

## TRIASSIC METOPOSAURID AMPHIBIANS

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## CONTENTS

INTRODUCTION . . . . .	405
Acknowledgments . . . . .	406
LOCALITIES AND HORIZONS FROM WHICH TRIASSIC METOPOSAURS HAVE BEEN COLLECTED.	408
A TAXONOMIC REVIEW OF THE METOPOSAURIDAE . . . . .	410
The Described Genera and Species of Metoposaurs . . . . .	410
SOME CONSIDERATIONS OF METOPOSAUR OSTEOLOGY . . . . .	424
Skull and Jaws . . . . .	424
Postcranial Skeleton . . . . .	426
BIOMETRIC ANALYSIS OF AMERICAN METOPOSAURS . . . . .	429
Bivariate Characterization . . . . .	430
Bivariate Discrimination Test . . . . .	433
Estimation of Bivariate Overlap . . . . .	434
Multivariate Characterization . . . . .	437
Summary of Results . . . . .	438
THE GENERA AND SPECIES OF METOPOSAURS . . . . .	443
Discussion . . . . .	443
Conclusions . . . . .	449
BIBLIOGRAPHY . . . . .	451





## INTRODUCTION

DURING LATE TRIASSIC TIMES the labyrinthodont amphibians entered the final stages of their evolutionary history. These were the terminal members of a long phylogenetic line that extended back to the close of the Devonian period, and as such they represented a group of vertebrates that had been persistently successful over a time lapse of more than 100 million years. Even though the labyrinthodonts were destined to become extinct at the close of Triassic times, these amphibians were numerous and successful throughout the Triassic period. Their demise was certainly not a slow and gradual process; rather the evolutionary development of these interesting amphibians continued with seeming vigor up to the end of the Triassic period, at which time they disappeared suddenly and completely from all the continents.

The first land-living vertebrates were labyrinthodonts, which appeared as direct descendants from certain crossopterygian fishes during the transition from Devonian to Carboniferous times. For a period of geologically brief duration the ancient labyrinthodonts had the land to themselves, but very soon the first reptiles arose from amphibian ancestors to share the land. Even with these active reptilian competitors around them, the labyrinthodonts continued as very successful tetrapods; indeed, they reached what was perhaps the culmination of their evolutionary history during the Permian period, when there were many large, aggressive reptiles in the world. Some of the rhachitomous labyrinthodonts of Permian times were themselves rather aggressive animals, and it is likely that they could compete actively and directly with many of their reptilian contemporaries. These amphibians were large and strong, well able to live either in streams and ponds, or out on the land. In some parts of the world the Permian labyrinthodonts were among the most numerous of the animals that constituted the faunas where they lived.

The success of the late Paleozoic labyrinthodont amphibians was carried over into Triassic times, but on a basis different from its Permian expression. The Triassic labyrinthodonts belonging to the Order Stereospondyli

were descended from the Permian labyrinthodonts of the Order Rhachitomi. But whereas the Permian forms were strong and well adapted to life either in the water or on the land, the Triassic types were characteristically adapted to an almost complete aquatic existence. Some of the Triassic labyrinthodonts were even larger than their Permian forbears (in fact certain genera among the stereospondyls were the all-time amphibian giants, with skulls that were more than a meter in length), but they had weak vertebral columns and comparatively small, feeble limbs, which would seem to indicate that they may never have left the water. Yet they were obviously very successful in the environment to which they were adapted, for their remains in some regions are among the most common of Triassic fossil vertebrates.

One group of Triassic stereospondyl labyrinthodonts is that of the family Metoposauridae, so named from the European genus *Metoposaurus*. These amphibians were all of late Triassic age. The skeleton in the metoposaurs is commonly 2 meters or more in length and is characterized by the relatively enormous, flat skull. As is typical of the labyrinthodonts, the skull roof is complete, being pierced only by the openings for the orbits and the nostrils, and by the single pineal opening, placed along the median line near the back of the skull roof. The jaws are long and bear numerous labyrinthodont teeth, as do the premaxillary and maxillary bones in the skull. There are also teeth upon the palate. The palate is pierced by very large palatal vacuities, separated by a long parasphenoid bone which is suturally and firmly connected at the back with the pterygoid bones on either side.

The bones of the skull roof are extraordinarily thick and heavy and deeply sculptured on their dorsal surfaces. Certainly one reason for the abundance of metoposaur remains in upper Triassic continental sediments is to be found in the thick, comparatively indestructible nature of the skull bones. The same is true of the ventral bones in the shoulder girdle, namely, the interclavicle and the clavicles. These are thick bones, heavily sculptured.

In contrast to the thick bones of the skull and of parts of the shoulder girdle, the other parts of the skeleton in the metoposaurs are remarkably weak. The centra and the spines of the vertebra are solid enough, but otherwise there is evidence of a strong, secondary trend towards cartilage in the axial skeleton. For instance, although the limb bones and bones of the fingers and toes are well formed, they are comparatively small, while there is little evidence as to the structure of the wrist and ankle, these portions of the skeleton having been evidently mainly cartilaginous.

Considerable numbers of metoposaur skulls, interclavicles, and clavicles (and to a lesser extent other parts of the skeleton) have been found in the upper Triassic sediments of Europe and North America. These fossils give us an opportunity to learn something about the metoposaurs and about the world they lived in. For example, enough metoposaur remains have been found in close association at certain localities to give fair samples of populations.

No fewer than 10 genera and 19 species of metoposaurs from upper Triassic sediments have been described, of which eight genera and 14 species are North American. Many of the descriptions were based on single specimens, as was frequently necessary, and many of them were made without adequate comparisons to genera and species already known. This multiplication of names gives a variety to the lists of upper Triassic faunas of North America and creates the appearance of differences between the several faunas that may be more imaginary than real. Consequently the differences between the faunas have received undue stress, while the similarities have sometimes been overlooked.

The purpose of the present paper is to survey the upper Triassic metoposaurs of North America, in an attempt to place their relationships on as objective a basis as possible. First there is a survey of the known genera and species of metoposaurs of this continent. Then there is a study of certain populations, with an attempt to evaluate their relationships to one another. Finally, on the basis of these population studies, an attempt is made to determine the validity of the various genera and species and to indicate their interrelationships.

#### ACKNOWLEDGMENTS

We wish to express our deep appreciation to Prof. Alfred S. Romer, Director of the Museum of Comparative Zoölogy at Harvard College, for facilities and assistance that made possible the study and measurements of the metoposaurs found near Lamy, New Mexico, in that institution. Likewise, similar thanks and appreciation are due to Drs. C. Lewis Gazin and David Dunkle of the United States National Museum for making possible the study and measurements of the metoposaurs, also from the Lamy location, in Washington. Again, our thanks and appreciation go to Mr. Boone McClure and Mr. J. T. Hughes, Director and Curator, respectively, of the Panhandle-Plains Museum at Canyon, Texas, for the opportunity to study and measure their unusually large collection of metoposaurs from Potter County, Texas.

To Prof. Charles L. Camp and to Dr. S. P. Welles of the University of California we are indebted for permission to make measurements of some metoposaurs in the Museum of Paleontology at Berkeley, which were found near St. Johns, Arizona. We are also indebted to Dr. E. C. Olson of the University of Chicago and to Dr. Rainer Zangerl of the Chicago Natural History Museum for permission to study and measure the metoposaurs from Wyoming that are now in the collections of the Chicago Museum. Data on specimens in the universities of Michigan, Missouri, and Texas, and in Princeton University, were taken from publications, as were those for specimens in European museums.

Abbreviations for the above-mentioned institutions, and for the American Museum of Natural History, as used in this paper, are as follows:

- A.M.N.H., the American Museum of Natural History
- C.N.H.M., Chicago Natural History Museum
- M.C.Z., Museum of Comparative Zoölogy, Harvard College
- M.P.U.M., Museum of Paleontology, University of Michigan
- P.U., Princeton University
- U.C., University of California, Berkeley
- U.M., University of Missouri
- U.S.N.M., United States National Museum
- U.T., University of Texas

The drawings that illustrate this paper were made by Mr. Michael Insinna, and some of the graphs were prepared by Mr. William G. Heaslip.

In tables 1 through 9 the sample numbers indicate groups of specimens treated as statistical populations. The explanation of the sample numbers is as follows:

SAMPLE 1: Specimens from a quarry in the Chinle formation, near Lamy, New Mexico, in the Museum of Comparative Zoölogy and the United States National Museum.

SAMPLE 2: Specimens from a quarry in the Dockum formation, Potter County, Texas; Panhandle-Plains Museum, Canyon, Texas.

SAMPLE 3: Specimens from a quarry in the Dockum formation, Howard County, Texas, at the University of Texas.

SAMPLE 4: A single small skull from Howard County, Texas: original at the University of

Texas; cast in Texas Technological College Museum.

SAMPLE 5: The type of *Buettneria perfecta*, M.P.U.M. No. 7475.

SAMPLE 6: The type of *Buettneria bakeri*, M.P.U.M. No. 13055.

SAMPLE 7: Four specimens from the Popo Agie formation, between Lander and Bull Lake Creek, Wyoming, at the Chicago Natural History Museum and at the University of Missouri.

SAMPLE 8: Four specimens from the Chinle formation, between St. Johns and Cameron, Arizona, at the Museum of Paleontology, University of California.

In tables 1 through 4, groups of measurements of skulls, clavicles, and interclavicles are made on individual specimens, and there is no assurance of association among skulls and postcranial elements.

## LOCALITIES AND HORIZONS FROM WHICH TRIASSIC METOPOSAURS HAVE BEEN COLLECTED

THE FIRST METOPOSAUR to be made known to the scientific world was *Metopias diagnosticus*, described in 1842 by von Meyer, the type specimen of which was found in the upper Triassic or Keuper beds of Germany. In later years additional fossils have been discovered in southern Germany and described, but up to the present time not very many specimens of these amphibians have been found in the European region. Such fossils as have been found seem to be isolated specimens, most of them fragmentary. In spite of the intensive scouting of European Triassic exposures no associated populations have come to light (at least so far as can be determined from the literature); consequently it is necessary to turn to the North American discoveries in order to obtain an adequate knowledge of probable metoposaur relationships. The name *Metopias*, not being valid, was replaced by *Metoposaurus* by Lydekker in 1890.

Metoposaurs are known in the upper Triassic Maleri beds of central India. These fossils, reviewed by von Huene in 1940, are very fragmentary and consist of vertebral intercentra, portions of some occipital condyles of the skull, some pieces of the skull roof, and some sections of interclavicles and clavicles, one interclavicle being fairly completely represented. Von Huene did not attempt to give these fossils a formal name, a sound decision in view of the incomplete nature of the fossils.

The first metoposaurs from North America were discovered and described about a hundred years ago by Leidy and by Cope. Leidy described *Dictyocephalus*, which is a very small and fragmentary specimen that may be of metoposaurid relationships, from the sediments of the Newark group in North Carolina. Cope described *Eupelor*, an undoubted metoposaur, from the Newark beds of eastern Pennsylvania. Since then very little additional material has been found in the Newark sediments.

After Leidy's description of *Dictyocephalus* in 1856 and Cope's descriptions of *Eupelor* in 1866 and 1868, no further discoveries of

metoposaurs were made in North America until after the turn of the century. Then in 1904 Lucas described the interclavicle of a metoposaur from the Chinle formation of northern Arizona, the specimen having been found by Barnum Brown. At about the same time E. B. Branson described some skulls of metoposaurs from the Popo Agie formation, west of Lander, Wyoming; on these skulls he based his new genus *Anaschisma*.

Sinclair described a fragment of a jaw from the Newark group in 1917, and in 1920 Case described an interclavicle with associated clavicles from the Dockum formation of western Texas. Shortly thereafter, in 1922, Case described very fine materials from the Dockum formation, and on them he founded a new genus *Buettneria*. This was the first adequate description of metoposaurs from the southwestern Triassic.

Since that time numerous discoveries of metoposaurs have been made in the Dockum and Chinle formations of Texas, New Mexico, and Arizona, some of which have been described. In addition, Branson and Mehl described in 1929 some supplementary skulls and other skeletal materials from the Popo Agie formation of Wyoming.

At this place it might be well to mention three of the more important discoveries from the Triassic of the southwest, which receive special attention in this paper. These discoveries were made during the 1930's, two of them in the Dockum formation in western Texas, one in the Chinle formation in northern New Mexico. In all three instances the discoveries led to the opening of very rich quarries, from which abundant fossils, deposited in the greatest profusion, were collected.

The New Mexico locality is about 16 miles south of Lamy, at a place where outcrops of the Chinle formation are not far from Highway 285. This locality was first excavated by Robert V. Witter and T. E. White in 1938 for the Museum of Comparative Zoölogy at Harvard. A large and impressive block containing many skulls and other bones (illustrated in pl. 28, fig. 1, of the present paper)

was taken from the quarry. Subsequently David Dunkle of the United States National Museum obtained a second block (pl. 28, fig. 2) from this locality. The specimens in these two blocks represent one of the populations analyzed on subsequent pages of this paper, on the basis of measurements and studies of the original material made by the senior author.

