterior rising process of the quadrate ramus of the pterygoid. It consists of three processes: the basal process (BP), the ascending process (AP), and the otic process (OP).

The basal process is circular in outline, and the thin peripheral edges are rough for the attachment of cartilage. This cartilage was clearly the palatoquadrate, and it is apparent that the epipterygoid more or less "floated" in it because a layer of matrix occupying the position of the cartilage lost by decay separates it from the pterygoid and the parasphenoid below. In all probability the basal process had a cartilaginous posteromedial extension which attached to the lateroventral edge of the neurocranium.[1] The epipterygoid is clearly an ossified portion of the palatoquadrate cartilage and, therefore, cartilaginous extensions of the epipterygoid are considered parts of the palatoquadrate.

The ascending process of the epipterygoid, which is well developed, is oval in cross section. It expands gradually and ends dorsally in a concave surface that obviously held a cartilaginous plug. This cartilaginous surface faces a rough surface (Fig. 8, AAP) at the angle between the side wall of the brain case and

[1] The term "neurocranium" is here used for the part of the chondrocranium which encloses the brain.

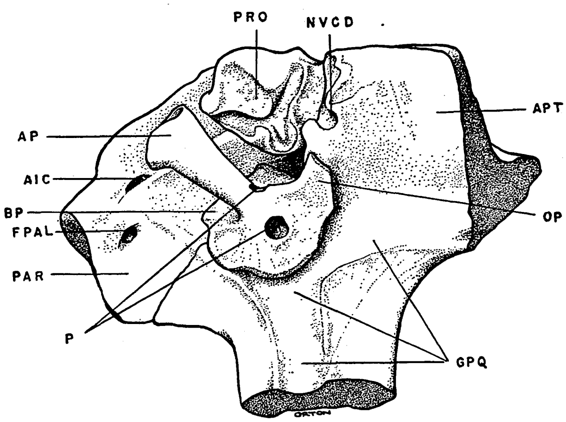


FIG. 1. Anterolateral view of a portion of the skull, with the roofing bones removed, showing the epipterygoid and the proötic. × ½

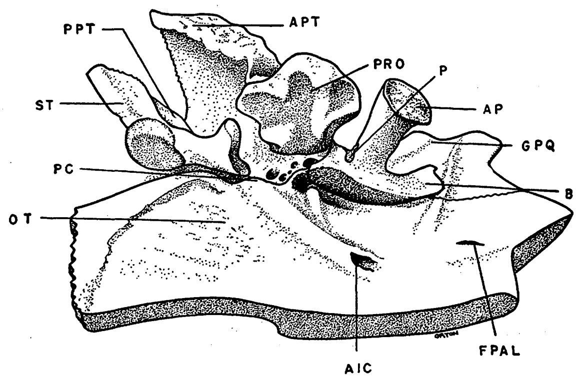


FIG. 2. Median view showing the epipterygoid, proötic, and stapes with the roofing bones removed. Anterior and posterior rising processes of the quadrate ramus of the pterygoid are cut. × ½

Abbreviations in Figs. 1–2: AIC, anterior foramen for the *a. carotis interna;* AP, ascending process; APT, anterior rising process of the quadrate ramus of the pterygoid; BP, basal process; FPAL, foramen for the *n. palatinus;* GPQ, groove for the palatoquadrate; NVCD, notch for the *v. capitis dorsalis;* OP, otic process; OT, ventral impression of the otic capsule; P, pits for the attachment of the *m. adductor pseudotemporalis;* PAR, parasphenoid; PC, parafenestral crista; PRO, proötic; PPT, posterior rising process of the quadrate ramus of the pterygoid; ST, stapes the roof of the skull slightly anterior to the parietal foramen. Such a condition is found in all labyrinthodonts in which the regions concerned are preserved.

On the anterolateral face of the base of the ascending process is a deep circular pit (P), and another pit is present on the dorsolateral edge of the same process extending onto the posterior surface. The significance of these pits was very puzzling at first. The relations of three typical processes of the epipterygoid, basal, ascending, and otic (described below), are understood, and they seem to have had no connection with the pits. The pits are found on both epipterygoids in the same position, so that they are certainly not accidents of preservation. Brock (1938) describes an attachment of the *m. adductor internus pseudotemporalis* to the epipterygoid in the gecko. The author believes that the pits represent similar muscle attachments. They are further described on page 98.

The otic process of the epipterygoid is a posterolateral continuation of the basal process. It lies on the anterior face of the anterior rising process of the quadrate ramus of the pterygoid. In *Buettneria* there was no contact of the otic process of the palatoquadrate cartilage with the proötic beneath the notch for the *v. capitis dorsalis* (NVCD). A small ridge on the pterygoid clearly separated the cartilage from any connection with the proötic at this point. There was, however, a dorsal cartilaginous attachment of the palatoquadrate which undoubtedly spread posteriorly over the top of the anterior rising process of the quadrate ramus of the pterygoid and the notch for the *v. capitis dorsalis* and attached to the squamosal and the anterodorsolateral edge of the otic capsule. This attachment will be further described on page 90.

The proötic (Figs. 1–2, PRO) is a large, heavy, somewhat globular bone. Both proötics were found undisturbed in their natural positions attached to the anterodorsomedial edge of the anterior rising process of the quadrate ramus of the pterygoid. Säve-Söderbergh (1936) assumes — and the author thinks justly so — that the smooth perichondral bone tissue delimits the area of the proötic which formed the outer surface of the auditory capsule. The rough enchondral bone tissue was enclosed within the cartilage of the capsule.

The proötic is complex in outline and has several grooves and facets. The anterior face has two distinct facets covered by perichondral bone. Of these the lateroventral facet is roughly oval and is very smooth. It may be assumed to mark the anterolateral boundary of the otic capsule. The second one, a quadrangular facet, occupies the dorsomedial corner of the anterior face. Its surface is covered by perichondral bone tissue, but is quite irregular. The two facets are separated by a groove which originates on the posterior part of the dorsal surface and passes anteroventrally to a point a little below the middle of the anterior surface. Just below the middle of the anterior face the groove divides into a deeper continuation, which runs in a medial direction, and a shallower one, which runs obliquely ventrolaterally. Both of these grooves lie just dorsal to the ventral edge of the anterior face.

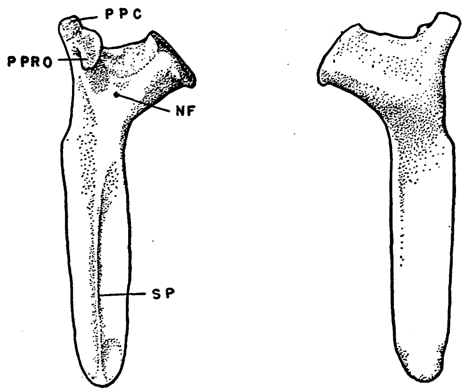
The dorsal face is divided into two areas by the continuation of the groove, already described, on the anterior face. The surface of the groove is covered with perichondral bone, and the surfaces of the two areas are covered with enchondral bone. The dorsolateral surface is inclined toward the outer side and might equally well be called a lateral surface. Evidently it served for the attachment of cartilage which helped connect the proötic with the dorsomedial end of the anterior rising process of the pterygoid. The dorsomedial surface of the proötic bears an irregular area of enchondral bone. Since the anterior portion of this surface is of denser bone than the posterior portion, it is evident that there was an increasing attachment of cartilage toward the rear.

The median face of the proötic is formed by enchondral bone. The ventral portion, which consists of denser bone than the dorsal, carries the same implications as those suggested above.

The posterior face is very irregular in outline. Posterolaterally there is a triangular concave surface of perichondral bone, which probably formed part of the lateral surface of the otic capsule. Posteromedially there are two deeply concave surfaces with enchondral bone tissue, indicating continuation of the cartilaginous otic capsule.

The ventral face is bipartite, with a lateral concave surface and a medial irregular surface, both of enchondral bone.

The stapes (Figs. 2–4, ST) is a long, thin, spatulate bone with a double proximal head. In natural position it lies just above the posterior rising process of the quadrate ramus of the pterygoid. The anteroventral head comes almost in contact with that part of the *parafenestral crista* (PC) which overhangs the



FIGS. 3–4. Dorsal (left) and ventral views of the stapes. × ½
Abbreviations: NF, nutrient foramen; PPC, process for the parafenestral crista; PPRO, process for the proötic; SP, spine

entrance of the *a. carotis interna.* From this anterior head of the stapes a smaller process (Fig. 3, PPRO) projects vertically; the distal end is recurved toward the body of the bone. The entire medial face of this smaller process is rough to hold a cartilaginous attachment for the proötic. When the stapes was in place the anterior head must have been attached to the lateral wall of the otic capsule. The attachments served to hold the stapes more firmly in position.

The functional head of the stapes is approximately oval in cross section; it is attached to the anterior head by a thin web of bone. The spatulate body of the stapes bears on its dorsal surface a prominent spine (SP), which originates a little anterior to the middle of the length of the bone, nearer the posterior edge, and continues almost to the distal end, where the spine is closer to the anterior edge. The spine probably separated muscles which held the stapes in position. The anterior edge of the stapes is very thin, and the thickest part of the bone is posteromedial to the diagonal spine. A small foramen (NF) is located on the dorsal surface of the bone near the proximal end. For reasons given on page 103 this is believed to be a nutritive foramen and not the foramen for the *a. orbitalis* (*stapedialis*).

A shallow groove passes diagonally across the stapes, just lateral to the nutritive foramen. The author is of the opinion that the *a. orbitalis* passed anteriorly in this groove.

Dorsal Surface of the Palate

The portion of the dorsal surface of the palate exposed on the parasphenoid and pterygoids has been described by Case (1922) from the type specimen. Several additions to this description can be made from a study of skull No. 21326 (Figs. 1–2).

Medial to the parafenestral crista (PC) and posterior to the tunnel that enclosed the *a. carotis interna* is a rough area indicating the position of a former cartilaginous attachment. This was the ventral attachment for the otic capsule (OT).