During the years 1939-1942 some excavations were made in Howard County, Texas, by government project workers, under the direction of paleontologists at the University of Texas. This work was done about 3 miles north of Otis Chalk, which is southeast of Big Spring. As a result quite a few metoposaur skulls and other bones were recovered, and this material was described by Sawin in 1945. The analysis of the population represented by these fossils is based on the data presented in Sawin's publication.

At about the same time an extraordinarily large series of skulls, jaws, and postcranial skeletal parts was excavated, also by government project workers, under the direction of C. Stuart Johnston of the Panhandle-Plains Museum at Canyon, Texas, from the Herring Ranch, Potter County, west of Amarillo, Texas. These fossils are now housed at the

museum in Canyon. Data for the analysis of this population were gathered by the senior author at Canyon in the spring of 1954.

In addition to these three large undoubted population samples, two suites of fossils cited in the present paper are here considered as representing population samples. One of these consists of several skulls, four of which were described and figured by Branson and by Mehl from the Popo Agie formation of Wyoming. These specimens, assigned to three genera and four species, were collected along the strike of the Popo Agie beds, as exposed in the area between Lander and Bull Lake. This exposure stretches over a linear distance of about 35 miles, which we consider as easily within the limits that might have been occupied by a single population. The other suite of fossils consists of a number of undescribed metoposaur skulls from Arizona, found between St. Johns and Cameron. Here the distance is about 150 miles, but again we do not consider such a distance as excessive for the range of a single population. These two suites are treated statistically in the same manner as are the large population samples from Potter County and Howard County, Texas, and from near Lamy, New Mexico.

## A TAXONOMIC REVIEW OF THE METOPOSAURIDAE

THE 19 SPECIES AND 10 GENERA of metoposaurs, mentioned above, are here listed, in chronological order of description, as follows:

- Metoposaurus diagnosticus* (Meyer), 1842  
*Dictyocephalus elegans* Leidy, 1856  
*Eupelorus durus* (Cope), 1866  
*Metoposaurus fraasi* Lucas, 1904  
*Anaschisma browni* Branson, 1905  
*Anaschisma brachygnatha* Branson, 1905  
*Metoposaurus stuttgartiensis* Fraas, 1913  
*Metoposaurus santaecrucis* (Koken), 1913  
*Calamops paludosus* Sinclair, 1917  
*Metoposaurus jonesi* Case, 1920  
*Buettneria perfecta* Case, 1922  
*Buettneria* (?) *major* Branson and Mehl, 1929  
*Borborophagus wyomingensis* Branson and Mehl, 1929  
*Koskinonodon princeps* Branson and Mehl, 1929  
*Kalamoiketos pinkleyi* Branson and Mehl, 1929  
*Buettneria bakeri* Case, 1931  
*Trigonosternum latum* Schmidt, 1931  
*Metoposaurus heimi* Kuhn, 1932  
*Buettneria howardensis* Sawin, 1945

Before an analysis of the populations with which this paper is particularly concerned and a general evaluation of the genera and species of metoposaurs are given, a review of the described forms and a general description of metoposaur osteology are presented, as a background against which the present study has been made.

The evidence as to the validity of genera and species included in the taxonomic review is presented in a subsequent section of the paper and is based on the results of the statistical studies of various populations of North American metoposaurs. It might be well to state here that opinions as to the numbers of genera and species of these amphibians have ranged from the extreme of splitting known fossils into a large array of forms to the other extreme of lumping them into a few taxonomic categories. Perhaps the extremity of metoposaur splitting is indicated by the list of genera and species that is presented above. Certainly 10 genera and 19 species of these amphibians make an imposing array for one family of late Triassic age.

The other end of the spectrum of taxonomic thought is adumbrated by some remarks made by Romer in his "Review of the

Labyrinthodontia," published in 1947. This author, a close and most competent student of the labyrinthodonts, had the following to say about metoposaur relationships:

"It is indisputable that the metoposaurs form a compact group of genera, between which there are but minor generic differences, and which have many common features contrasting strongly with other labyrinthodonts. There are, actually, only two distinguishable generic types (apart from the Indian forms with which I am not familiar), *Metoposaurus* and an American series of forms, most or all of which may prove to be identical with *Dictyocephalus*" (Romer, 1947, p. 256).

### THE DESCRIBED GENERA AND SPECIES OF METOPOSAURS

#### METOPOSAURUS LYDEKKER, 1890

*Metoposaurus* LYDEKKER, 1890, p. 152.

*Trigonosternum* SCHMIDT, 1931, pp. 258, 260.

GENOTYPIC SPECIES: *Metopias diagnosticus* Meyer, 1842.

TYPE OF SYNONYM: *Trigonosternum latum* Schmidt, 1931.

HORIZON AND DISTRIBUTION: Keuper, upper Triassic; Germany; for *Trigonosternum*, Lettenkohle.

DIAGNOSIS: "Skull broad, with obtuse muzzle; palatal vacuities expanded in front; premaxillary vacuities large and double; orbits large, oval, situated in the anterior half of the skull, and widely separated from one another; lyra enclosing an oblong space between orbits and nares; nares terminal, large, rounded, and approximated; frontals pointed behind, and excluded from the border of the orbit by the junction of the postfrontal with the prefrontal; squamosal, postorbital, and postfrontal elongated. Teeth apparently arranged like those of *Capitosaurus*. Each cranial bone strongly pitted at the centre, and radiately grooved at the periphery. Median plate (interclavicle) of thoracic buckler with a rounded posterior extremity and distinct lateral wings; lateral plates (clavicles) meeting in a long suture in advance of the median plate. Dentition weak; teeth strongly fluted externally, especially at the base, with but

slight internal foldings" (Lydekker, 1890, pp. 152-153). To this should be added the fact that the lacrimal bone does not enter the margin of the orbit.

In order to give the reader the background for our taxonomic conclusions, we include here the original diagnoses and other pertinent taxonomic data for genera and species that we consider as junior subjective synonyms.

DIAGNOSIS OF *Trigonosternum*: "Der Umriss [of the interclavicle] ist breit dreieckig mit, soweit der Rand genügend zu erkennen ist, gerundetem Zuschnitt aller drei Ecken. Die Gesamtform war jedenfalls symmetrisch. Zwei schmälere, aber im Knochen in der Mitte mindestens 4 mm starke Fortsätze dehnen sich an der längsten, fast geraden, jetzt noch 125 mm langen Seite des Dreiecks aus. Der Eine von ihnen lässt einen stumpf zugespitzt zungenförmigen Umriss gut erkennen. Der dritte, wesentlich kürzere Fortsatz steht senkrecht zur Verbindungslinie der beiden anderen. Er ist im Knochen nur bis etwa 2 mm stark, aber wesentlich breiter, etwa 10 mm vom Ende noch reichlich 40 mm. Auch er scheint eine stumpfe mediane Zuspitzung besessen zu haben, die aber nicht mehr deutlich erhalten ist. Die beiden zu dem dritten Fortsatz aufsteigenden Seiten sind etwas eingebuchtet" (Schmidt, 1931, p. 259).

***Metoposaurus diagnosticus* (Meyer), 1842**

*Metopias diagnosticus* MEYER, 1842, p. 302.

*Labyrinthodon diagnosticus* (Meyer), OWEN, 1861, p. 216.

*Metoposaurus diagnosticus* (Meyer), LYDEKKER, 1890, p. 153.

*Metoposaurus stuttgartensis* FRAAS, 1913.

*Metopias santaecrucis* KOKEN, 1913.

*Trigonosternum latum* SCHMIDT, 1931.

*Metoposaurus heimi* KUHN, 1932.

HORIZON AND LOCALITY: Keuper, including Lettenkohle, upper Triassic; southern Germany and Austria. The type is from Württemberg.

TYPE: A partial skull.

DIAGNOSIS: A metoposaur in which the skull is comparatively long and narrow. The diagnosis of the genus *Metoposaurus* by Lydekker, quoted above, was based on skulls of the type species, *Metoposaurus diagnosticus*. The characters that Lydekker cites as

typical for *Metoposaurus* may be accepted as generally descriptive of the species now under consideration. They are also applicable to most of the known metoposaurs, an indication of the general morphological uniformity so characteristic of these amphibians. The one feature that seems to be distinctive for the species *Metoposaurus diagnosticus* is the rather long and narrow skull. This form may be regarded as one of the few truly valid species of metoposaurs. Further consideration of *Metoposaurus* will be found on a subsequent page, in the discussion of "*Metoposaurus*" *fraasi*.

***Metoposaurus stuttgartensis* Fraas, 1913**

*Metoposaurus stuttgartensis* FRAAS, 1913, pp. 285-288, pl. 17, figs. 4, 5.

HORIZON AND LOCALITY: Keuper, upper Triassic ("Lehrbergstufe, dicht unter dem Semi-notussandstein"); Sonnenberg, near Stuttgart, Württemberg, Germany.

TYPE: An interclavicle and a left clavicle, some ribs and vertebrae, in the Stuttgart Museum.

DIAGNOSIS: "*M. stuttgartensis* ist eine kleine Art, etwa nur halb so gross als *M. diagnosticus*, sonst aber mit diesem übereinstimmend. Der Kehlbustapparat, welcher am besten bekannt ist, zeigt eine breite Form der herzförmig gestalteten Mittelplatte, die Seitenplatten bilden nach vorn eine kurze Symphyse, tragen aber einem stark verbreiterten clavicularen Fortsatz. Die vorderen Rippen sind im distalen Ende ausserordentlich verbreitert und zeigen einen wohlausgeprägten *Processus uncinatus*. Die Wirbel des vorderen Rumpfteiles bilden flache, amphicoele Scheiben, während im hinteren Rumpfteil halbkreisförmige, aus dem Hypozentrum gebildete Hülsen auftreten" (Fraas, 1913, p. 288).

DISCUSSION: The clavicle and interclavicle described and figured by Fraas represent a very small metoposaurid, and it seems reasonable to think that perhaps these bones come from an immature individual. Both bones are broad as contrasted with their length; could this be an age character rather than a feature of taxonomic significance? One of the ribs figured by Fraas represents an amphibian of rather large size, which raises the question as to whether the materials attributed to *Metoposaurus stuttgartensis* represent a single



form or rather are a mixed lot of bones. However that may be, the ribs described by Fraas are rather unusual in that they are greatly expanded distally, much more so than is the case in *Metoposaurus diagnosticus*. In addition, these bones have uncinat processes. The description of the vertebrae, which unfortunately were not figured by Fraas, does not indicate any unusual features. These seem to be typical stereospondyl vertebrae.

In general, this species is difficult to evaluate on the basis of the incomplete and all too scanty material described by Fraas.

***Metoposaurus santaecrucis* (Koken), 1913**

*Metopias Santae Crucis* KOKEN, 1913, pp. 20-24, pls. 1, 2.

**HORIZON AND LOCALITY:** Keuper, upper Triassic; north of Heiligenkreuz, Austria.

**TYPE:** A partial skull, in the University at Tübingen, Germany.

**DIAGNOSIS:** "Als artliche Unterschiede von *M. diagnosticus* nenne ich die geringere Grösse und die oben schon hervorgehobenen Abweichungen in der Skulptur der Deckplatten" (Koken, 1913, p. 24).

**DISCUSSION:** The type specimen of the species described by Koken consists of a partial skull, in which some of the most important parts are missing. Koken distinguished the form largely on the basis of its rather small size and the nature of the sculpturing on the roof of the skull. These characters are anything but diagnostic, and in the case of this particular specimen they are probably representative of a particular growth stage. On the basis of the material this is an indeterminate form, but there is good reason to suspect that the type specimen represents a young individual of *Metoposaurus diagnosticus*.

***Metoposaurus heimi* Kuhn, 1932**

*Metoposaurus heimi* KUHN, 1932, pp. 112-119, pl. 4.

**HORIZON AND LOCALITY:** Middle Keuper, upper Triassic; near Ebrach, Germany.

**TYPE:** A skull, in the Staatssammlung für

Paläontologie und Historische Geologie, Munich, Germany.

**DIAGNOSIS:** "Schädel sehr flach und gross werdend, sehr grosses Foramen quadrate zwischen Quadratojugale Quadratum und Squamosum, grosses Loch für den Supraoccipitalknorpel, darunter ein kleineres Foramen magnum. Das Squamosum reicht am Hinterhaupt sehr weit nach unten und verbindet sich mit dem Quadratum" (Kuhn, 1933, p. 119).

**DISCUSSION:** Among the named European species of metoposaurs, *Metoposaurus heimi* is the only one in addition to the type species that has been based on adequate material. The skull described by Kuhn in 1932 is essentially complete and of characteristic metoposaur form. Whether or not the specific diagnostic characters cited by Kuhn are truly distinctive is a question that must wait for detailed comparisons of the skull he described with type and other materials of *Metoposaurus diagnosticus*. The skull of *Metoposaurus heimi* would appear to be broader in proportion to its length than is the case in the type species of this genus. In some respects this skull bears striking resemblances to the skulls of metoposaurs of North America.

***Trigonosternum latum* Schmidt, 1931**

*Trigonosternum latum* SCHMIDT, 1931, pp. 258-261, pl. 4, fig. 20.

**HORIZON AND LOCALITY:** Lettenkohle, upper Triassic; near Kölleda, in the Thuringian region of southern Germany.

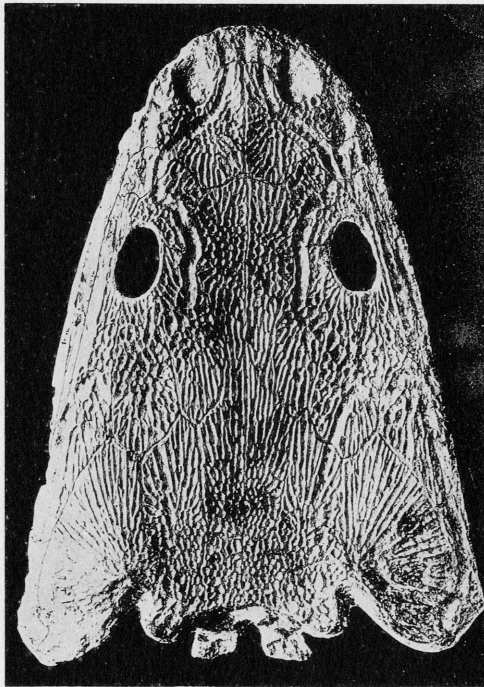
**TYPE:** A partial interclavicle.

**DIAGNOSIS:** See the diagnosis of the genus *Trigonosternum* above.

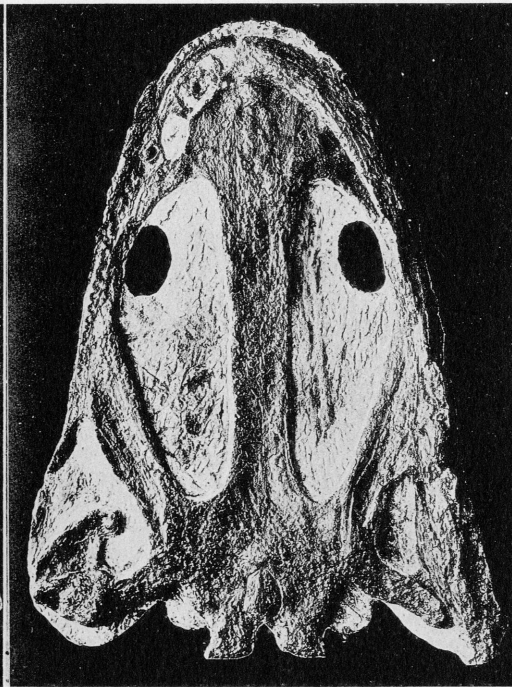
**DISCUSSION:** It would appear that Schmidt's definition of this new genus and species is based on a misinterpretation of a normal stereospondyl type of interclavicle. Schmidt thought that he had a very broad, short interclavicle, quite unlike the same bone in other metoposaurids. It seems to us, however, that, if the figure in his plate is rotated about 90 degrees and viewed in this new aspect, it then appears to have an out-

PLATE 25

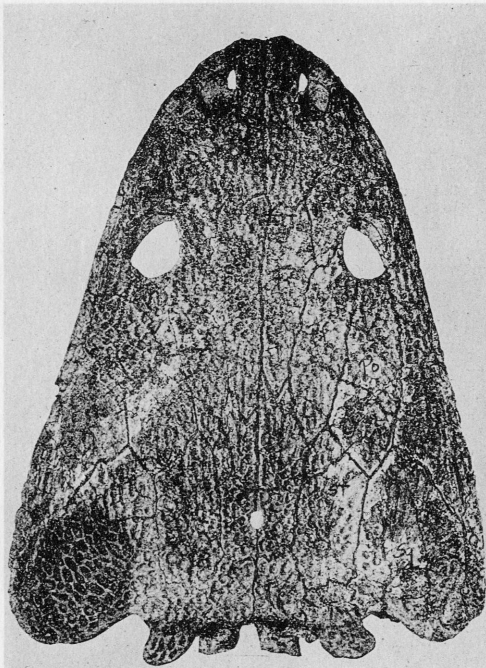
- 1, 2. Skull of *Metoposaurus diagnosticus*. 1. Dorsal view. 2. Palatal view.  $\times \frac{1}{2}$ . From Fraas, 1896.
- 3, 4. Skull of *Eupelor fraasi jonesi*. This is the type of *Buettneria perfecta* Case. 3. Dorsal view. 4. Palatal view.  $\times \frac{1}{2}$ . From Case, 1922.



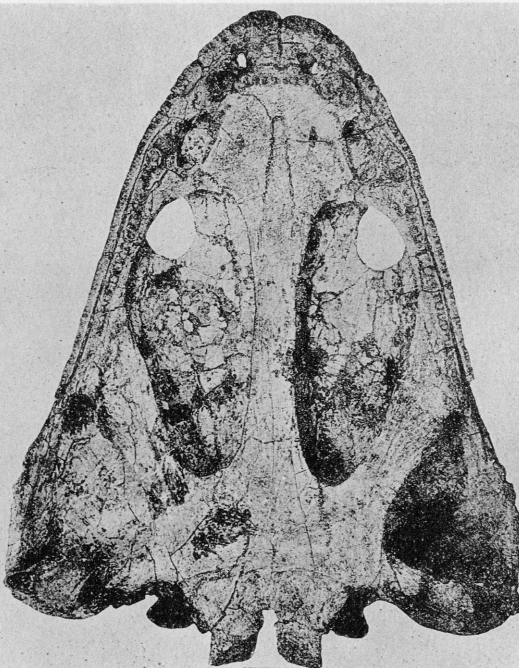
1



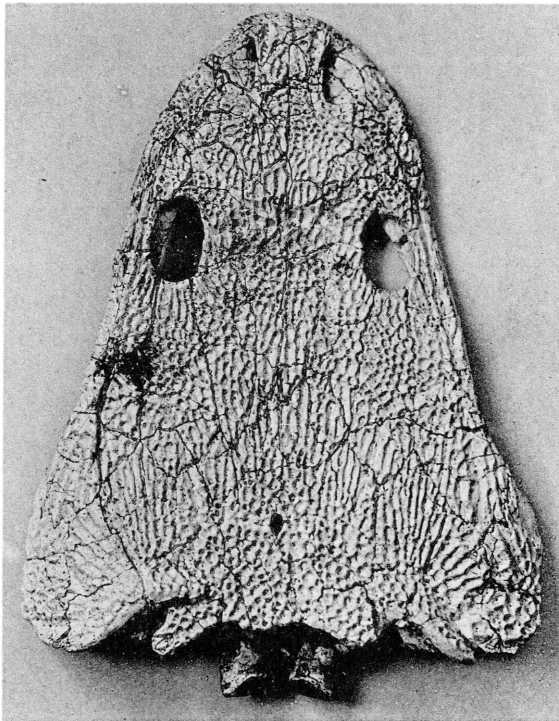
2



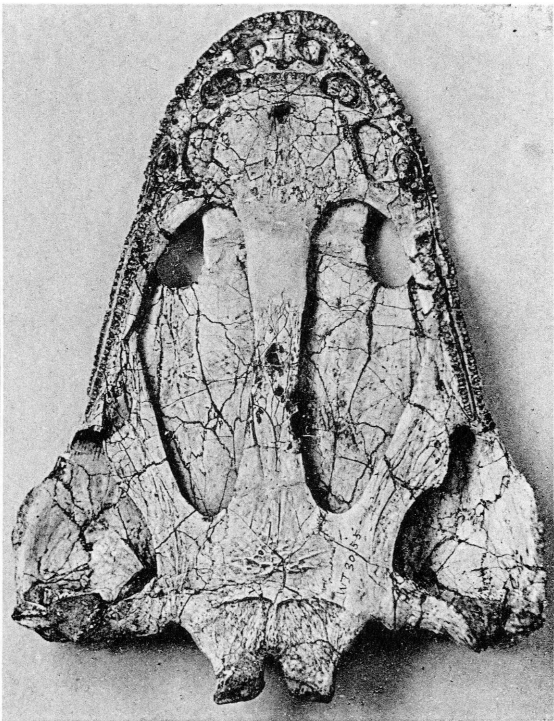
3



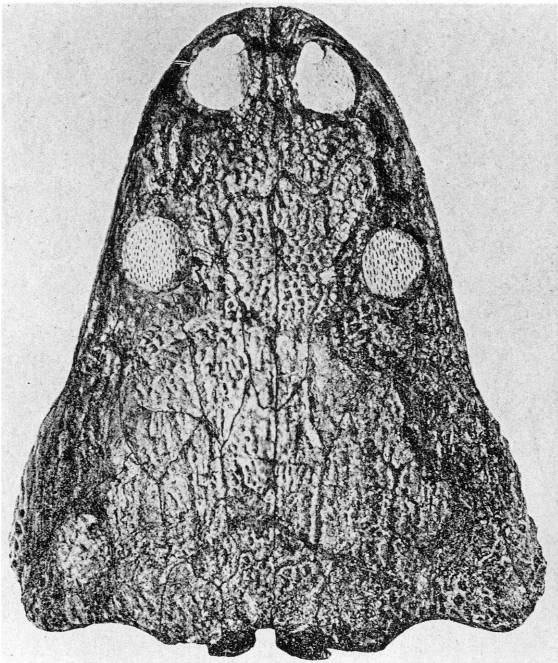
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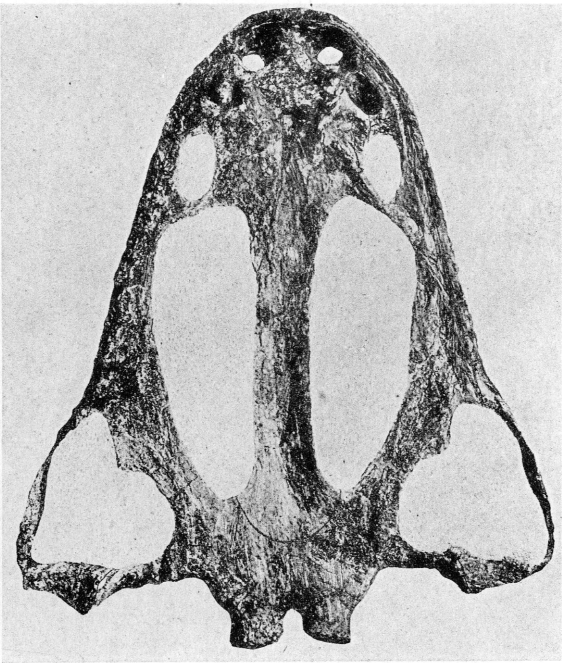
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line very similar to that seen in other metoposaur interclavicles.

Even so, the type specimen is so incomplete that it must be regarded as indeterminate.

**DICTYOCEPHALUS** LEIDY, 1856

*Dictyocephalus* LEIDY, 1856, p. 256.

GENOTYPIC SPECIES: *Dictyocephalus elegans* Leidy, 1856.

HORIZON AND DISTRIBUTION: Newark group, upper Triassic; North Carolina.

DIAGNOSIS: "Plates of the cranium covered with reticular ridges in a general radiant manner. Parietals comparatively short, broader in front than behind; parietal foramen near the centre of the bones. Occipitals [post-parietals] quadrate, a little longer than broad. Posterior outline of the cranium with a superficial transverse concavity on each side and not a deep sinus" (Leidy, 1856, p. 256).

***Dictyocephalus elegans* Leidy, 1856**

*Dictyocephalus elegans* LEIDY, 1856, p. 256.

TYPE: A.M.N.H. No. 5661, portion of a skull roof.

HORIZON AND LOCALITY: Newark group, upper Triassic; Chatham County, North Carolina.

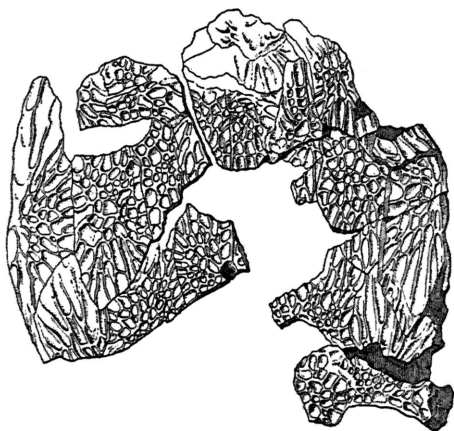


FIG. 1. Fragmentary skull roof of *Dictyocephalus elegans* in its present state of preservation. A.M.N.H. No. 5661, type. Natural size.