The grooves for the palatoquadrate cartilage (GPQ) on the dorsal surface of the pterygoids can be easily identified. The anterior termination of the groove which carried the *commissura quadrato-cranialis anterior* is on the anterodorsomedial surface of the palatine, where it joins the prevomer. From this point the groove runs laterally to the anterolateral edge of the orbit and turns posteriorly. It proceeds posteriorly along the palatine to the pterygoid, becoming more prominent as it nears the epipterygoid. At the epipterygoid the outer edge of the groove curves laterally and ends at a rough area on the medial face of the quadrate. The medial edge of the groove turns posteromedially, continues for about a centimeter beyond the epipterygoid, and flattens out on the parasphenoid. The palatoquadrate cartilage is discussed on page 91.

The ethmoidal region of the dorsal surface of the palate

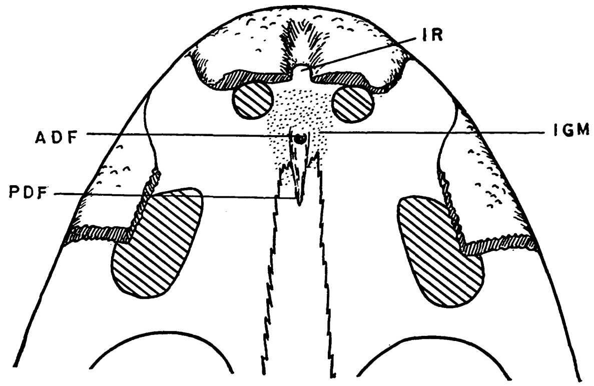


Fig. 5. Dorsal surface of the ethmoidal region of the palate, showing the area of the *glandula intermaxillaris.* $\times \frac{1}{3}$

Abbreviations: ADF, anterior dorsal foramen of the gland; IGM, position of the gland; IR, interrostral fenestra; PDF, posterior dorsal foramen of the gland

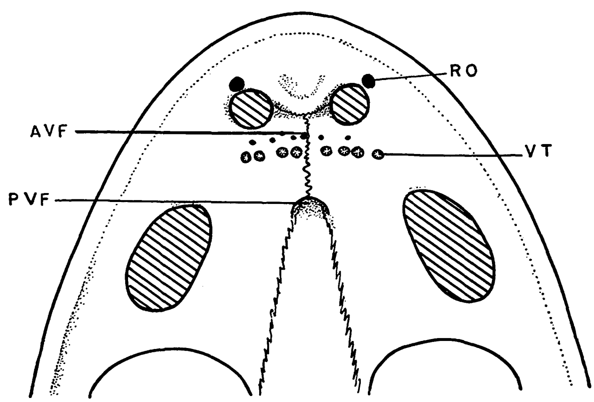


Fig. 6. Ventral surface of the ethmoidal region of the palate, showing the foramina for the tubules of the *glandula intermaxillaris.* $\times \frac{1}{3}$

Abbreviations: AVF, anterior ventral foramen of the gland; PVF, posterior ventral foramina of the gland; RO, foramen for the *r. terminalis medialis* of the *r. ophthalmicus profundus;* VT, vomerine teeth

(Figs. 5–7) shows several structures hitherto unknown in *Buettneria.* On the palatal lamina of the premaxillaries and the anteromedial portion of the prevomers is a very finely pitted area (IGM) surrounded by smooth bone. In the center of the pitted area a large foramen (ADF) is formed by a widening of the median suture between the prevomers. This foramen leads into a canal that passes anteroventrally. On the ventral surface of the palate just anterior to the vomerine teeth can be seen a transverse row of foramina. The foramen in the median line (AVF) is a little larger than the others. The author believes that the canal which leads anteroventrally from the pitted area breaks up into small tubules

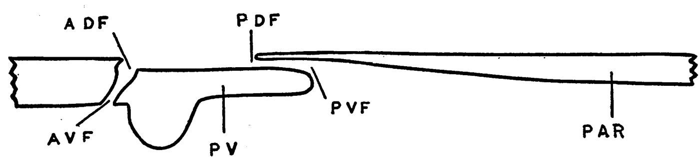


Fig. 7. Cross section along the median line of the ethmoidal region of the palate, showing the foramina of the *glandula intermaxillaris.* $\times \frac{1}{3}$

Abbreviations: ADF, anterior dorsal foramen of the gland; AVF, anterior ventral foramen of the gland; PAR, parasphenoid; PDF, posterior dorsal foramen of the gland; PV, prevomer; PVF, posterior ventral foramen of the gland

that have their exit in this series of foramina. The foramina seem too large and too regularly spaced over a small area to be for nutritive vessels. Their function will be discussed on page 81.

A groove on the prevomer leads posteriorly from the large dorsal foramen between two anterior extensions of the cultriform process. It gradually descends until it reaches the lower part of the parasphenoid (PDF). It appears on the ventral surface of the palate (PVF) in the deep recess where the parasphenoid disappears above the prevomers. The relationship of these foramina is shown in the diagrammatic sagittal section (Fig. 7).

There is a very shallow depression anterior to the pitted area on the prevomers and between the vacuities for the tusks of the lower jaw. The anterior limit of this shallow depression is just beneath a median fenestra (IR) that leads up between the premaxillaries onto the dorsal surface of the skull. The walls of the fenestra gradually expand upward until they form a wide opening on the upper surface of the skull.

Without doubt the pitted area on the prevomers marks the location of the *glandula intermaxillaris.*

Säve-Söderbergh (1935), in describing the interrostral (internasal) bone, discusses the interrostral fenestra of *Micropholis, Trematops, Zatrachys,* and *Dasyceps.* He states the problem of the intermaxillary gland thus:

> Now this gland (see especially Wiedersheim, 1876) has a somewhat different position in the *Anura* and the *Urodela.* In the *Urodela* it lies in the internasal cavity, between the nasal capsules. In the *Anura* it is situated mainly in front of but also within the nasal capsules . . . .
>
> In spite of these differences the intermaxillary glands of the two groups are, at least usually, regarded as equivalent and homologous . . . .
>
> To me, however, this homology does not seem quite so clearly established.
>
> The gland of a Urodele like *Cryptobranchus, Desmognathus,* or *Triton* (see Wiedersheim, 1877, figs. 22, 103, 111) opens in a longitudinal slit-like fenestra between the vomeres, in the middle of the median length of those bones. On the other hand the intermaxillary gland of an Anure, like *Rana* (see Wiedersheim, 1876, Taf. III, figs. 14, 15, 16; cf. Ecker-Wiedersheim-Gaupp, 1896, fig. 14) has its openings in a transverse, bent row in front of the vomeres, between these bones and the "premaxillaries."
>
> In the *Ichthyostegalia* and *Labyrinthodontia* the gland must conceivably have opened in the anterior palatal vacuity. Thus it is comparable with that of the *Anura,* but its homology to the gland of the *Urodela* seems at least very uncertain.

The perfection of the preservation of the *Buettneria* skull No. 21326 throws considerable light on the homology of the *glandula intermaxillaris* as found in the *Anura* and the *Urodela.* The evidence points to *Buettneria* having the conditions seen in both:

1. The canal that leads in a posteroventral direction from the location of the *glandula intermaxillaris,* between the prevomers and to the ventral surface of the cultriform process, is suggestive of the condition noted in the *Urodela.*

2. The canal that leads anteroventrally and then breaks up into numerous tubules is suggestive of the conditions found in the *Anura.* It may be argued by some in opposition to this idea that the canal and tubules in the frog are directed posteriorly. It is conceivable, however, that with a loss of the posterior portion

of the *glandula intermaxillaris* and emphasis on the more anterior portions of the gland the canals and tubules would become directed posteriorly.

The author does not wish to convey the idea that such a highly specialized stereospondyl as *Buettneria* has any connection whatsoever with living Amphibia. *Buettneria* seems, however, to have preserved a primitive condition in the structure of the *glandula intermaxillaris.*

The depressions for the nasal capsules can be seen very plainly on the dorsal surface of both prevomers. The grooves for the *processus maxillaris anterior* and the *processus maxillaris posterior* are situated at the posterolateral corner of the internal nares. On the palatine are two foramina that appear to be connected by a canal that passes lateral to a process that is identifiable as the *processus dorsalis* (Fig. 10, PD) of the palatine, described by Säve-Söderbergh (1936). It was impossible to excavate this canal because of the filling of very hard hematite, but it may be assumed with safety that the two foramina are connected.

The anterior portion of the *processus maxillaris posterior* was separated from the palatoquadrate cartilage by a thin shelf of bone of the palatine that projects medially. The shelf extends 1.3 cm. in a posterior direction from the posterior edge of the *processus dorsalis* of the palatine.

The *processus maxillaris anterior* lay on a shelf that projects medially from the palatine. The *processus maxillaris anterior* and *posterior* were probably connected by cartilage that passed through the canal lateral to the *processus dorsalis.* Between the posterior edge of the shelf and the *processus dorsalis* is a depression in which lay the cartilaginous connection between the *processus maxillaris anterior* and the *commissura quadrato-cranialis anterior*. Beneath the shelf for the *processus maxillaris* runs a groove which in all probability housed the main trunk of the *r. lateralis terminalis Vth* (Francis, 1934, p. 141).

A finely pitted area, which is similar to that found on the prevomers and which is thought to have been covered by the intermaxillary gland, occurs on the maxillary bone at the posterolateral edge of the choanae. This area corresponds to the position of the *glandula nasalis lateralis* in the frog (Ecker, Wiedersheim, and Gaupp, 1904, p. 627). It is suggested that the gland was present in *Buettneria.*

Around the peripheral margins of the dorsal surface of the palate in the ethmoidal region are various foramina for the cutaneous branches of the *r. maxillaris Vth.*

Ventral Surface of the Roof of the Skull

The ventral surface of the roof of the skull (Fig. 8) shows with remarkable clarity the sutures of the dermal bones and the impressions of the structures that form the endocranium. The dorsal surface of the brain case, the otic capsule, the anterior attachment of the neurocranium that enclosed the olfactory bulbs and nerves, and certain of the scars of attachment of the more prominent muscles can be traced with certainty.

The dorsal outline of the brain case (Figs. 8–9, DBC) is the most prominent feature on the ventral surface of the skull roof. The area occupied by the brain posterior to the parietal eye is surprisingly small for an animal of this size. The brain case was subtriangular and was elongated in an anterior direction. This outline is shown by descending ridges from the dermsupraoccipitals, the parietals, and the frontals. These ridges are very strong on either side of the parietal foramen.

The posterior limit of the brain case is marked by a curved ridge that is directed transversely in about the middle of the anteroposteral length of the dermsupraoccipital. The curve of the ridge is concave anteriorly. The greatest width is reached about one centimeter anterior to the posterior limit of the brain case. From the points of greatest width the ridges on the dermsupraoccipitals and their continuations on the parietals gradually come together until they meet in the area just anterior to the parietal foramen.

The ventrally extended ridges on the dermsupraoccipitals and the parietals obviously served for the dorsal attachments of the cartilaginous walls of the brain case. What appears to be a remnant of the sphenethmoid is found on the ventral edge of the

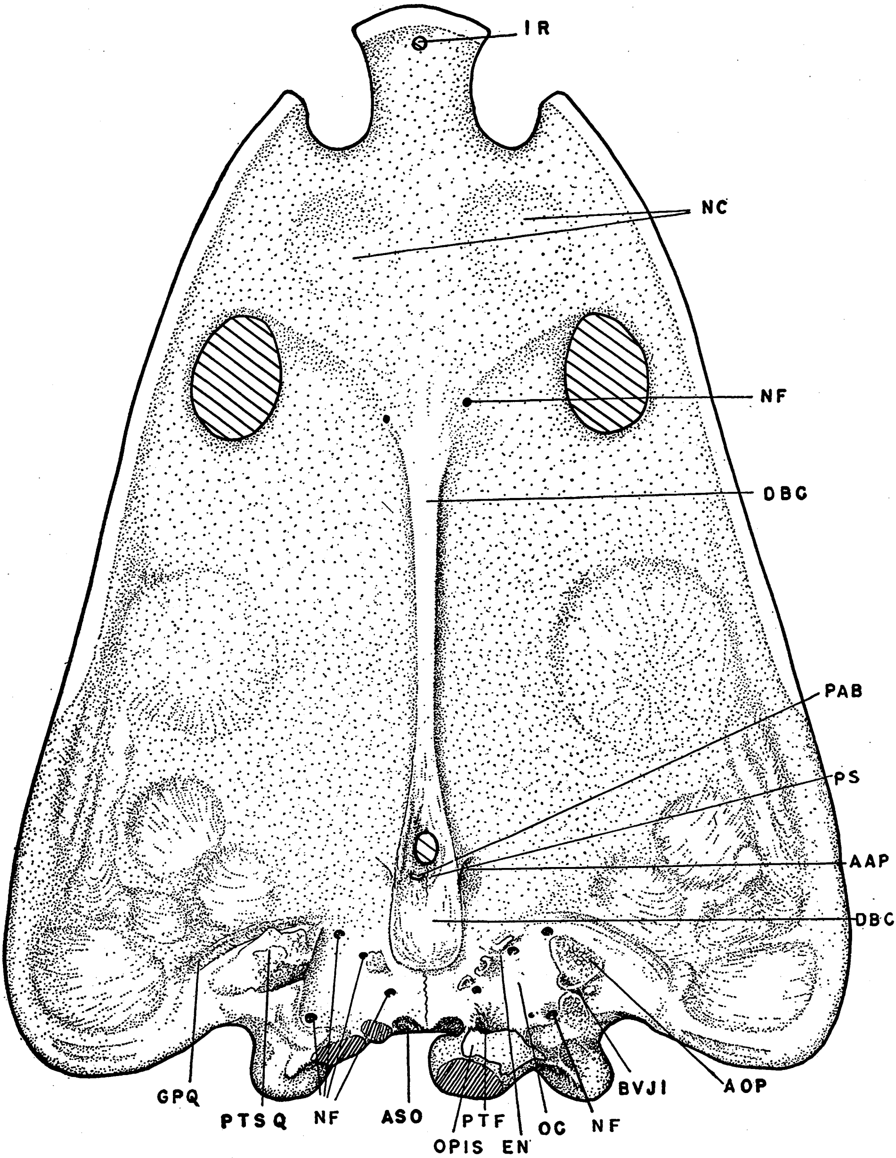


FIG. 8. For caption and abbreviations see bottom of opposite page

descending flange of the parietal on either side of the parietal foramen. The descending flanges were broken, and a break 1.2 cm. ventral to the roof of the skull appears to be on the line of a suture. The rest of the descending portion of the flange, 0.8 cm. long, would then be sphenethmoid. Its length is only 2.4 cm. The ventral edge of the sphenethmoid (?) is marked by two notches, which appear to be the dorsal edges of two foramina. If they are, they locate the position of escape for the *n. occulomotorius* and the *a. ophthalmica.*

The portion of the brain case which surrounds the parietal foramen reveals several surprising things. Just posterior to the parietal foramen and a little to the right (with the skull in the natural position) is a depression (PAB). The author ventures to suggest that it is a dorsal impression of the parapineal organ upon the roof of the skull. The anterior portion of the depression opens directly into the parietal foramen. The posterior portion is just slightly deeper than the anterior. There is no sharp lip separating the parietal foramen from the depression. The right-hand wall of the depression continues directly anteriorly almost parallel to the mid-line, but with a slight lateral curvature (to the right). The left-hand wall proceeds anterolaterally, crosses the mid-line at an angle of about 20°, and gradually merges into the parietal foramen about 4 mm. medial to the right-hand wall of the parietal foramen. Between the left wall of the depression and the brain case is a shallow groove (PS). It begins slightly posterior and a little to the left (skull in natural position) of the depression just described and passes anterolaterally (to the left),

---

FIGURE 8

Ventral surface of the skull roof. × about $\frac{1}{3}$

Abbreviations: AAP, dorsal attachment of the ascending process; AOP, attachment for the cartilaginous otic process; ASO, attachment for the supraoccipital; BVJI, lateral branch of the *v. jugularis interna;* DBC, dorsal side of the cartilaginous brain case; EN, notch for the endolymphatic duct; GPQ, groove for the palatoquadrate; IR, interrostral fenestra; NC, dorsal impression of the nasal capsule; NF, nutrient foramen; OC, otic capsule; OPIS, opisthotic; PAB, dorsal impression of the parapineal body; PS, impression for stalk of pineal organ; PTF, posttemporal fenestra; PTSQ, pterygoid-squamosal complex

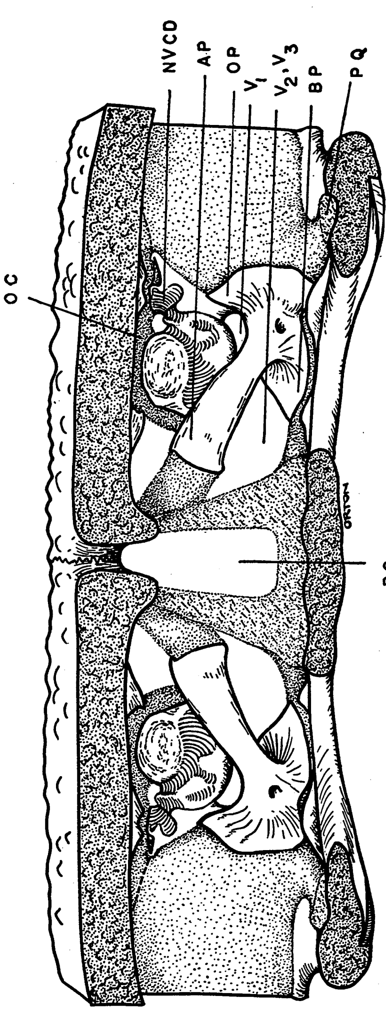


FIG. 9. Semidiagrammatic view looking in a posterior direction at the anterior portion of the brain case to show the relationship of the epipterygoid to the palatoquadrate, and the proötic. The cartilage areas are stippled. Sections of the cut cartilage are stippled with straight lines; sections of cut bone, with curved lines. × about $\frac{1}{3}$

Abbreviations: AP, ascending process; BC, brain case; BP, basal process; NVCD, notch for the *v. capitis dorsalis;* OC, otic capsule; OP, otic process; PQ, palatoquadrate; V_1, *r. ophthalmicus profundus V;* V_2, *r. maxillaris V;* V_3, *r. mandibularis V* ending in the left posterior corner of the parietal foramen. This groove, if correctly interpreted, is the impression of the stalk of the pineal organ.

If this interpretation is correct — and to the author the evidence presented seems convincing — the conditions of the epiphysial complex in *Buettneria perfecta* shed light on the developmental history of recent Amphibia and correspond very closely to the conditions described by Cameron (1903):

> 1) The epiphysis in certain types of Amphibia (*Rana, Bufo, Triton*) arises in the form of two primary outgrowths from the roof of the fore-brain. These are placed, one on either side of the mesial plane.
>
> 2) The outgrowth which is situated to the right of the middle line disappears at an early stage of development by blending with the left outgrowth.
>
> 3) The latter shows the most active growth, and the effect of this in most cases is to cause the epiphysial opening to become situated to the left of the mesial plane. The left outgrowth is therefore the more important of the two in Amphibia.

In *Buettneria* it is evident that the parapineal organ was of considerable size.

The portion of the brain case anterior to the parietal foramen is V-shaped. The apex of the V is directed forward and is closed by a thickening of the parietal bones. The side walls in this area are prominent, with the outer side slightly concave dorsoventrally. A median ridge continues in an anterior direction from the junction of the side walls and gradually flattens and spreads laterally until it disappears on the frontals.

The dorsal impressions of the otic capsules can be clearly seen on the ventral surfaces of the dermsupraoccipitals, the tabulars, and the supratemporals. The impression is more clearly shown on the left side and is used as the basis of the following description.

There is a deep groove which completely separates the impression of the otic capsule from that of the brain case. This, in all probability, corresponds to the *fossa Bridgei* of Säve-Söderbergh (1936). It differs, however, from the *fossa Bridgei* as described in *Lyrocephalus*, *Platystega*, and *Aphanerama*, in which forms the impressions of the otic capsule and brain case are not completely separated. The *fossa Bridgei* will be further discussed on page 94.