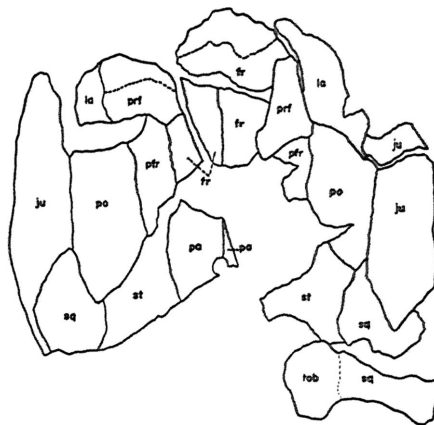


FIG. 2. Key to the bones shown in figure 1. Abbreviations: fr, frontal; ju, jugal; la, lacrimal; pa, parietal; pfr, prefrontal; po, postorbital; prf, postfrontal; sq, squamosal; st, supratemporal; tab, tabular.

DIAGNOSIS: See diagnosis of genus above.

DISCUSSION: The diagnosis given by Leidy of *Dictyocephalus elegans*, the most important section of which is quoted above, does not give much to characterize this genus in comparison with other genera that might be related to it. Certainly *Dictyocephalus elegans* is a small labyrinthodont amphibian. The skull bones show a pattern of sculpturing that can be compared closely with the patterns on the skull bones of well-known metoposaurids. Beyond this it is difficult to reach any definite conclusions because of the fragmentary nature of the type specimen.

The general proportions of the known skull bones, as cited by Leidy, afford less light on this problem than seems to be apparent at first glance. He mentions the generally quadrate shape of the postparietals—a character that is duplicated in other North American labyrinthodonts of late Triassic age, especially those from the Triassic sediments of Wyoming. As for the seemingly short parietals, it appears to the senior author that this condition is in part an illusion, the result of the skull's having been subjected to distor-

PLATE 26

1, 2. Skull from Potter County, Texas, population of *Eupelor fraasi jonesi*. 1. Dorsal view. 2. Palatal view.  $\times$  about  $\frac{1}{2}$ . Photographs furnished by Mr. J. T. Hughes with permission of Mr. Boone McClure, Director of the Panhandle-Plains Museum, Canyon, Texas.

3, 4. Skull of *Eupelor browni*. This is the type of *Anaschisma browni* Branson. 3. Dorsal view. 4. Palatal view.  $\times \frac{1}{2}$ . From Branson and Mehl, 1929.

tion or pressures, whereby the bones of the circumorbital series have been pushed back to some degree, to ride over the bones of the cranial roof. If this be so, then the anterior portions of the parietals are obscured by the postfrontals and postorbitals that cover them in part. Unfortunately the type skull has been damaged and has suffered loss of bone since Leidy made his study and since the figure that is reproduced in Emmons' "American geology," published in 1857, was drawn. This section of the skull roof is not now complete enough for a satisfactory resolution of the problem.

Perhaps the most striking character of *Dictyocephalus elegans* is its small size, which makes comparison with the large metoposaurs of western North America difficult. This specimen may very well represent the juvenile stage of a large metoposaurus, closely comparable to some of the metoposaurs of the western states, but in view of the fragmentary nature of the specimen there is no way to prove or disprove this possibility.

#### EUPELOR COPE, 1868

*Eupelor* COPE, 1868, p. 221.

*Anaschisma* BRANSON, 1905, pp. 570-571.

*Calamops* SINCLAIR, 1917, p. 319.

*Buettneria* CASE, 1922, p. 13.

*Borborophagus* BRANSON AND MEHL, 1929, pp. 65, 79.

*Koskinonodon* BRANSON AND MEHL, 1929, pp. 51, 79.

*Kalamoiketos* BRANSON AND MEHL, 1929, pp. 70, 73.

GENOTYPIC SPECIES: *Mastodonsaurus durus* Cope, 1866.

TYPES OF SYNONYMS: *Anaschisma browni* Branson, 1905; *Calamops paludosus* Sinclair, 1917; *Buettneria perfecta* Case, 1922; *Borborophagus wyomingensis* Branson and Mehl, 1929; *Koskinonodon princeps* Branson and Mehl, 1929; *Kalamoiketos pinkleyi* Branson and Mehl, 1929.

HORIZON AND DISTRIBUTION: Upper Triassic continental sediments of North America; Brunswick formation of the Newark group in Pennsylvania and adjacent states; Dockum formation of Texas; Chinle formation of New Mexico, Arizona, and Utah; Popo Agie formation of Wyoming.

DIAGNOSIS: "One of the former [postorbital] is four inches six lines long; both [post-

orbital and parietal] are pitted medially (about  $3\frac{1}{2}$  pits in an inch) and marked with short coarse sulci posteriorly. The parietals are two inches nine lines wide behind, and four inches wide between the anterior parts of the postorbitals. On what is probably the posterior part of the interorbital region (a small part of the posterior margin of the left orbit is preserved) commence two smooth, shallow sulci 1 in. 2 l. apart, which are probably the posterior extremities of the superficial channels of the face of the Labyrinthodonts. Between them the surface is pitted (four or five to the inch). The parietal bones are throughout longitudinally sulcate (four and one-half to the inch), with obtuse ridges between" (Cope, 1869, p. 25, reprinted verbatim from the original description of 1866).

In order to give the reader the background for our taxonomic conclusions, we include here the original diagnoses and other pertinent taxonomic data for genera and species that we consider as junior subjective synonyms.

DIAGNOSIS OF *Anaschisma*: "Skull large, subtriangular. Bones of the roof all deeply sculptured. Frontals excluded from orbits by the junction of the pre- and postfrontals; all of the bones behind the orbits, excepting the supraoccipitals and epiotics, elongated; lachrymal forming part of the posterior border of the nares. Opisthotics short, not coalesced with the exoccipitals. Parasphenoid with a long, narrow, cultriform process anteriorly; exoccipitals meeting in the median line in the floor of the skull. Parietal foramen small, subcircular; no auditory notches; orbits very large, subcircular, situated in anterior half of skull, and widely separated from each other; premaxillary vacuities large, double, penetrating the roof of the skull at the anterior end of the nares; nares terminal, large, ovate. Base of skull with large quadrate foramina; foramen magnum large, with no inward projections of the exoccipitals. Palatine foramina expanded anteriorly. Teeth with labyrinthine structure much like that of *Mastodonsaurus*; a large tooth on each ramus of the mandible near the symphysis. Mandible broad and thin, breadth and thickness as 4 to 1; a strong postcotylar process present" (Branson, 1905, pp. 570-571).



**DIAGNOSIS OF *Calamops*:** "The portion of the jaw preserved is straight lengthwise, except toward the forward end where it curves inward toward the symphysis . . . Apparently the teeth are without enamel, with smooth or but slightly grooved crowns, circular in cross section at the base and, in the case of some of them, with the crown slightly flattened laterally toward the tip, with acute anterior and posterior edges. In thin section, cut transversely to the crown, radial prolongations of the pulp cavity are seen toward which numerous fine dentine tubules seem to converge from the outer wall of the tooth. Labyrinthine infoldings of cement have not been made out. . . . On the outer side of the jaw, the matrix has an irregular hummocky surface suggestive of pittings in the bone . . . *Calamops* is larger than any labyrinthodont hitherto described from the Newark group and is the largest amphibian thus far reported from the Triassic of North America" (Sinclair, 1917, pp. 319-321).

**DIAGNOSIS OF *Buettneria*:** "The general resemblance to the skull of *Anaschisma* from the Popo Agie beds of Wyoming is apparent, but the arrangement of the teeth and the bones of the lower surface show that the two forms can not be placed in the same genus, and render it doubtful whether they should be placed in the same family. A comparison with Branson's figures shows that the skull was a little broader, proportionately, than in *Anaschisma* and that the orbits were a little farther forward. . . . In this region [the lower surface of the skull] the skull shows very decided differences from *Anaschisma*. [But most of the differences cited by Case, particularly the supposed differences in number and arrangement of teeth on the vomers and palatines, and the supposed long median suture between the exoccipitals, have proved to be non-existent.] The quadrate foramen is relatively larger than in *Anaschisma*" (Case, 1922, pp. 13-17).

In addition to these diagnostic characters, there seems to be a real difference between the skulls described as *Buettneria* and *Anaschisma* in the proportions of the postparietal bones, these elements being rather elongated in the former genus, as contrasted with their approximately equal lengths and widths in the latter form. Also, *Buettneria* has, accord-

ing to Case, a deep pit on the occipital surface of the skull along the suture between the postparietal and the tabular, as contrasted with the open foramen (the "posttemporal foramen") in *Anaschisma* as figured by Branson, 1905. Examination of other specimens described as *Buettneria* indicates that this is a variable individual character. (See Sawin, 1945.)

**DIAGNOSIS OF *Borborophagus*:** "Skull with breadth and length proportions of about 3:4, sharply rounded anteriorly. Orbits slightly elongate antero-posteriorly, situated just anterior to the mid-length of the skull. External nares comparatively narrow and elongate. Deck bones exceptionally thin and delicately sculptured. Mucus canals narrow. Supraorbital canals ending on postfrontals near level of posterior border of orbits. Jugal and temporal canals forming a unit with which the infraorbital canal apparently fails to connect. Palate similar to that of *Koskinonodon* but with relatively smaller narial openings and cultriform process relatively narrow at mid-length. Clavicular girdle units thin and delicately sculptured. Interclavicle with weakly developed median dorsal boss. Clavicles narrow with high scapular ridge confluent anteriorly and posteriorly with the lateral and postero-lateral margins (Branson and Mehl, 1929, pp. 79-80).

**DIAGNOSIS OF *Koskinonodon*:** "Skull large, somewhat elongate with proportions of width to length of about 7:9. Orbits very slightly in front of the mid-length of the skull. Nares large. Nasals comparatively long and narrow. Dermosupraoccipitals short. Supraorbital canal ending near posterior end of postfrontal. Jugotemporal canal a separate unit. An antero-posterior cross-commissure between the infraorbital and supraorbital canals. Palate like that of *Anaschisma* but with short palatines and long ectopterygoids, and somewhat narrower cultriform process. Internal nares exceptionally large. Exoccipitals long . . . Clavicles short and broad with slightly convex lateral margin outlines" (Branson and Mehl, 1929, p. 79).

**DIAGNOSIS OF *Kalamoiketos*:** "Deck bones of skull exceptionally thin and delicately sculptured. Dermosupraoccipitals about twice as long as tabulare. Parietal foramen relatively far forward. Exoccipitals very

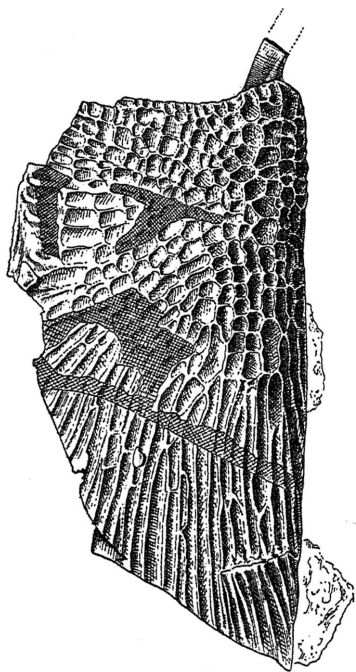


FIG. 3. Left clavicle of *Eupelor durus*, A.M.N.H. No. 1850. External view,  $\times \frac{1}{4}$ . From von Huene, 1921.

short. Cartilaginous basioccipital very likely appearing at the base of the intercondylar notch. Cultriform process exceptionally narrow at mid-length. Anterior and posterior lateral bars of pterygoid narrow" (Branson and Mehl, 1929, p. 80).

*Eupelor durus* (Cope), 1866

*Mastodonsaurus durus* COPE, 1866, pp. 249-250.  
*Calamops paludosus* SINCLAIR, 1917.

HORIZON AND LOCALITY: Newark group, upper Triassic; Phoenixville, Pennsylvania.

TYPE: Not definitely determinable. In the American Museum of Natural History collection are the following numbered specimens: A.M.N.H. No. 1850, a left clavicle; A.M.N.H. No. 1863, portion of an interclavicle; A.M.N.H. No. 1868, fragments: A.M.N.H. No. 3927, fragment of a clavicle and some possible impressions in the rock. It is possible that the type is included among these specimens.

DIAGNOSIS: See diagnosis of the genus *Eupelor* above.

DISCUSSION: Cope, in his original descrip-

tion of 1866, stated that *Mastodonsaurus durus*, "which is of considerable size, is represented by portions of two crania and numerous teeth." Subsequently, in 1868, he erected the genus *Eupelor*, the type being *Mastodonsaurus durus*. In the latter paper he based his discussion entirely on the teeth that had been found with the undoubted amphibian bones. Then in 1869 (p. 26), after a fairly detailed discussion of these teeth, he came to the conclusion that they should not be assigned to *Eupelor durus* but rather to the Thecodontia. "As the tooth from which the description of *Eupelor* was derived, is from the same stratum as the *Belodon* and *Clepsysaurus*, and some distance above the horizon of the cranial bones described, after an examination of the series in possession of Wheatley, I am disposed to refer all these teeth to the Thecodonts, and restrict the name *Eupelor durus* m. to the cranial bones only."

Even though Cope limited his definition of the genus *Eupelor* to the teeth, which he subsequently and justifiably removed from any amphibian relationships, the genus is still

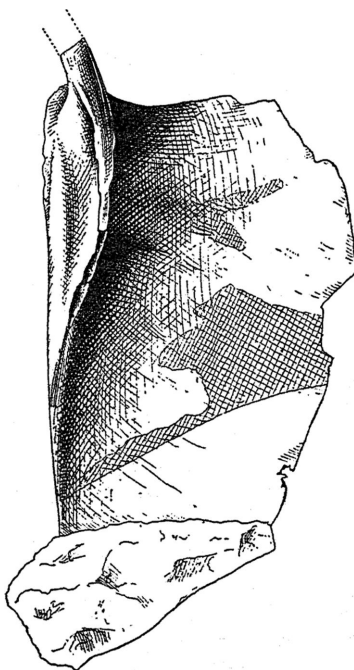


FIG. 4. Left clavicle of *Eupelor durus*, A.M.N.H. No. 1850. Internal view,  $\times \frac{1}{4}$ . From von Huene, 1921.

good because he designated *Mastodonsaurus durus* as the type species, and his original description clearly indicated large bones as well as teeth as constituting the type. Thus the definition of the species must go back to the so-called skull bones that were described in his paper of 1866.

In Cope's original description, and in the subsequent descriptions, he mentions "a portion of the table of the cranium of a large labyrinthodont." Then he speaks of the largest fragment being 8 inches long and  $8\frac{1}{2}$  wide. There is no bone in the collection from Pennsylvania showing these dimensions, although the lower part of the clavicle measures about 8 inches in length by about 6 inches in width. Is it possible that Cope was looking at this, and thinking of it as coming from the skull?

In the collection are two rock fragments with labels attached to the back, probably in Wheatley's writing. Both of these read "Cranial bones of *Mastodonsaurus durus* Cope. Phoenixville Tunnel Pennsylvania." These may show impressions of the cranial roof, but they are certainly not very clear. They do not accord with the dimensions given by Cope.

There is the portion of an interclavicle in the Pennsylvania material, correctly identified and figured by von Huene in 1921. Again,

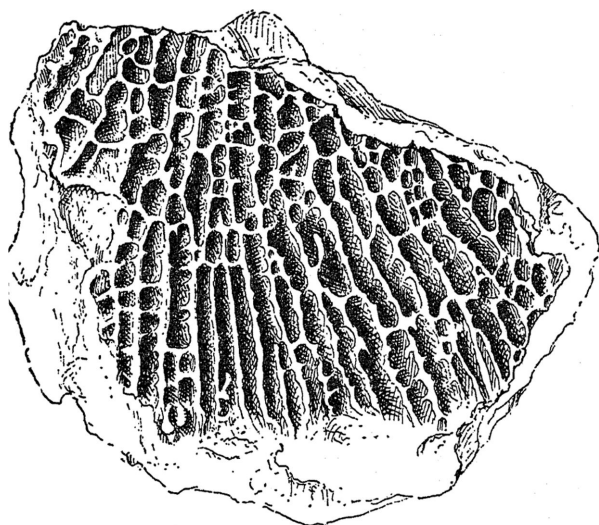


FIG. 5. Portion of interclavicle of *Eupelorus durus*, A.M.N.H. No. 1863. External view,  $\times\frac{1}{4}$ . From von Huene, 1921.

is there a chance that this may have been described by Cope in his original paper and mistakenly referred to the top of the skull? Perhaps, yet the dimensions of this bone do not accord with those given by Cope, although it is barely possible that the specimen in its present condition may be less complete than it was originally. With this specimen is a slip of paper that reads "part of cranium of Saurian Mines York pa.," which is initialed "CMW"—obviously Wheatley.

Two reverse molds in the rocks are included in the Pennsylvania materials. Neither has any number or identifying label. One of these may represent a portion of a skull roof, perhaps in the vicinity of the postorbital, or the anterior region of an interclavicle. The other, from a larger animal, is difficult to identify. Both of these specimens indicate a large metoposaur, of the same type as that represented by the clavicle, but as data are missing it is perhaps best to ignore them.

Such is our knowledge of *Eupelorus durus* at the present time, as based on Cope's descriptions and on the materials collected by Wheatley and now in the collections of the American Museum of Natural History. It seems that some of this material probably represents the specimen or specimens on which Cope based his original description of the species. But the problem of determining which fossils should be regarded as types is difficult, if not insoluble. Cope unfortunately published no figures, and his descriptions are so general that no positive identification of the specimens can be made from them.

There can be no doubt of the fact that the amphibian bones from Pennsylvania represent a large metoposaur very similar to the metoposaurs that have been described from western North America. In 1921 von Huene published excellent figures of the portion of an interclavicle and of the clavicle, mentioned above, that show in detail what these fossils are like.

#### *Calamops paludosus* Sinclair, 1917

*Calamops paludosus* SINCLAIR, 1917, pp. 319-321.

HORIZON AND LOCALITY: Newark group, upper Triassic; Holicong, Bucks County, Pennsylvania.



TYPE: P. U. No. 12302, front part of the left mandibular ramus.

DIAGNOSIS: See the diagnosis of the genus *Calamops* above.

DISCUSSION: *Calamops paludosus* is founded on such inadequate material that it must be regarded as indeterminate at the present time.

**Eupelor fraasi fraasi** (Lucas), 1904

*Metoposaurus fraasi* LUCAS, 1904, pp. 194-195, pl. 3.

*Kalamoiketor* (?) *fraasi* (Lucas), BRANSON AND MEHL, 1929, p. 81.

*Buettneria major* BRANSON AND MEHL, 1929.

*Kalamoiketor pinkleyi* BRANSON AND MEHL, 1929.

HORIZON AND LOCALITY: Chinle formation, upper Triassic; about 5 miles east of Tanners Crossing, Little Colorado River, Arizona.

TYPE: U.S.N.M. No. 2152, an interclavicle.

DIAGNOSIS: "The species is characterized by the coarseness of the sculpturing of the episternum and the fact that the markings of the center of the plate consist of irregular pits which, toward the margin, are transformed into radiating grooves. These grooves are most marked on the anterior portion of the bone. The portions of clavicles present also have the ornamentation in the shape of pits rather than as grooves, and in this respect and in the greater coarseness of the sculpture the present species differs from the European *Metoposaurus diagnosticus* of von Meyer. It is furthermore characterized by the extent of the articulation of the clavicle with the episternum, the posterior end of the clavicle being well behind a line drawn through the center of the plate. The postero-internal angle of the clavicle is very much rounded instead of being decidedly angular, as it is in *Metoposaurus diagnosticus*" (Lucas, 1904, p. 194).

DISCUSSION: Most of the statements in Lydekker's diagnosis of *Metoposaurus*, quoted on a preceding page, apply with perfect validity to the metoposaurs that have been found in North America, an indication either that his diagnosis has been expressed in terms too broad for its purpose or that the American forms should rightly be included within the genus. Although it has been suggested that the American forms, which have

received various generic designations, should all be assigned to the genus *Metoposaurus*, certain constant differences between these metoposaurs and *Metoposaurus* of Germany indicate rather clearly true generic differentiations. These may be discussed briefly.

In the first place, although Lydekker failed to make this point, the lacrimal bone of the skull is never in contact with the orbital margin in *Metoposaurus*. In the American forms this bone always forms a part of the orbital border. This constant difference in itself seems sufficient justification for regarding *Metoposaurus* as generically distinct from the metoposaurs of North America. Again Lydekker mentions the fact that the clavicle meet along a long border in front of the interclavicle in *Metoposaurus*, which is certainly not the case in the American forms. This may not be a very great difference but it is a constant one, and as such reinforces the evidence shown in the relationship of the lacrimal bone. This relationship between clavicles and interclavicle can be correlated with another relationship between these bones. In *Metoposaurus* of Germany a line drawn between the posterior edges of the clavicles passes somewhat in front of the center from which the sculpture of the interclavicle radiates and is about midway between the front and the back of the sculptured bone surface. In the American forms, on the other hand, such a line passes through the center from which the sculpture radiates and is definitely behind the midpoint of the sculptured surface.

Finally, as Lucas indicated in his description of the interclavicle that he called *Metoposaurus fraasi*, the sculpture of this bone is coarser in the American form than it is in the type species of *Metoposaurus* and is marked by a considerable area of irregular pits in the central part of the bone, as contrasted with an almost complete absence of such pits in the European form. In other words, there is a combination of central pits from which grooves radiate, in the interclavicle from Arizona, whereas the sculpture consists almost completely of grooves in *Metoposaurus diagnosticus*. What Lucas had to say about the specimen he was describing applies generally to all known specimens of this bone found in North America.

Because of these considerations, it is here

suggested that *Metoposaurus* of Germany is a genus distinct from any of the metoposaurs that have been so far discovered in North America.

Therefore the interclavicle described by Lucas from Arizona must be placed in a genus other than *Metoposaurus*.

**Buettneria** (?) *major* Branson and Mehl,  
1929

*Buettneria* (?) *major* BRANSON AND MEHL,  
1929, p. 79.

HORIZON AND LOCALITY: Chinle formation, upper Triassic; near Joseph City, Arizona.

TYPE: U.M. No. 511V.P., a large clavicle.

PARATYPE: U.M. No. 582V.P., a vertebra.

DIAGNOSIS: "This species is based on an exceptionally large right clavicle of striking characteristics from the lower part of the Chinle near Joseph City, Arizona. A single vertebra from the same locality probably belongs to this species" (Branson and Mehl, 1929, p. 79).

DISCUSSION: The "striking characteristics" of the clavicle cited and figured by Branson and Mehl are indeed hard to recognize. There seem to be no features about this bone, as figured in plate 14 of their paper, that set it off distinctly from other metoposaur clavicles that have been found in southwestern United States. This species may be regarded as inadequately defined and therefore of uncertain status.

**Kalamoiketos** *pinkleyi* Branson and Mehl,  
1929

*Kalamoiketos pinkleyi* BRANSON AND MEHL,  
1929, pp. 73-75, 80.

HORIZON AND LOCALITY: Chinle formation, upper Triassic; about 8 miles northwest of Adamana, Arizona.

TYPE: U.M. No. 554V.P., posterior portion of a skull.

DIAGNOSIS: See the diagnosis of the genus *Kalamoiketos* above.

DISCUSSION: *Kalamoiketos pinkleyi* is based on a fragmentary portion of a skull representing an animal of relatively small size. Therefore some of the characters cited by the authors can be regarded as juvenile rather than taxonomic features. Other characters, such as the long postparietals and the short exoccipitals, are what might be expected in

the metoposaurs of the southwestern United States, generally described under the name of *Buettneria*.

**Eupelor** *fraasi jonesi* (Case), 1920

*Metoposaurus jonesi* CASE, 1920, p. 3.

*Buettneria jonesi* (Case), BRANSON AND MEHL,  
1929, p. 78.

*Buettneria perfecta* CASE, 1922.

*Buettneria bakeri* CASE, 1931.

*Buettneria howardensis* SAWIN, 1945.

HORIZON AND LOCALITY: Dockum formation, upper Triassic; western Texas.

TYPE: M.P.U.M. No. 3814, associated interclavicle and clavicles.

DIAGNOSIS: "The interclavicle is rhomboidal in form with the center of ossification and sculpture in the posterior half. The clavicles articulate with the interclavicle by overlapping suture at the posterior end; the contact was preserved by strong ridges and grooves. The clavicles are decidedly convex at the posterior end and the center of sculpture is presented laterally rather than downward. The loss of the broken tips of the slender processes of the anterior ends of the bones was slight and they did not meet in the median line; the intervening space must have been filled with cartilage" (Case, 1920, pp. 1-2).

DISCUSSION: Among the considerable series of clavicles and interclavicles described as or referred to *Buettneria perfecta*, there are many specimens that match very closely the type material of *Metoposaurus jonesi*.

**Buettneria** *perfecta* Case, 1922

*Buettneria perfecta* CASE, 1922, pp. 13-25.

HORIZON AND LOCALITY: Dockum formation, upper Triassic; Sand Creek, Crosby County, Texas.

TYPE: M.P.U.M. No. 7475, a complete skull.

PARATYPES: M.P.U.M. Nos. 7469, left mandibular ramus; 7503, a lower jaw; 7265, 7364, 7366-7368, 7448, and 7449, interclavicles, clavicles, and other miscellaneous bones.

DIAGNOSIS: See the diagnosis of the genus *Buettneria* above.