The otic capsule was enclosed anteriorly by the partly ossified proötic and posteriorly by a cartilaginous opisthotic. A thin plate of bone lies on the anterior face of the descending process of the dermsupraoccipital, the tabular, and the rising process of the exoccipital. A similar bone found in the type specimen was interpreted by Case (1922) as the "opisthotic (?)." If it is the opisthotic — and certainly it is in the correct position — it probably formed little or no support for the otic capsule. It almost covers the posttemporal fenestra, which is open dorsally to the opisthotic. The criteria used for locating areas of cartilaginous attachment of the otic capsule on the proötic can be applied to the opisthotic. The entire anterior surface of the opisthotic is of perichondral bone tissue, with the exception of one very small area on the anterodorsal edge, which is perhaps enchondral bone. This small edge might have been in contact with the posterior wall of the cartilaginous otic capsule. It is serrated and lies within a line projected from the dorsal impression of the otic capsule on the dermsupraoccipital to the ventral impression on the parasphenoid.

The posterolateral edge of the capsule is clearly outlined by a thick crescent-shaped area of cartilage attachment, probably a part of the cartilaginous opisthotic.

The anterolateral corner of the impression of the otic capsule is bounded by another thick area of cartilage attachment. This area is the dorsal attachment of the otic process of the palatoquadrate. The anterior rising process of the quadrate ramus of the pterygoid approximates the otic capsule, and the extension of the otic process of the palatoquadrate fuses with or actually forms the anterolateral corner of the otic capsule. This unusual condition is further discussed on page 91.

A groove separates these two areas of cartilage attachment. It was probably closed ventrally by cartilage, so that in life it formed the dorsal portion of a canal. The opening of the groove into the otic capsule is broad. Laterally the groove narrows, then widens out again. It is thought to have been occupied by a median dorsal branch of the *v. jugularis interna*.

A large foramen is in the posterolateral corner of the dorsal impression of the capsule on the tabular. It is constant and has been found in the same position in six tabulars examined. It leads dorsally into the extremely thick bone of the tabular. The author could find no outlet for this foramen and believes that a large nutrient vessel passed through the foramen to nourish the thick bone above. There are three other foramina which lead into the bone above the otic capsule. In all probability they also are nutrient foramina. It must be concluded that there were numerous blood vessels above the otic capsule. More details will be given in the section on the angiology of *Buettneria* (p. 101).

On the median edge of the impression of the otic capsule are two small descending processes. The anterior edge of the anterior process is extended and shares in the anterolateral edge of the otic capsule, and the posterior edge of the posterior process is extended and shares in the median side of the otic capsule. Between the processes is a smooth notch. The endolymphatic duct probably passed through this notch into the otic capsule.

The difference in thickness of the lateral wall of the otic capsule and the median wall as indicated by attachments is very noticeable. The median wall is 0.6 cm. thick at its thickest part; the lateral wall, 2.1 cm. This is due, perhaps, to the fact that the posterior lateral wall of the capsule in *Buettneria* was exposed at the back part of the skull and, therefore, the great thickness of cartilage was developed to protect and strengthen it.

In the ethmoidal region of the ventral surface of the skull roof the dorsal impression of the nasal capsules can be seen on the nasal bones.

On the median line lying between the dorsal laminae of the premaxillaries is the rather large fenestra that has been mentioned in the description of the *glandula intermaxillaris*. This fenestra is undoubtedly homologous to the interrostral fenestra of *Trematops*, *Zatrachys*, *Dasyceps*, and *Micropholis*.

The only other structures that are noticeable in the ethmoidal region on the ventral surface of the skull roof are grooves on the posterolateral edges of the dorsal laminae of the premaxillaries and the anterolateral edges of the nasals. These grooves probably carried the *cartilago obliqua;* they are further discussed on page 95.

Posterior Face of the Skull

The pterygoid-squamosal complex in skull No. 21326 is more clearly shown than that in the type specimen. This region has been described and figured in detail by Case (1922) for *Buettneria* and by Branson and Mehl (1929) for *Koskinodon.*

A descending process of the squamosal interlocks with two ascending processes of the pterygoid. The same condition was found and figured in the type specimen by Case (1922, fig. 2B). In skull No. 21326 a thick layer of bone lies on the anterior face of the anterior rising process of the quadrate ramus of the pterygoid. It reaches up almost to the squamosal. From the direction of the bone fibers, however, the author does not believe that this layer is a part of either the squamosal or the pterygoid. The fibers of the layer are directed dorsolaterally, and those of the descending process of the squamosal are directed ventrally. It is suggested that the layer of bone is a perichondral ossification of the palatoquadrate cartilage.

An extra ossification in the palatoquadrate seems strange, since it is generally accepted that the tendency in the stereospondyls is toward chondrification. It must be remembered, however, that the roof of the skull was very heavy, and the anterior rising process of the quadrate ramus of the pterygoid and the descending process of the squamosal, along with the exoccipital-tabular "pillar," were the only means of supporting the posterior thickened parts of the skull roof. It is possible that in the older animals an ossification was developed in the palatoquadrate to strengthen further the heavy posterior region of the skull.

The anterior ascending process of the quadrate ramus of the pterygoid is in contact with the squamosal for about 5 cm. The anteromedial portion was separated from the squamosal by cartilage, which can only have been part of the palatoquadrate that spread up between the pterygoid and the squamosal. This cartilage also formed a strong attachment to the anterodorsolateral walls of the otic capsule slightly lateral to the ossified portion of the proötic. It must represent the attachment of the otic process of the palatoquadrate to the otic capsule. It seems to the author to be abnormally high on the otic capsule, but the structure of the skull will not permit it to be restored otherwise.

The figures of Säve-Söderbergh (1936) for *Lyrocephalus* (Fig. 16) and *Aphanerama* (Fig. 37) show no structure where this cartilage is indicated in *Buettneria.* It is thought that perhaps in the Spitsbergen forms the palatoquadrate continued dorsal to the groove for the *v. capitis dorsalis* and attached to the anterolateral edge of the otic capsule.

On the ventral surface of the squamosal there is a deep groove that lies just anterior to the anterior rising process of the quadrate ramus of the pterygoid. It lies posterior to the ossified portion of the palatoquadrate and above a layer of matrix that separates this ossified portion posteriorly from the rising process of the pterygoid. The palatoquadrate must have occupied the space now filled by matrix and probably extended up into the groove on the lower surface of the squamosal.

Chondrocranium

The four parts of the chondrocranium of *Buettneria perfecta,* namely, the palatoquadrate, the brain case, the otic capsules, and the ethmoidal region (Fig. 10, left side), will now be described.

The palatoquadrate may be restored with a minimum of doubt. The *commissura quadrato-cranialis anterior* lies in a distinct groove on the dorsal surface of the median process of the palatine. It thins posterolaterally, as is indicated by the groove for it on the main body of the palatine, and becomes less distinct in that direction. The cartilage continues posteriorly and posteromedially on the dorsal surface of the palatine ramus of the pterygoid. At the mid-point of the free portion of the palatine ramus of the pterygoid the palatoquadrate cartilage expands laterally. It contracts again just before it unites posteromedially with the epipterygoid.

The epipterygoid is supported by the palatoquadrate, which surrounds the ossified basal process. The palatoquadrate extends a short distance posteromedially and forms the *commissura quadrato-cranialis basalis.* The anterior boundary of this *com-*

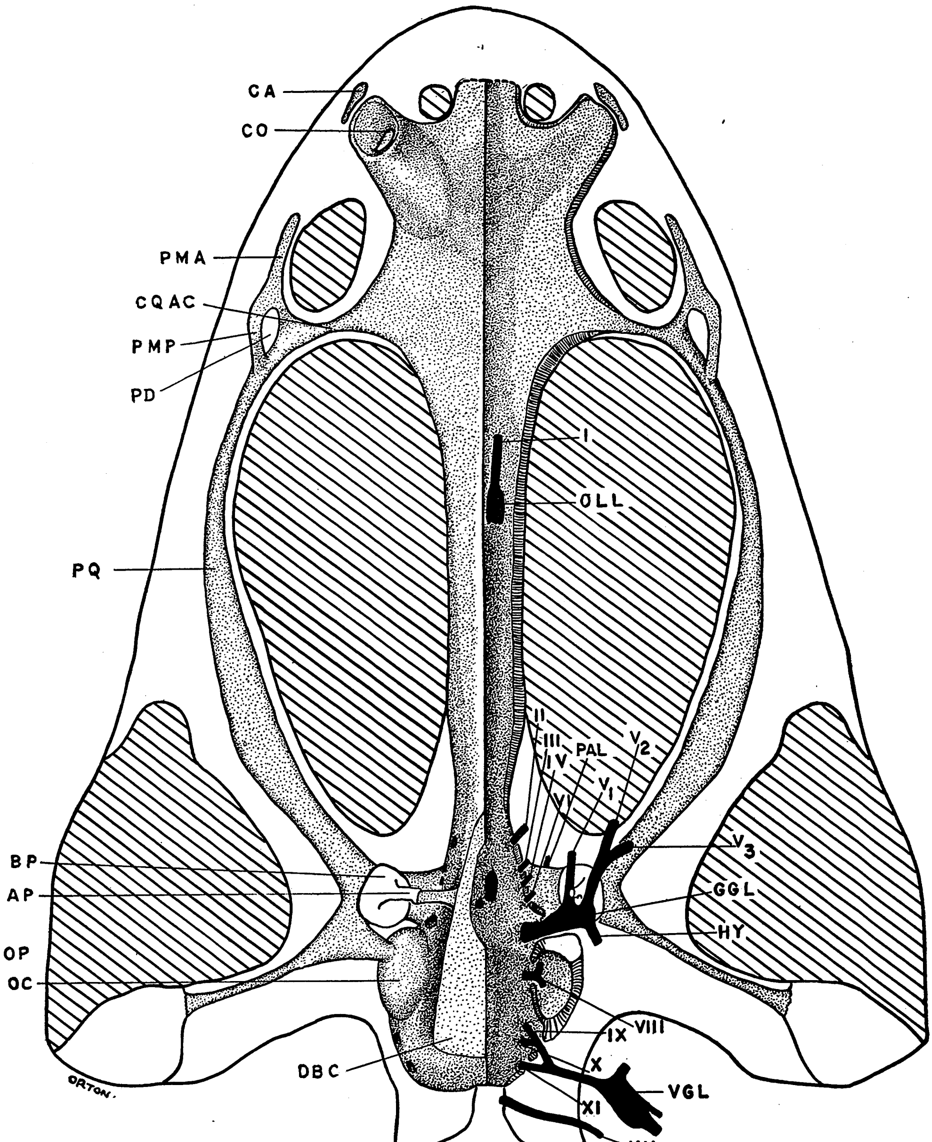


FIG. 10. For caption and abbreviations see bottom of opposite page

missura is clearly limited by a ridge on the parasphenoid directed toward the internal opening for the *a. carotis interna,* which flattens out 2 cm. anterolaterally to it.