DISCUSSION: The metoposaur described by Case from the Dockum formation of Texas is distinctly different from the form described as *Anaschisma*, of the Popo Agie formation,

as indicated in the quoted generic diagnosis above. Since the time of Case's original description of *Buettneria*, a great deal of material has been collected from the Dockum formation, and this material gives us a broad and excellent base for the characterization of the Dockum form. Indeed, the biometric studies of metoposaur populations that make

PARATYPES: M.P.U.M. Nos. 14098 and 14154, skulls; 13027 and 13029, interclavicles; 13028, clavicle; 12946, femur; several other femora found in association with the skulls.

HORIZON AND LOCALITY: Dockum formation, upper Triassic; Scurry County, Texas.

DIAGNOSIS: "The elongation of the pits of the sculpture extending over the frontal and

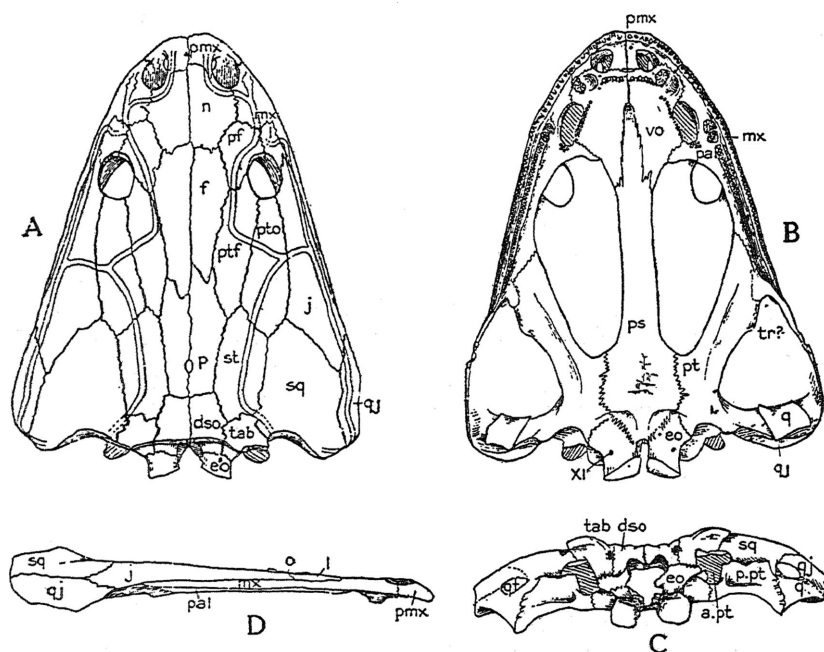


FIG. 6. Skull of *Eupelor fraasi jonesi*, M.P.U.M. No. 7475. (This is the type of *Buettneria perfecta* Case.) A. Dorsal view. B. Palatal view. C. Occipital view. D. Right lateral view. All  $\times \frac{1}{4}$ . From Case, 1922.

up the latter part of this paper are based to a considerable extent on the Dockum fossils. Such being the case, no attempt is made to offer extended remarks here concerning the resemblances and differences of Dockum metoposaurs to related forms from other parts of North America. However, it might be well to mention that the form now under consideration is a metoposaur in which the orbits are far forward and are bordered by the lacrimal bone, and in which the postfrontals, postorbitals, and postparietals are relatively rather long.

*Buettneria bakeri* Case, 1931

*Buettneria bakeri* CASE, 1931, pp. 187-206, pls. 1-3.

TYPE: M.P.U.M. No. 13055, a skull

the postorbital regions, the incomplete sensory canal system, the extension of the palatal vacuities anterior to the orbits, the narrower and more elongate skull, and the smaller size distinguish this species from *Buettneria perfecta*, the genotype" (Case, 1931, pp. 187-188).

*Buettneria howardensis* Sawin, 1945

*Buettneria howardensis* SAWIN, 1945, pp. 362-399.

COTYPES: U.T. Nos. 31100-124, 31220-1, 31100-42, 31100-30, 31100-161, 31100-122, skulls, with which are associated mandibles and various portions of the postcranial skeletons.

HORIZON AND LOCALITY: Dockum formation, upper Triassic; Howard County, Texas.

**DIAGNOSIS:** "The difference in proportions in the Dockum species of the genus *Buettneria* is but slight. *B. perfecta* has a narrower skull than *B. howardensis* and differs slightly in other ratios, (Table I-A)" (Sawin, 1945, p. 396). An examination of Sawin's table I-A reveals no significant differences in the ratios other than length to width of skull, except

preorbital region and a lack of a connection between the jugal and temporal canals in the midjugal region, the jugal canal here curving down to the margin and closely approaching the upcurving temporal canal" (p. 365). "These fenestrae [paraquadrate fenestrae] . . . are considerably larger and of different proportions than the opening figured by Case

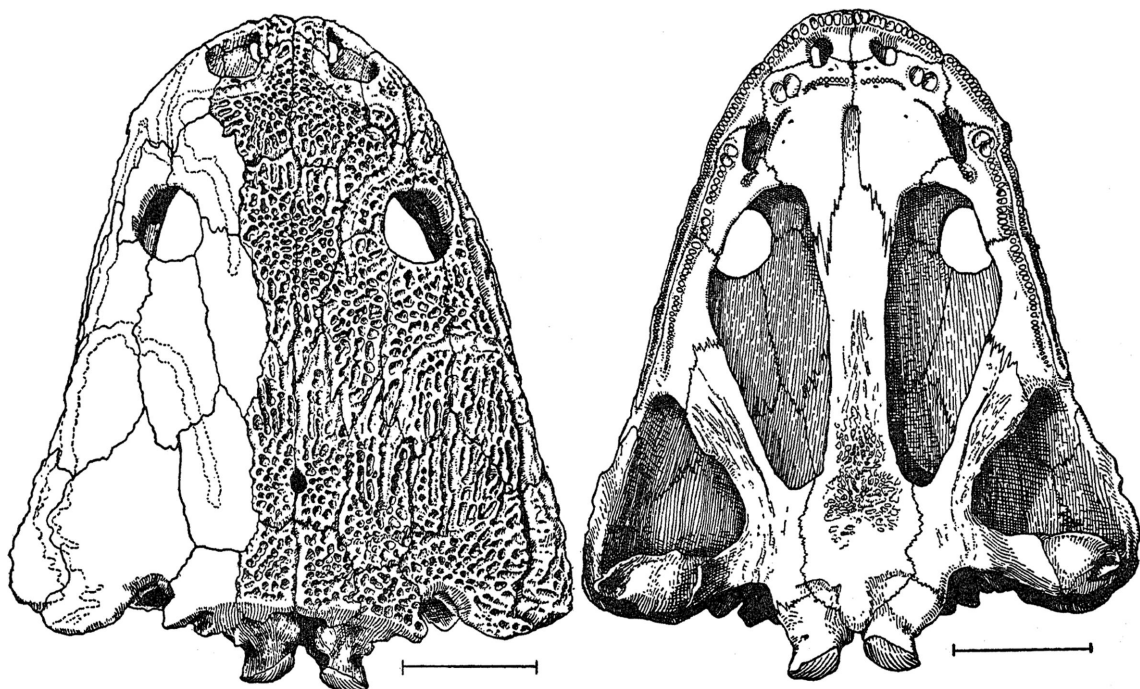


FIG. 7. Skull of *Eupelor fraasi jonesi*, based on U.T. Nos. 31100-122, and 31220-1. (This is a composite from the material on which *Buettneria howardensis* was based.) Dorsal and palatal views,  $\times \frac{1}{2}$ . From Sawin, 1945.

for the size of the palatal vacuities. It would appear that perhaps these openings are proportionately slightly larger in the species described by Sawin than they are in *Buettneria perfecta*. Other possible differences indicated by Sawin as distinctive of his species may be quoted in the following statements: "The pattern of this system [of slime canals] is similar to that described for *Anaschisma* by Branson and Mehl and consequently differs with that described for *Buettneria perfecta* by Case in the absence of a connection between the supraorbital and temporal canals. Other departures from the systems as described for *Buettneria perfecta* and *Anaschisma* include separate channels for the supraorbital and infraorbital canals in the

for *Buettneria perfecta*" (p. 366). "The largest of these [nutrient foramina on vomers] is on the midline at the intersection of sutures with the premaxilla, extends into the bone, but fails to perforate it. In *Buettneria perfecta* (Wilson, 1941) it penetrates the bone as the anteroventral foramen for the intermaxillary foramen for the intermaxillary gland" (p. 374). "Sixty or more conical teeth with oval bases are borne on the upper margin of the dentary and 7 small teeth are directed posteriorly from a ridge near the symphysis in back of the regular row. . . . The specimens here examined do not differ in any important detail from those described for *Buettneria perfecta* or *Anaschisma* except for the symphyseal row of teeth" (p. 382).

DISCUSSION: Although Sawin described *Buettneria howardensis* in considerable detail, he did not present a diagnosis or a summary of characters, to show how the species he was describing might differ from other species described as belonging to this genus. Some of his statements that might be considered as diagnostic are quoted above.

Generally speaking, the form described by Sawin is very close to the metoposaur described as *Buettneria perfecta*, and most of his descriptions can be applied with complete validity to the type species. Such differences as can be picked out to distinguish *Buettneria howardensis* from *Buettneria perfecta* are indeed very slight.

*Eupelor browni* (Branson), 1905

*Anaschisma browni* BRANSON, 1905, pp. 585-587.

*Anaschisma brachygnatha* BRANSON, 1905.

*Borborophagus wyomingensis* BRANSON AND MEHL, 1929.

*Koskinonodon princeps* BRANSON AND MEHL, 1929.

HORIZON AND LOCALITY: Popo Agie formation, upper Triassic; near Lander, Wyoming  
TYPE: C.N.H.M. No. UC-447, a skull.

DIAGNOSIS: "Skull broad posteriorly; proportion of greatest length to greatest width about 10 to 9. Bones of roof of skull coarsely sculptured, pitting predominating anteriorly, ridges and furrows posteriorly. Mucous canals of the lyra beginning in a deep depression just inside the postero-inner corner of the orbit. The main part of the posterior mucous canals begins on the postfrontals, and passes backward in a broad curve to a point in front of the middle of the postorbitals, where the part passing forward on the postorbitals meets it. It then turns at a sharp angle and passes outward and forward. Eyes large, subcircular, situated in anterior half of skull; nares large, approximated; infra-temporal foramina very broad; internal nares close to the palatine foramina. Maxillary and premaxillary teeth small; a few small teeth on the vomers in a row parallel to those on the premaxillae; mandibular teeth compressed, with the long axis transverse to the long axis of the jaw; a very large tooth on each palatine a little in front of the internal nares; a few teeth on the transverse" (Branson, 1905, pp. 585-587).

DISCUSSION: The first metoposaurid from North America named on the basis of adequate skull material was *Anaschisma*, described and figured by Branson in 1905. Some preceding remarks in the present paper, made with regard to Lydekker's description of *Metoposaurus*, may now be applied with equal validity but in the opposite way at this place, namely, that much of the generic diagnosis of *Anaschisma* is equally good for *Metoposaurus*. In their diagnoses both Lydekker and Branson were outlining for the most part characters that are common to all the metoposaurs.

In their monograph on the Triassic amphibians of the Rocky Mountain region, published in 1929, Branson and Mehl corrected some errors that had been made by Branson in his original diagnosis of *Anaschisma*. Thus it became evident in their later work that the back of the skull in this amphibian is similar to the same region in other metoposaurs, and that what Branson had thought were differences in his original study were actually the result of breakage and weathering of the specimen. Moreover, in their later work these authors pointed out that the lacrimal bone does not border the nares, as Branson had originally indicated, and that the exoccipitals do not meet medially. These characters of *Anaschisma* are similar to those of other North American metoposaurs.

In certain characters, however, the metoposaur described as *Anaschisma* is quite distinct from *Metoposaurus*, the one other genus of this group of amphibians that was known from adequate skull materials when *Anaschisma* was first described. Of particular importance is the fact, brought out by Branson and Mehl, that the lacrimal bone, although it does not border the nares, does form a portion of the orbital border. In *Metoposaurus* this bone is quite isolated from the eye, as we have seen. In addition, there is less elongation of the bones forming the back portion of the skull roof in *Anaschisma* than in *Metoposaurus*. This is particularly apparent in the postparietal bones, which in the European genus are definitely elongated, but which in the American form are as broad as they are long.

The relative breadth of the postparietals in *Anaschisma* is reflected in the proportions of the squamosals and perhaps in other bones

forming the back section of the skull roof, all of which is an indication of the fact that the back portion of the skull in the North American genus is relatively broader than it is in the European form. Indeed, there is a distinct transverse flare in the skull roof of *Anaschisma* at the back, as is not the case in the skull roof of *Metoposaurus*.

It should be mentioned also that the orbits are somewhat more posteriorly placed in *Anaschisma* than in *Metoposaurus*.

All these characters indicate that *Anaschisma* can be readily differentiated from *Metoposaurus*.

*Anaschisma brachygnatha* Branson, 1905

*Anaschisma brachygnatha* BRANSON, 1905, pp. 588-589.

HORIZON AND LOCALITY: Popo Agie formation, upper Triassic; near Lander, Wyoming.

TYPE: C.N.H.M. No. UC-448, a skull.

DIAGNOSIS: "This species differs from *Anaschisma browni* as follows: Skull much narrower posteriorly in proportion to the length; proportion of length to breadth about 5 to 4. Eyes not as far forward; nares farther apart. Bones in roof of skull with finer pitting, and broader, more rounded ridges between the pits. Mucous canals of the lyra beginning farther back, and in a broader, shallower depression. The posterior canals beginning in a broad, shallow depression on the postorbitals, instead of on the postfrontals. Infra-temporal foramina much narrower; internal nares much farther from the palatine foramina" (Branson, 1905, pp. 588-589).

DISCUSSION: There is every reason to think that *Anaschisma brachygnatha* is probably a small individual of the same type of metoposaur that Branson described as *Anaschisma browni*. Careful analysis will show that the characters cited by Branson as separating this species from the other are of doubtful validity. For instance, the position of the eyes in the skull is essentially the same in both specimens, as is apparent from statistical studies and graphs on following pages of the present paper. It is difficult to see that the nares are farther apart in one specimen than they are in another. And certain other differences, such as the finer pitting in the smaller skull, are almost certainly attributable to age differences.

Finally, and this is of particular importance, the two specimens were found close together, which makes it appear that they were very probably two individuals in a single population. (In 1948 Branson mentions "the pit from which the skulls were taken about 20 feet from the top of the Popo Agie.")

*Borborophagus wyomingensis* Branson and Mehl, 1929

*Borborophagus wyomingensis* BRANSON AND MEHL, 1929, pp. 65-73, 80, pls. 10-12.

HORIZON AND LOCALITY: Popo Agie formation, upper Triassic; Sage Creek, Fremont County, Wyoming.

TYPE: U.M. Nos. 517, a skull, and 513, a clavicle associated with the skull.

PARATYPE: U.M. No. 583, several vertebrae, discovered near the skull and clavicle.

DIAGNOSIS: See the diagnosis of the genus *Borborophagus* above.

DISCUSSION: *Borborophagus wyomingensis* is almost certainly a juvenile, and the supposedly distinctive characters cited by the authors in their description are such as might be expected in a young individual of the metoposaur described by Branson as *Anaschisma*.

*Koskinonodon princeps* Branson and Mehl, 1929

*Koskinonodon princeps* BRANSON AND MEHL, 1929, pp. 51-65, 79, pls. 4-9.

HORIZON AND LOCALITY: Popo Agie formation, upper Triassic; Bull Lake Creek, Fremont County, Wyoming.

TYPE: U.M. No. 537V.P., a skull.

PARATYPES: U.M. Nos. 504V.P., 505V.P., and 527V.P., three skulls; 567V.P., a mandibular ramus; also a second mandibular ramus; 512, a clavicle; 506, an interclavicle; 556, an ilium; 521, an interclavicle; also some fragmentary interclavicles.

DIAGNOSIS: See the diagnosis of the genus *Koskinonodon* above.

DISCUSSION: The type is a very large metoposaur; otherwise it is not unusual. It may therefore be considered as very probably a large individual of the characteristic upper Triassic metoposaurs found in the Popo Agie beds.

## SOME CONSIDERATIONS OF METOPOSAUR OSTEOLOGY

### SKULL AND JAWS

ONE OF THE FACTS that must be faced at the beginning of any analytical study of the metoposaurs is the remarkable uniformity of structure that characterizes these large amphibians. Metoposaurs have been found in Europe and India (although the specimens so far known from this latter region are so fragmentary that they are as yet of little value except for locality records) and from various parts of North America, and in general the fossils from these widely scattered regions are all pretty much alike. Such differences as exist are mainly those of detail; yet nine or possibly 10 genera have been named. For the moment let us forget the taxonomic problem and review the osteological features typical of all metoposaurs.

It is not necessary to describe in detail the skull and jaws of a metoposaur or of several metoposaurs. For such detailed descriptions the reader is referred to the papers by Fraas, by Case, by Sawin, and by Wilson. The last three of these students have presented rather detailed accounts of the skull and jaws of metoposaurs from Texas, generally placed within the genus *Buettneria*. In the papers by Fraas fossils of *Metoposaurus* are described. Romer (1947) presents excellent summary discussions of all the metoposaurs.

The metoposaurs are large stereospondylous labyrinthodonts, with a total length of 2 meters or more. The head in these amphibians is very large in relation to the body, as is characteristic of the stereospondyls in general, so that skulls having a length of 400 or 500 mm. are quite common. In the largest specimens the skull may approach a meter in length, while in the smallest known specimen the skull is little more than 150 mm. long. These varying sizes may be regarded for the most part as indicative of growth stages rather than as valid taxonomic characters. Certainly the metoposaurs, as did other amphibians, began life as small larval forms, and it is to be expected that the fossil materials should show various stages in the ontogenetic development of these animals.

The metoposaur skull is extraordinarily flat, which is typical of the stereospondyls, and is generally very broad in comparison

with its length. In the narrowest of the known skulls the greatest breadth is about three-fourths of the greatest length, and in the broadest skulls the breadth is almost equal to the length. This last condition probably is not natural but rather represents the effect of crushing. In what appear to be uncrushed skulls from Texas and New Mexico the ratio of breadth to length is about 4/5.

Five openings pierce the roof of the metoposaur skull, namely, the two external nares, the two orbits, and the single pineal opening. The nares are bounded by the premaxillae, the maxillae, and the nasal bones. The orbits are separated from the frontal bones on each side by the prefrontal and postfrontal bones and are bounded posteriorly and laterally by the postorbital and jugal bones. In *Metoposaurus* the jugal bone extends forward and around the front of the orbit to meet the prefrontal, so that the lacrimal bone is completely excluded from the front border of the eye. In all the North American metoposaurs, on the other hand, it would seem that the lacrimal bone forms part of the anterior border of the orbit, so that it separates the prefrontal from the jugal. This is an important qualitative difference between the Eurasiatic and North American forms; indeed it is perhaps the only clear-cut difference in the skull that can be used for separating the Old World from the New World forms. The pineal is located near the back of the skull, on the suture between the two parietal bones.

The orbits of the metoposaurs are located far forward in the skull, so that the distance from the front of the premaxillaries to the anterior border of the orbits is commonly only about a third of the distance from the front of the eyes to the back of the skull roof. It would appear, as Romer has pointed out, that there was actually a forward migration of the eyes during the phylogenetic history of the metoposaurs, so that the orbits occupy a more anterior position with relation to the various elements of the skull in these amphibians than they do in other labyrinthodonts. An alternative suggestion has been that the skull was shortened in front of the eyes and lengthened behind. But, as Romer has shown, it is a significant

fact that the orbits are opposite the anterior portions of the frontals, not the posterior, while there has been little change in the position of palatal or endocranial structures during the shift of the orbits. Correlated with the forward movement of the eyes in these amphibians, there have been changes in the proportions of the skull bones, so that the elements of the skull roof in front of the orbits

this again reflects changes in the proportion of skull bones that have taken place during the phylogenetic history of these amphibians. Thus much of the skull roof is sculptured by deep, irregularly rounded or roughly hexagonal pits or depressions, but in some areas these pits have been elongated into irregular grooves. In the American metoposaurs such elongation of the sculpturing is seen for the

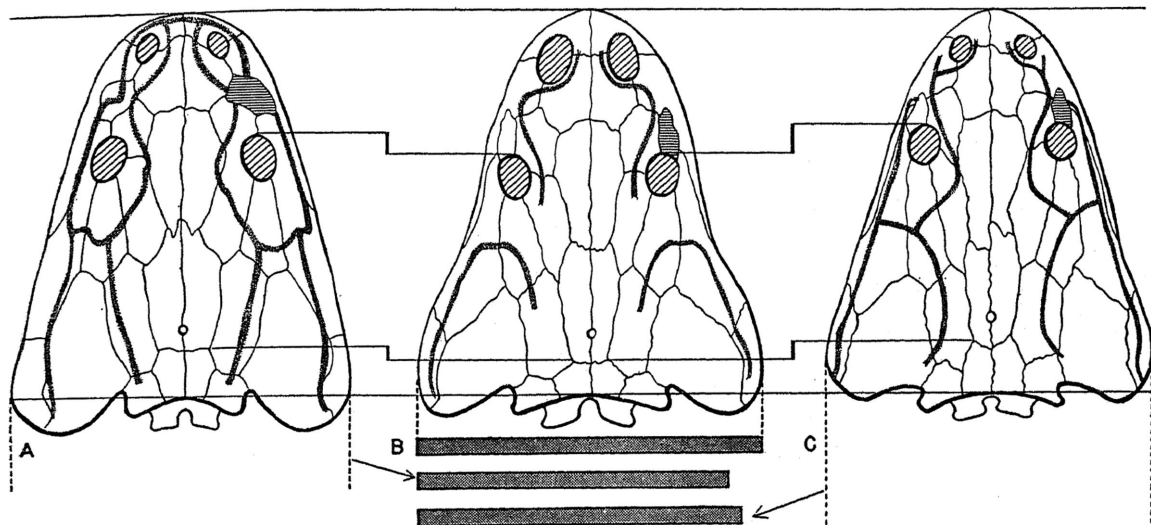


FIG. 8. Comparison of skull proportions in three metoposaurs as seen in dorsal view. Lengths of skull roofs drawn to unit scale. A. *Metoposaurus diagnosticus*, after Fraas, 1896. B. *Eupelor browni* ("Anaschisma" *browni*), after Branson and Mehl, 1929. C. *Eupelor fraasi jonesi* ("Buettneria perfecta"), after Case, 1922. This figure shows a comparison of relative widths (as indicated by bars at bottom of figure), of differences in position of orbits, of relative lengths of postparietal bones, and of position of lacrimal bone with reference to orbit.

are rather square or short, while some of the bones behind the eyes are greatly elongated. This last feature is particularly characteristic of the frontals, parietals, postfrontals, postorbitals, jugals, and supratemporals.

It would appear that there has been more postorbital elongation in the skull roof bones in *Metoposaurus* than in the North American forms. For instance, the bones already listed above are proportionally somewhat longer in the European form than in the North American types, while the squamosal and the postparietals are definitely elongated bones in *Metoposaurus*, as contrasted with their considerably broader dimensions in the skulls from North America.

The sculpture of the skull roof is particularly characteristic of the metoposaurs, and

most part on the parietals, supratemporals, postfrontals, postorbitals, and squamosals. In *Metoposaurus* from Europe a similar development on these bones, especially the squamosal, is apparent, but the elongation of the sculpturing into grooves is more marked than in the American forms. Moreover, there is a certain amount of such elongation on the front portion of the frontals and the back of the nasals in *Metoposaurus*, whereas in the American metoposaurs the sculpturing tends to be more nearly rounded or hexagonal in this front region of the skull. Here is a qualitative difference between the skulls of the European and North American metoposaurs, but it is a difference that is not clear cut.

Some authors have placed reliance on differences in the expression of the so-called



slime canals of the lateral line system on the skull roof of the various metoposaurs. Differences are to be seen in this respect in the skulls designated as *Metoposaurus*, *Anaschisma*, and *Buettneria*. Nevertheless a careful analysis will show that such differences are more apparent than real. *Metoposaurus* has a well-developed system of such slime canals. The slime canals of *Buettneria* are essentially similar in relationships and development to those of *Metoposaurus*, except that there has been some reduction in the nasal region. In *Anaschisma* there has been consid-

There are teeth on the vomers and palatines, and each of these bones bears on each side two large tusks or fangs. The teeth in the metoposaurs show a well-developed labyrinthodont structure.

The internal nares are large and are located on each side at the junctions of the vomer, palatine, and maxillary bones. At the front border of the palate is a pair of prenasal apertures, located within the premaxillae but bordered in part by the vomers. These openings evidently were for the accommodation of the large fangs of the lower jaws.