The palatoquadrate turns laterally almost at right angles as it passes onto the quadrate ramus of the pterygoid and assumes a vertical position against the anterior ascending process of the quadrate ramus of the pterygoid. At this point the basal process of the epipterygoid is 0.7 cm. within the edge of the cartilage. As has previously been stated, the palatoquadrate cartilage could not have had an attachment to the anterior face of the proötic. The surface for cartilage attachment of the otic process faces posterolaterally; to have a cartilaginous connection with the anterior face of the proötic it would have to face dorsomedially. Because of the position it is obvious that the cartilaginous otic process was attached to the dorsolateral corner of the otic capsule above the notch for the *v. capitis dorsalis* rather than to the anterior face of the proötic and beneath the *v. capitis dorsalis,* as in other stereospondyls.

The vertical quadrate ramus of the palatoquadrate continues posterolaterally to unite with an anteromedial surface of the quadrate. The unexpected "layer of bone," identified as an ossified portion of the palatoquadrate, lies between the epiptery-

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FIGURE 10

Diagrammatic dorsal view of the skull with the roofing bones removed, showing on the left side the dorsal surface of the endocranium; on the right side the top of the endocranium has been removed to show the exits of the cranial nerves. The cartilage is stippled; the nerves are black. × about $\frac{1}{3}$

Abbreviations: AP, ascending process; BP, basal process; CA, *cartilago alaris;* CO, *cartilago obliqua;* CQAC, *commissura quadrato-cranialis anterior;* DBC, dorsal side of the cartilaginous brain case; GGL, Gasserian ganglion; Hy, *r. hyomandibularis V;* OC, otic capsule; OLL, olfactory lobe; OP, otic process; PAL, *n. palatinus;* PD, *processus dorsalis;* PMA, *processus maxillaris anterior;* PMP, *processus maxillaris posterior;* PQ, palatoquadrate; VGL, *vagus ganglion;* I, *n. olfactorius;* II, *n. opticus;* III, *n. occulomotorius;* IV, *n. troclearis;* V_1, *r. ophthalmicus profundus V;* V_2, *r. maxillaris V;* V_3, *r. mandibularis V;* VI, *n. abducens;* VIII, *n. acusticus;* IX, *n. glossopharyngeus;* X, *n. vagus;* XI, *n. accessorius;* XII, *n. hypoglossus* goid and the quadrate, separated from the anterior rising process of the quadrate ramus of the pterygoid by a layer of matrix which replaced the cartilage. Dorsally, the edge of the palatoquadrate cartilage fitted into a groove on the lower surface of the squamosal.

The ascending process of the epipterygoid was attached by a cartilaginous extension to a depression on the dorsolateral wall of the brain case at the angle of the descending flange of the parietal.

The neurocranium can be restored with almost as much certainty as the palatoquadrate. In the occipital region the supraoccipital was entirely cartilaginous. It attached ventrally to a free upper surface of the exoccipital and dorsally to notches in the posteroventral surface of the dermsupraoccipital. Laterally it was bounded by the descending processes of the tabular. Without doubt the cartilaginous supraoccipital fused with the posterodorsal margin of the brain case, although the posterior margin of the actual brain case is anterior to the supraoccipital. As previously stated, the *fossa Bridgei* separated the otic capsule from the dorsal part of the brain case.

The dorsolateral walls of the brain case and the impression of the ventral surface on the palate have been described in other connections (pp. 78 and 83). The area occupied by the ventral portion of the brain case seems greater than that occupied by the dorsal portion. It must be remembered, however, that there was no ventral separation between the median wall of the otic capsule and the brain case, such as is present on the dorsal surface. The ventral impression is of both brain case and otic capsule.

The orbitotemporal region anterior to the olfactory lobes must have been a long tube of subtriangular outline. The base of the triangle rested upon the broad flat cultriform process and the dorsal apex attached to the median ventral flanges of the parietals and frontals. It appears to be the exact reverse of the condition found in the Spitsbergen forms.

The ethmoidal region cannot be restored with as much accuracy as the other parts of the chondrocranium. On the dorsal side of the prevomers and on the ventral side of the nasals are depressions that indicate the position of the nasal capsule. A rough estimate suggests that the nasal capsules were rather large, perhaps 5 cm. long.

The dorsal surface of the premaxillary that is exposed through the external nares carries a broad groove, which might have served either for muscles or for the *cartilago alaris*. Because of the depth of the groove the author is inclined to believe that the latter suggestion is more nearly correct. The muscles about the choanae were, in all probability, not strong enough to cause such a scar.

A deeper, narrower groove occurs on the dorsomedian rim of the external nares on the lateral edge of the premaxillary and nasal bones. It also seems too deep to have been caused by muscles, and the author therefore tentatively suggests that it was occupied by the *cartilago obliqua*.

The relationships of the *processus maxillaris anterior* and the *processus maxillaris posterior* have already been noted (p. 82). The ventral surface of the roof of the skull shows only the impressions of the nasal capsules, so that nothing more can be ascertained concerning the dorsal surface of the chondrocranium in the ethmoidal region. The *commissura quadrato-cranialis anterior* has previously been discussed (p. 82).

Myology

The scars of several of the muscles of *Buettneria* show very plainly in skull No. 21326 (Fig. 8). An attempted restoration of the areas of origin of these muscles, outlined in red, is given in Figures 11–12. The right-hand side of Figure 11 represents the origins of muscles on the ventral surface of the roof of the skull; the left-hand side, those of muscles on the ventral surface of the palatal bones. Figure 12 shows the origins of certain of the muscles of the back of the skull. It will be noticed that the outlines of the scars and the areas of muscle attachment are not in all cases the same. This is due, of course, to the fact that the scar represents only the point of strongest attachment. The restoration must be accepted as diagrammatic only.

In the following paragraphs the names of muscles are in accordance with the terminology of Luther (1914) and Brock (1938).

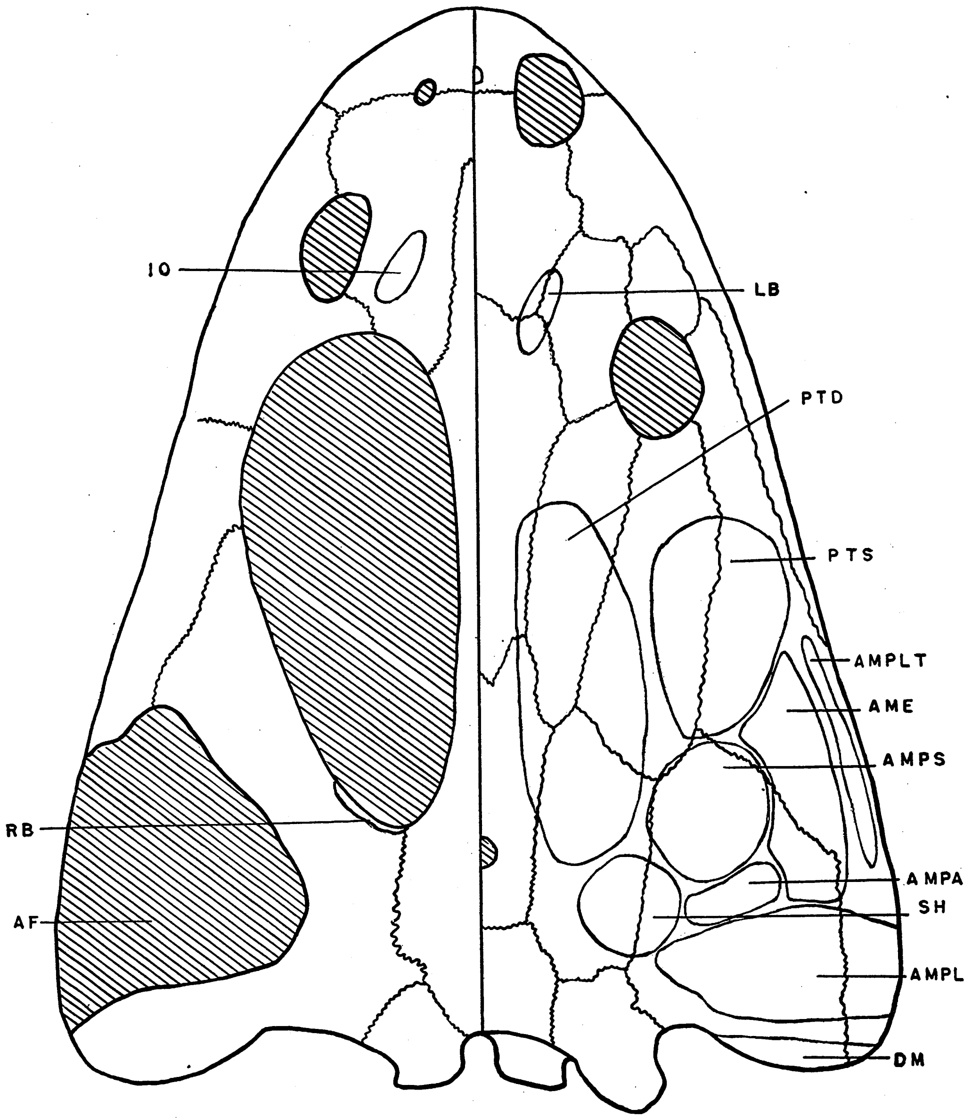

FIG. 11. For caption and abbreviations see bottom of opposite page

It is not the intention of the author to homologize the muscles of *Buettneria* with those of any one living form. The names are used for convenience only.

The *adductor mandibulae* muscles of *Buettneria* are quite numerous, numbering eight in all. The arrangement corresponds most closely to that of the larval *Anura*.

The *m. pterygoideus* in *Buettneria* is apparently divided into a deep and a superficial portion, both originating on the roof of the skull and not upon the pterygoid. The palatine ramus of the pterygoid is marked by ridges and grooves that apparently served to protect the blood vessels and nerves of the roof of the mouth. These can in no wise be interpreted as muscle scars.

The deep portion of the *m. pterygoideus* (PTD) originated in a very shallow depression that lies lateral to the median descending flange of the parietals and frontals. The depression seems to extend over the posterior part of the postfrontal, the posteromedial part of the postorbital, and the anteromedial part of the supratemporal.

Laterally, on the lateral portion of the postorbital and the median portion of the jugal, is a rather deep smooth depression which apparently was the origin of the superficial portion of the *m. pterygoideus* (PTS).

Posterior to the superficial portion of the *m. pterygoideus* and almost entirely upon the anterior end of the squamosal is a deep depression for the *m. adductor mandibulae posterior subexternus* (AMPS).

FIGURE 11

The right side shows the muscle attachments, outlined in red, on the ventral surface of the roof of the skull and also their relation to the sutures; the left side shows the muscle attachments on the ventral surface of the palatal bones. × about $\frac{1}{3}$

Abbreviations: AF, adductor fenestra; AME, *m. adductor mandibulae externus;* AMPA, *m. adductor mandibulae posterior articularis;* AMPL, *m. adductor mandibulae posterior longus;* AMPLT, *m. adductor mandibulae posterior lateralis;* AMPS, *m. adductor mandibulae posterior subexternus;* DM, *m. depressor mandibulae;* IO, *m. obliquus inferior;* LB, *m. levator bulbi;* PTD, deep portion of the *m. pterygoideus;* PTS, superficial portion of the *m. pterygoideus;* RB, *m. retractor bulbi;* SH, *m. suspensorius hyoideus*

Posterior and slightly lateral to the *m. adductor mandibulae posterior subexternus* is a depression for the *m. adductor mandibulae posterior articularis* (AMPA). It is the smallest but also the deepest. This muscle must have been a powerful one.

Lateral to the *m. adductor mandibulae posterior articularis, m. adductor mandibulae posterior subexternus,* and the posterior portion of the superficial portion of the *m. pterygoideus* is an elongate depression that probably served as the origin for the *m. adductor mandibulae externus* (AME). It is on the posterior portion of the jugal and the anterolateral portion of the squamosal.

The *m. adductor mandibulae posterior lateralis* (AMPLT) had its origin in a long shallow groove lateral to the origin of the *m. adductor mandibulae externus.* The *m. adductor mandibulae posterior longus* (AMPL) had its origin, in part, on the anterior surface of the squamosal, just anterior to the quadrate.

A muscle must have originated in a depression just anterior to the attachment of the quadrate ramus of the palatoquadrate to the roof of the skull. This attachment was probably for the *m. suspensorius hyoideus* (?) (SH), which supported the hyoid apparatus. In this case, however, the author is less certain than in the others.

The *m. adductor internus pseudotemporalis* has an origin on the epipterygoid in *Sphenodon, Lacertilia,* and *Chelonia.* The only way in which the author can explain the pits on the epipterygoid is to suggest that they were the places of origin of two slips of the *adductor internus pseudotemporalis.*

All the *adductor mandibulae* muscles passed through the adductor fenestrae (AF; subtemporal fenestra) and were inserted on the lower jaw. Unfortunately there is not a lower jaw that is well enough preserved to show these insertions.

There are several other muscle attachments (Figs. 11–12) that can easily be discerned on the ventral surface of the roof of the skull of *Buettneria.* The *m. depressor mandibulae* (DM) undoubtedly originated in a shallow groove on the extreme posterior edge of the squamosal. A shallow groove on the ventral surface of the skull roof is directed diagonally on the anterior portion of the frontal, the posterolateral surface of the nasal, and the median surface of the prefrontal; it probably served as the place of origin for the *m. levator bulbi* (LB).

The left-hand side of Figure 11 represents the ventral surface of the palate. Several muscle scars can be found, but only two are identified with confidence. A sharp groove on the pterygoid at the posterior margin of the interpterygoid vacuity probably was the place of origin for the *m. retractor bulbi* (RB). In the Spitsbergen forms a similar groove is mentioned by Säve-Söderbergh (1936) as situated on the dorsal surface at the base of the cultriform process.

A groove on the ventral surface of the prevomer directed posterolaterally was probably the origin of the *m. obliquus inferior* (IO).

Two very prominent muscle scars partly cover the ventral surfaces of the exoccipital, the parasphenoid, and the pterygoid close to the posteromedian end of the skull. The muscles that originated here must have been attached to some part of the shoulder girdle and are indeterminate.

Four muscle attachments on the posterior face of the skull (Fig. 12) can be identified with certainty. The terminology of Evans (1939) is used for the posterior muscles. A small triangular pit directly above the *foramen magnum* undoubtedly served as the origin of the *mm. spinalis capitis* and *rectus capitis posterior* (SC + RCP). Lateral to this is a very deep pit that lies on the suture between the dermsupraoccipital and the tabular. This pit, it is thought, was the place of origin for the *m. longissimus capitis pars articulo-parietalis* (LCA). The *m. obliquus capitis magnus* (OCM) apparently had its origin in another pit directly below the one occupied by the *m. longissimus capitis pars articulo-parietalis.* Just dorsal to the occipital condyles a shallow depression is the origin for the *m. longissimus capitis pars transversalis capitis* (LCTC).

Other scars which served as places of origin for muscles that united the clavicular apparatus with the skull are found on the back of the skull. The author does not feel, however, that they can be identified with enough certainty to make the attempt worth while.

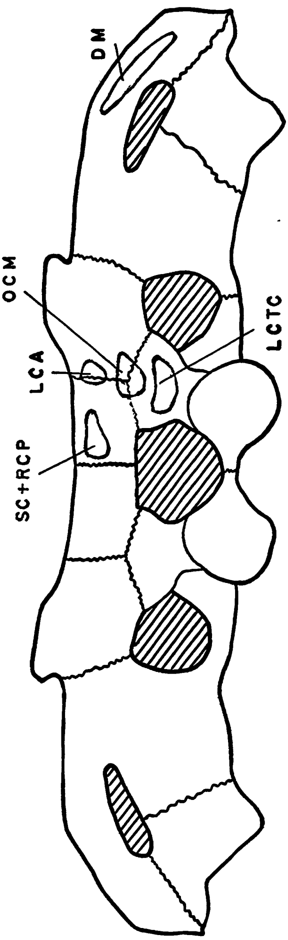

FIG. 12. Muscle attachments, outlined in red, on the back of the skull

Abbreviations: DM, *m. depressor mandibulae;* LCA, *m. longissimus capitis pars articulo-parietalis;* LCTC, *m. longissimus capitis pars transversalis capitis;* OCM, *m. obliquus capitis magnus;* SC + RCP, *m. spinalis capitis + rectus capitis posterior*

Neurology

The exits of the cranial nerves (Fig. 10, right side) are restored with confidence because of their relation to certain fixed points in the skull. The impressions of the olfactory lobes in the sphenethmoid were found by Säve-Söderbergh (1936) to be extended anteriorly for a considerable distance in *Lyrocephalus*. Because of the close similarity of the endocranial anatomy of *Buettneria* and *Lyrocephalus* it is assumed by the author that the olfactory lobes (OLL) of *Buettneria* were also quite long. The exit of the *n. opticus* (II) has not been found, but it must have left the brain case slightly anterior to the epiphysis.

The foramen for the *n. occulomotorius* (III) has been described on page 85. As suggested by Säve-Söderbergh, the *n. trigeminus* (V) and the *n. facialis* (VII) probably left the brain by a common foramen. The *r. palatinus* proceeded in an anterior direction medial and ventral to the basal process of the palatoquadrate. In all probability its posterior foramen is beneath the basal process of the epipterygoid. The anterior foramen (Fig. 1, FPAL) is anterolateral to the median foramen for the *a. carotis interna*. The *r. ophthalmicus profundus V* (V_1) left the Gasserian ganglion (GGL) and passed forward dorsal to the basal process and ventromedial to the ascending process of the epipterygoid. The *r. maxillaris V* (V_2) and the *r. mandibularis V* (V_3) passed dorsal to the basal process and lateral to the ascending process of the epipterygoid. The *truncus hyomandibularis* (HY) left the posterolateral portion of the Gasserian ganglion, proceeded in a posterolateral direction, and passed out of the skull dorsal to the proximal end of the stapes. The *n. acusticus* (VIII) entered the otic capsule directly. The *n. glossopharyngeus* (IX) and the *n. vagus* (X) in all probability had separate roots which united before entering a common foramen. In the middle of the exoccipital they were joined by the *n. accessorius* (XI), which left the brain case by a different foramen. The three roots then left the exoccipital by a common foramen and passed posterolaterally to form the large vagus ganglion. The *n. hypoglossus* (XII) left the medulla at a point about halfway through the *foramen magnum* and passed through a foramen in the exoccipital posterior to the foramen for the IX, X, and XI.

A few other foramina can be seen which were obviously connected with the nervous system. On the anterodorsal surface of the prevomers are foramina for the *rr. palatini* (Fig. 13), which probably accompanied the *a. palatina.* Along the inner angle formed by the roof of the skull and the palate are numerous foramina for cutaneous branches of the *r. maxillaris V.* The foramina for the *r. palato-nasalis* (Säve-Söderbergh, 1936) are found medial to the *processus dorsalis* of the palatine bone.

A large foramen is on the posteroventral side of the premaxillary just beneath the anterior edge of the fenestra for the ventral tusk. It is believed by the author that the *r. terminalis medialis* of the *r. ophthalmicus profundus* (Fig. 6, RO) passed through this foramen and then branched out into its various cutaneous endings on the snout. A fortuitous break across this foramen shows several small canals radiating to the dorsal surface of the snout. They were for the cutaneous branches.

Angiology

Säve-Söderbergh (1936) describes the arterial and venous systems of *Lyrocephalus.* An attempt is made here to do the same for *Buettneria,* and the results on the whole seem to corroborate Säve-Söderbergh's work. Certain foramina which are well known were taken as starting points. With the works of Goodrich (1930), Ecker, Wiedersheim, and Gaupp (1899), Francis (1934), and Säve-Söderbergh (1936) a small part of the vascular system of *Buettneria* can be reconstructed (Figs. 13–14).

Of the arterial system (Fig. 13) only the branches of the *a. carotis interna* (CI) can be restored with any confidence. The *a. carotis interna* enters the back of the skull a little anterior to the suture of the pterygoid and the exoccipital. Just before it reaches the pterygoid a ventral branch is given off, the *a. palatina.*

The *a. palatina* (APAL) passes in an anterior direction in a groove on the ventral surface of the pterygoid. A lateral branch corresponding to the *r. mucosi postorbitalis* of the frog (Ecker, Wiedersheim, and Gaupp, 1899) is given off at the base of the palatine ramus of the pterygoid. The groove for the *r. mucosi postorbitalis* (RMP) can be followed more than half the length of the palatine ramus of the pterygoid.

The main stem of the *a. palatina* continues in an anterior direction to the anterior edge of the interpterygoid vacuity, where it proceeds over the dorsal surface of the prevomer. The larger portion of the *a. palatina* (TPAL) seems to pass somewhat medial and to enter an anterior foramen. A smaller terminal branch enters another foramen a little posterolateral to it. The *r. communicans* leaves the lateral terminal branch of the *a. palatina* and passes posterior to the internal nares to meet a *r. communicans* of the *a. maxillaris.* From this anastomosis a *r. palatonasalis* (RPN) extends anteriorly.

The main stem of the *a. carotis interna* gives off the *a. orbitalis* (AORB) slightly anterior to the junction of the *a. palatina.* The *a. orbitalis* passes in a posteromedial dorsal direction to a groove on the posterior edge of the stapes. This groove lies on the dorsal surface of the stapes and crosses it diagonally in an anterior direction. The *a. orbitalis,* which must have occupied this groove, passes over the stapes and not through it, as in *Lyrocephalus* (Säve-Söderbergh, 1936). It will be noted that a foramen was found on the stapes in the proper position for a stapedial foramen, but for two reasons the author is convinced that it did not conduct the *a. orbitalis.* First and more convincing, no exit for this foramen can be found on the ventral surface of the stapes. Secondly, the foramen is very small and could not have been occupied by an artery that must have been of considerable size.

The *a. orbitalis,* after leaving the dorsal surface of the stapes, passed anteriorly through the *cavum epipterieum.* A short distance anterior to the *cavum epiptericum* it gave off a lateral branch, the *a. mandibularis* (AMD). This artery probably accompanied the *n. mandibularis* to the lower jaw.

The main stem of the *a. orbitalis* continued anteriorly, and gave off another lateral branch, the *a. maxillaris* (AMX). This artery probably accompanied the *n. maxillaris.* The *a. maxillaris* proceeded lateral to the internal angle of the roof of the skull and the palate and probably gave off several cutaneous branches.

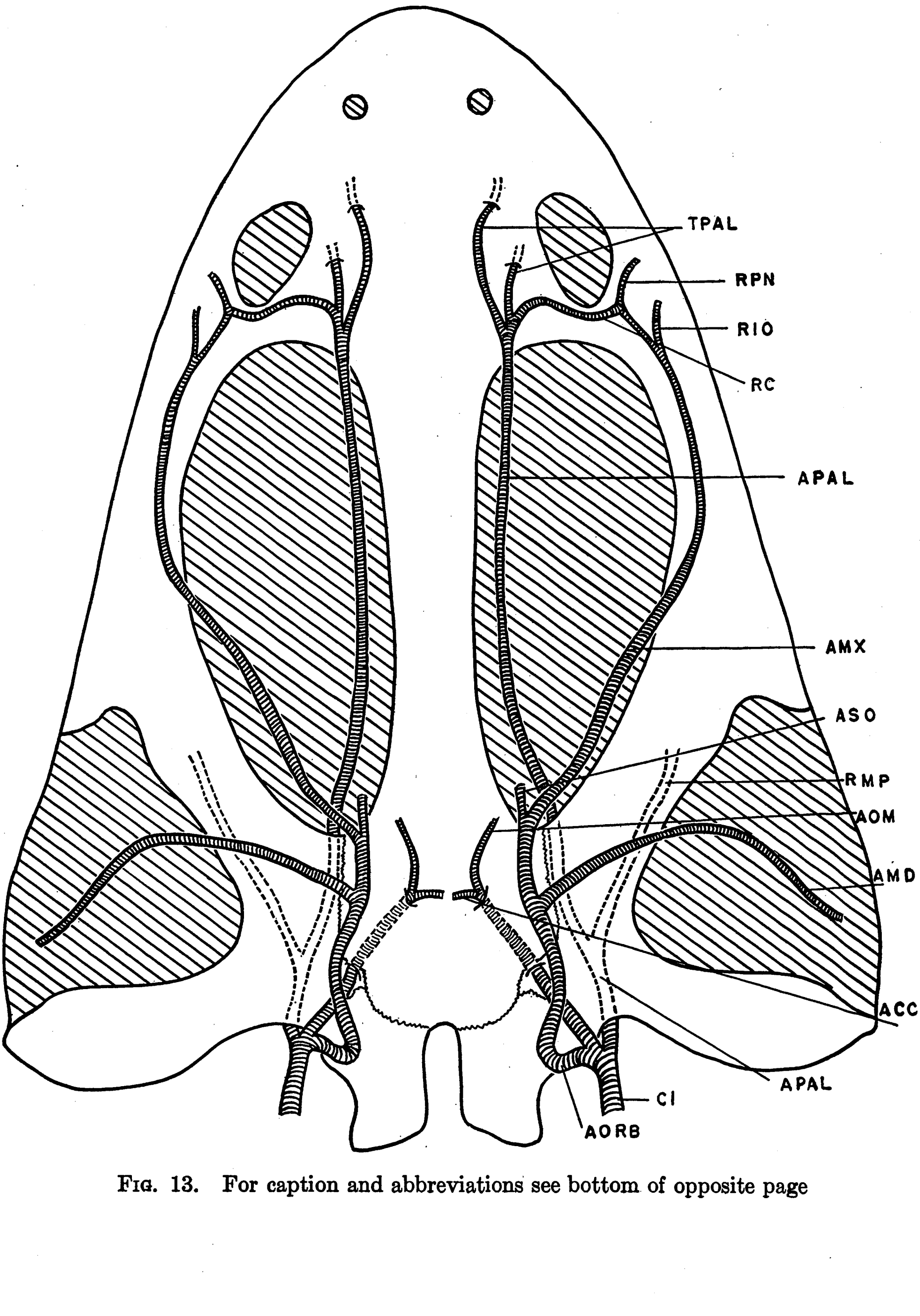

FIG. 13. For caption and abbreviations see bottom of opposite page

It then passed in an anteromedial direction, ventral to the orbit, and just anterior to the orbit gave off an *a. infraorbitalis* (RIO). The main stem of the *a. maxillaris*, termed by Säve-Söderbergh the *r. communicans* of the *a. maxillaris*, continued anterior and joined the *r. communicans* of the *a. palatina*.

The internal carotid, after giving off the *a. orbitalis*, passed anteromedially into a tunnel on the parasphenoid. The author agrees with Säve-Söderbergh (1936) and Watson (1919) and differs with the published opinion of Case (1922) on the direction taken by the *a. carotis interna* as they passed through the tunnel on the parasphenoid. Case states his view thus: " . . . the internal carotid arteries entered the skull through the posterior part of the palatine vacuities and then turned backward." In numerous conferences Dr. Case gave the author permission to state that he admits the possibility of the present interpretation, which is held by others, but he by no means considers it proved.

The *a. carotis interna* emerged from the anterior end of the tunnel on the parasphenoid inside the brain case. It gave off a median branch, the *a. carotis cerebralis* (ACC), to supply blood to the brain. The main stem of the *a. carotis interna* passed anteriorly and left the brain case as the *a. ophthalmica* (AOM).

The venous system of *Buettneria* cannot be restored with the same degree of confidence as the arterial system, owing to the fewer fixed relationships of it and the bones of the skull (Fig. 14).

The passage of the *v. jugularis interna* (VJI) through the *cavum epiptericum* is a constant character, so that it may be restored with confidence.

Another point of the venous system of the stereospondyls seems to be well established in the literature — the passage of the

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FIGURE 13

Diagrammatic reconstruction of the course of the *a. carotis interna* and some of its main branches. × about $\frac{1}{3}$

Abbreviations: ACC, *a. carotis cerebralis;* AMD, *a. mandibularis;* AMX, *a. maxillaris;* AOM, *a. ophthalmica;* AORB, *a. orbitalis;* APAL, *a. palatina;* ASO, *a. suborbitalis;* CI, *a. carotis interna;* RC, *ramus communicans* of the *a. palatina;* RIO, *a. infraorbitalis;* RMP, *r. mucosi post orbitalis* of the *a. palatina;* RPN, *r. postnasalis;* TPAL, terminal branches of the *a. palatina*

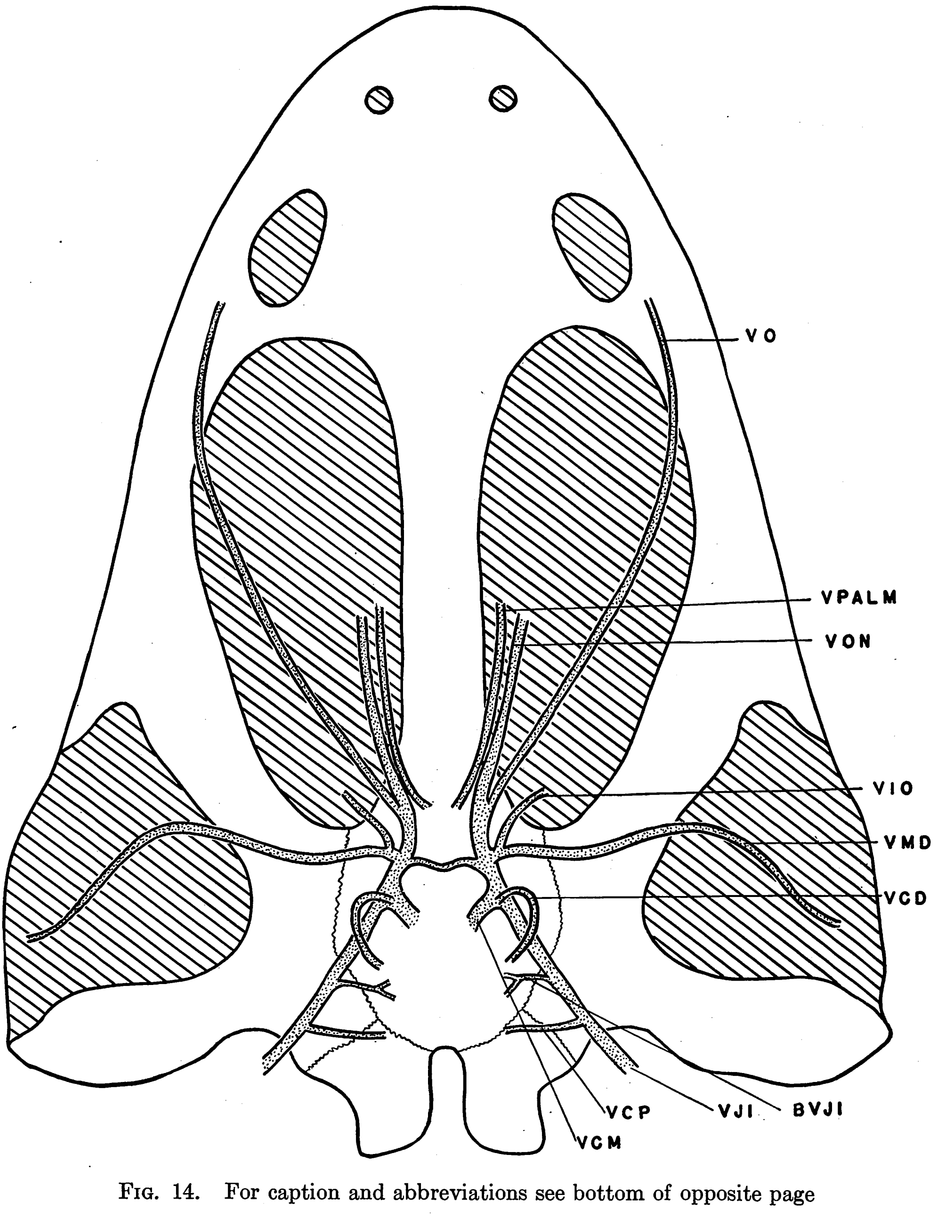

FIG. 14. For caption and abbreviations see bottom of opposite page

v. capitis dorsalis (VCD) through a groove that lies on the dorsal part of the suture between the proötic and the quadrate ramus of the pterygoid.

The *v. jugularis interna* must have left the skull close to the entrance of the *a. carotis interna,* but dorsal to the stapes.

A groove in the dorsal surface of the otic capsule is thought to have been occupied by a branch of the *v. jugularis interna.*

These points are all that can be tentatively or certainly identified for the venous system. The diagram of the venous system as given by Säve-Söderbergh seems, however, to represent correctly the conditions that must have been common to most stereospondyls. It is therefore repeated in part since it would apply to *Buettneria* with several additions and modifications.

MORPHOLOGICAL CONCLUSIONS

This study of the cranial anatomy of *Buettneria* from a nearly complete specimen has given the following morphological results:

1. Well-ossified epipterygoids, stapes, and proötics are present.
2. The ethmoidal region provides evidence for the presence of an intermaxillary gland that had certain features which are present in both the *Anura* and the *Urodela,* which seems to substantiate the theory that the gland is homologous in the two groups.
3. An interrostral fenestra found on the roof of the skull was occupied by an anterior portion of the intermaxillary gland.
4. There is evidence that a *glandula nasalis lateralis* was present.
5. An impression posterior to the parietal foramen probably was occupied by the parapineal organ.
6. A partial ossification of the opisthotic is found in its proper position.

FIGURE 14

Diagrammatic reconstruction of the course of the *v. jugularis interna* and some of the main branches. × about $\frac{1}{3}$

Abbreviations: BVJI, lateral branch of the *v. jugularis interna;* VCD, *v. capitis dorsalis;* VCM, *v. capitis medialis;* VCP, *v. capitis posterior;* VIO, *v. infraorbitalis;* VJI, *v. jugularis interna;* VMD, *v. mandibularis;* VO, *v. ophthalmicus;* VON, *v. orbitonasalis;* VPALM, *v. palatina medialis*

7. The presence of a descending process of the squamosal interlocking between two ascending processes of the quadrate ramus of the pterygoid is confirmed.

8. A partial ossification of the palatoquadrate cartilage between the epipterygoid and the quadrate is discovered for the first time.

9. The chondrocranium can be restored from impressions on the dorsal surface of the palate and the ventral surface of the roof of the skull.

10. The outline of the origins of several of the cranial muscles can be traced.

11. Important morphological structures that are closely related to the nervous system can be identified so that the exits of the cranial nerves can be located.

12. Important morphological structures that are closely related to the vascular system of the head are determined, so that the course of certain arteries and veins may be postulated.

GENERAL CONCLUSIONS

Buettneria is a stereospondylous amphibian which belongs to the family *Metoposauridae* and the subfamily *Buettneriinae*. Other well-known members of the subfamily are *Anachisma*, *Koskinodon*, *Borborophagus*, and *Kalamoïketor*. All the North American genera of Upper Triassic *Stereospondyli* so far discovered are very similar and can be placed in this one subfamily. It is a sharp contrast to the great variety of Upper Triassic stereospondyls which are found in Europe. Of the European forms *Metoposaurus* is most closely related to *Buettneria*.

The ancestor of the *Metoposauridae* is believed to have been some Permian rachitimous form. Säve-Söderbergh (1935), in classifying the Amphibia by means of the dermal bones of the skull roof, describes the ancestors of the *Metoposauridae* thus:

> Another quite remarkable instance of a rachitimous type, apparently nearly related to a stereospondylous family, is furnished by *Trimerorhachis*. Together with the two genera *Micropholis* and *Broiliellus*, certainly nearly related to each other, — possibly also with the other *Dissorophidae*, which are very incompletely known, — *Trimerorhachis* forms a group, which seems rather

clearly to belong to the line, represented, among the "*Stereospondyli*," by the *Metoposauridae* . . . .

Together with the *Metoposauridae* the mentioned rachitimous *Labyrinthodontia* (*Trimerorhachidae, Broiliellus, Micropholis, Dissorophidae?*) may be included in a superfamily *Metoposauroideae* . . . .

It must be remembered that Säve-Söderbergh's classification is based on the dermal bones of the skull and that he has rejected the established one based on the character of the vertebrae. His proposal has not been accepted in its entirety.

In the author's opinion *Trimerorhachis* had already become in the Permian a specialized form representing the end point of a group of aquatic rachitimous forms. Certain structures were so speciaized that it could not have been the ancestor of any stereospondylous type.

Several conditions in the skull of *Trimerorhachis* which seem to exclude it from the line of ancestry of the *Buettneriinae* are:

1. No ossified proötic has ever been found.
2. No ossified epipterygoid has ever been found.
3. The *a. carotis interna* seems to enter the brain case anterior to the articulation of the pterygoids with the parasphenoids.
4. There is a cartilaginous, not sutural, attachment between the pterygoids and the basisphenoids.

The evaluation of these characters will be further discussed by the author in a study of *Trimerorhachis*.

ADDENDUM

Since this paper was completed there has been received a detailed account of the osteology of *Benthosuchus sushkini* Efremov.[2] The English summary does not contain a full description of all details, but, with a careful study of the figures, it shows that Bystrow and Efremov have proposed nothing that conflicts with the present interpretation of *Buettneria*.

[2] Bystrow, A. P., and Efremov, J. A., "Benthosuchus sushkini Efr., a Labyrinthodont from the Eo-Triassic of Sharzhenga River," *Travaux de l'Institut paléontologique*, Académie des sciences de l'Union des République socialistes soviétiques, Tome X, Livre 1, 1940.

There are two things that the author wishes to mention:

1. There is in *Benthosuchus* an interrostral fenestra which is called by Bystrow and Efremov "the *foramen interpraemaxillare.*" The other structures that were associated with the *glandula intermaxillaris* in *Buettneria* do not appear in *Benthosuchus.*

2. In the description of the pterygoid Bystrow and Efremov make this statement: "Behind the base of the lamina ascendens lies a very distinct hollow — excavatio tympanica (fig. 6b), which served as the anterior wall of tympanical cavity." It is assumed by the author that by "tympanical cavity" Bystrow and Efremov mean the *cavum tympanum.* A cavity that lies in the same relative position as the *excavatio tympanica* of *Benthosuchus* can be found in *Buettneria* just posterior to the base of the anterior rising process of the quadrate ramus of the pterygoid and medial to the base of the posterior rising process of the quadrate ramus of the pterygoid. In *Buettneria* this cavity is 2 cm. lateral and slightly anterior to the outer wall of the proötic. From the relationship of this cavity to the proötic in *Buettneria* it seems more probable that the "*excavatio tympanica*" marks the origin of some muscle which connected with the shoulder girdle.

In *Buettneria* the otic capsule lies medial to the external entrance of the tunnel for the *a. carotis interna* on the parasphenoid, and the suggestion is now made that in *Benthosuchus* it lay just medial to the ridge on the parasphenoid called by Bystrow and Efremov the "crista parapterygoidea."

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