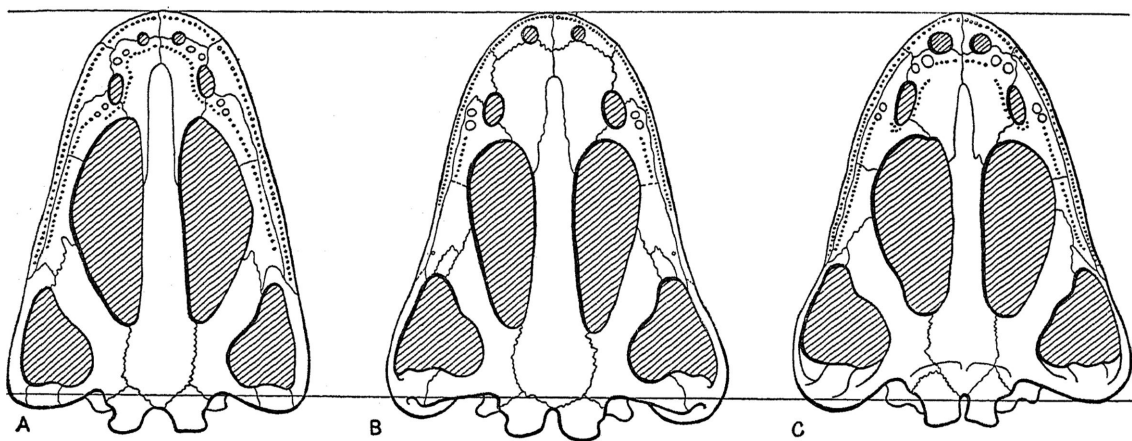


FIG. 9. Comparison of skull proportions in the same three metoposaurs illustrated in figure 8, as seen in palatal view. Drawn on basis of skull roofs at a unit scale. A. *Metoposaurus diagnosticus*. B. *Eupelor browni*. C. *Eupelor fraasi jonesi*.

erable reduction of these canals on the skull roof.

In palatal aspect the skull of the metoposaurs is characterized by the enormous vacuities on either side of the long parasphenoid bone. Watson (1951) has shown that the development of such large vacuities was necessary in the very flat-skulled labyrinthodonts as accommodations for the bulk of the eye and of its musculature. In the metoposaurs the palatal vacuities are of such size that they separate the pterygoid bone from the palatine on either side.

In these amphibians the posterior portion of the long parasphenoid meets the pterygoid bones on either side in long sutural articulations. At the back of the skull the exoccipital bones, forming a distinct condyle on each side, project far back beyond the limits of the skull roof and are prominent in both dorsal and palatal aspects.

The mandible in the metoposaurs is heavy and rather deep and is sculptured on its external lateral surface. The depth of the mandibular ramus is due in part to the prominence of the coronoid region—an indication of strong muscles for the closure of the jaw. At the back there is a well-developed retroarticular process for the insertion of the depressor mandibulae muscles.

#### POSTCRANIAL SKELETON

The very thick, strongly sculptured, and heavy interclavicle and clavicles are particularly characteristic of the postcranial skeleton in the metoposaurs, and fragments of these bones, together with pieces of the cranial roof, constitute the most abundant fossils found in some parts of the upper Triassic sediments of southwestern North America. In contrast to these large, heavy bones, most of the postcranial skeleton in the metoposaurs is re-

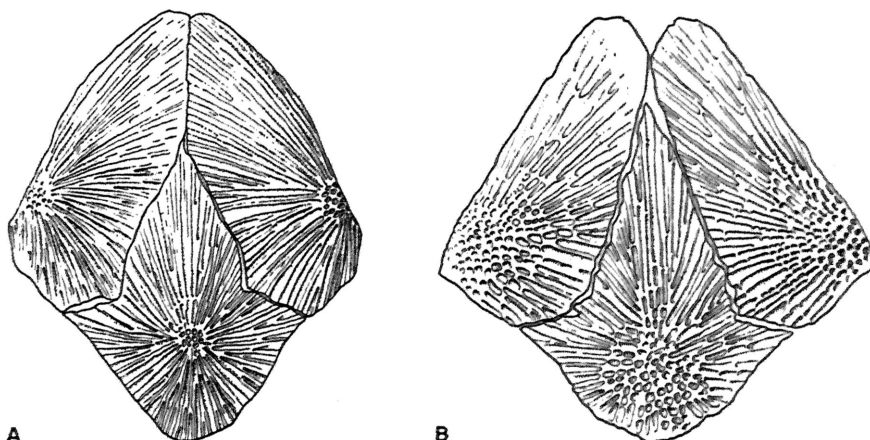


FIG. 10. Comparison of the clavicles and interclavicle in two metoposaurs, as seen in ventral view. Drawn to unit scale. A. *Metoposaurus diagnosticus*, after Fraas, 1896. B. *Eupelor fraasi jonesi* ("*Buettneria howardensis*"), after Sawin, 1945. Note restricted area of circular pits in interclavicle and clavicles of *Metoposaurus* as compared with *Eupelor*; also extended contact between clavicles of *Metoposaurus* and lack of such contact in *Eupelor*.

markedly weak and poorly ossified. Because of these differences in ossification, the interclavicle and clavicles are frequently well preserved, making them useful for statistical studies, while other postcranial bones are comparatively rare.

The interclavicle is a flat, rather diamond-shaped bone, with a long area on either side for articulation with the clavicles. At the

center of the external surface of the bone are irregularly sculptured pits, and from these, elongated depressions radiate to the lateral margins of the bone. In ventral view the clavicle is a sort of wing-shaped bone, thick at its posterolateral portion, on the outer surface of which is a sculpturing of irregular pits. From this portion of the bone long pits radiate to the thinner edges of the bone. A blade

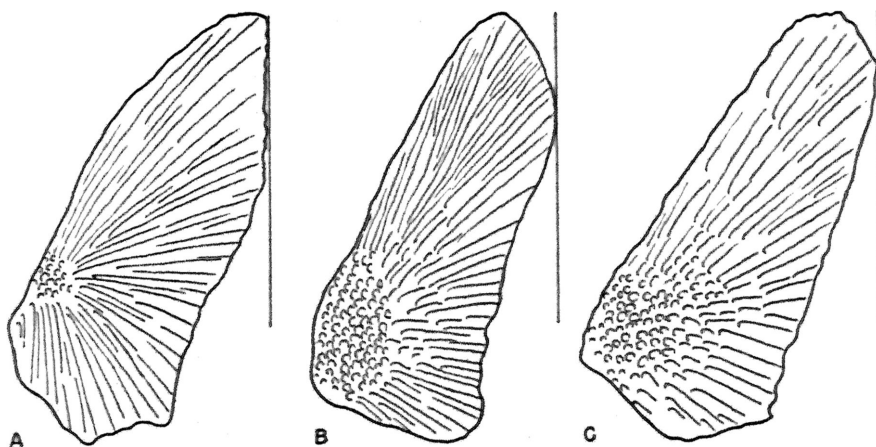


FIG. 11. Diagrammatic figure, drawn to unit scale, to compare clavicles in three metoposaurs, showing general proportions, relative areas of pits and grooves in external surfaces, and lines or points of contacts with clavicle of opposite side. A. *Metoposaurus diagnosticus*, after Fraas, 1896. B. *Eupelor browni* ("*Anaschisma*" *browni*), after Branson and Mehl, 1929. C. *Eupelor fraasi jonesi* ("*Buettneri howardensis*"), after Sawin, 1945.

extends upward from the external lateral edge of the clavicle, for articulation with other elements of the shoulder girdle.

It is pointed out above that there seems to be a qualitative difference in the sculpturing of the skull roof that distinguishes European from North American metoposaurs. In short, there is a greater development of elongated grooves in the skulls of the Old World forms than in those of the New World forms. A similar situation appears to be true of the interclavicle and the clavicles. In *Metoposaurus* of Europe there is a very small area of rounded or hexagonal depressions at the very center of the interclavicle, and from this area long grooves radiate laterally to all edges of the bone. In the American metoposaurs, on the other hand, the area of rounded pits is of considerable extent, and the development of long grooves extending radially to the edges of the bone is correspondingly reduced. Similarly the elongated grooves cover more of the surface of the clavicle in *Metoposaurus* than they do in that of the American forms. In these bones of the shoulder girdle the differences appear to be more pronounced between Old World and New World types than they are in the skull and appear to constitute good characters for distinguishing the metoposaurs of the two hemispheres.

The cleithrum in the metoposaurs is small, and the scapulocoracoid, though rather stout, is also of comparatively small size.

Thus the interclavicle and the clavicles are the dominant elements of the shoulder girdle.

The pelvis is reduced in size and shows none of the sculpturing that is so characteristic of the lower surfaces of the interclavicle and the clavicles in the pectoral girdle.

As might be expected, the limbs and feet are comparatively small and weak, for which reason they are not commonly found among the fossilized materials of metoposaurs. Many of the bones in the feet were evidently cartilaginous.

Vertebral centra of metoposaurs are fairly common in the upper Triassic continental sediments of western North America. These vertebrae are solid, with no indication of a notochordal perforation. The evidence indicates that these are enlarged intercentra, the pleurocentra having been completely suppressed. Neural spines were placed dorsally upon these intercentra, while double-headed ribs articulated with them in the presacral region.

According to Romer, the intercentra in *Metoposaurus* (at least in the specimen figured by Fraas) are "hemicylinders of no great thickness, although with parallel anterior and posterior margins. . . . It is reasonable to believe that there was present in cartilage a solid 'centrum' similar to that of *Buettneria*. Whether the incomplete ossification is a generic or, as one may suspect, an age character cannot be said" (Romer, 1947, p. 252).

## BIOMETRIC ANALYSIS OF AMERICAN METOPOSAURS

PREVIOUS TAXONOMIC WORK on metoposaurs has been based almost entirely on the study of single specimens or very small samples. Collections of this sort are, of course, poor materials on which to base estimates of ontogenetic and individual variation, and it is not surprising to find that published descriptions of metoposaur species and genera seem generally to underestimate the importance of infraspecific variability.

In the preparation of the present paper,

width (*GW*), and orbital width (*OW*); for the interclavicle, extreme interclavicle length (*IL*) and interclavicle width (*IW*); and, for the clavicle, clavicle width (*CW*) and clavicle length (*CL*). Measurements of these characters are presented in tables 1-4.

Statistical treatment of linear measurements made on metoposaurs is somewhat complicated by the fact that objective criteria are lacking to identify the adult or any other particular growth stage. In general,

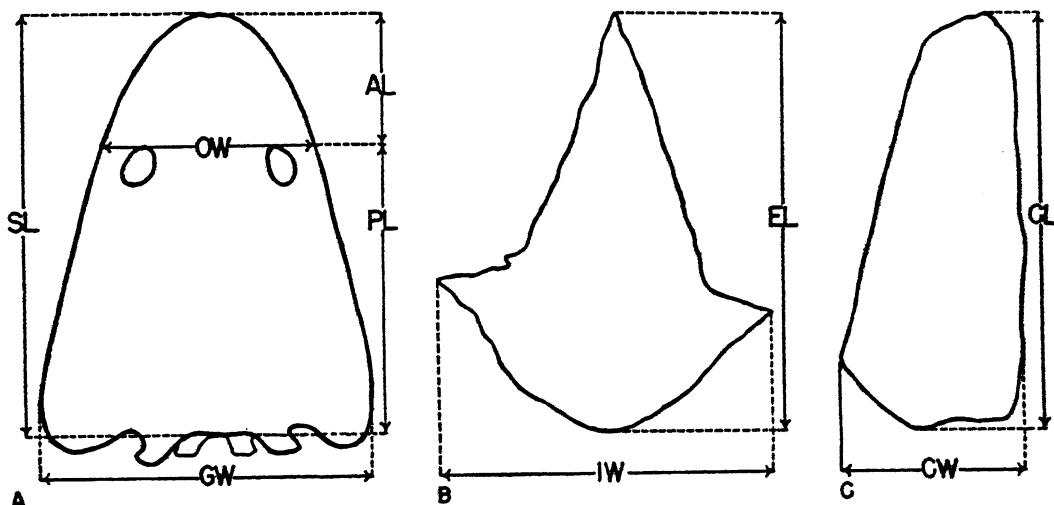


FIG. 12. Diagram to show manner in which measurements of skull, interclavicle, and clavicle were made. A. Skull: *SL*, skull length; *GW*, greatest width; *OW*, orbital width; *AL*, antorbital length; *PL*, postorbital length. B. Interclavicle: *EL*, extreme length; *IW*, interclavicle width. C. Clavicle: *CL*, clavicle length; *CW*, clavicle width.

the authors have had the opportunity of studying four stratigraphically homogeneous collections, each of which contains enough individuals to shed light on the structure of seemingly typical metoposaur populations. In order to take full advantage of this material it was felt desirable to treat the problem biometrically.

The first and most important step in any biometrical investigation is the selection of characters to be analyzed. Careful study and comparison of materials available to us indicate that nine skeletal dimensions are among the most significant unit taxonomic characters (fig. 12). These are, for the skull, antorbital length (*AL*), postorbital length (*PL*), skull roof length (*SL*), greatest skull

of course, it may be assumed that larger specimens are older than smaller specimens, but this assumption does not permit taxonomic conclusions to be based on direct comparisons of linear measurements of different samples. The collection from New Mexico, for example, contains 18 individual skulls ranging in length from 314 to 543 mm., with an average length of 439 mm. How should this sample be compared with that from Howard County, Texas, with seven individuals ranging in length from 353 to 504 mm., and with an average length of 420 mm.? If we base our comparison on the largest skull observed in each case, there is at least a reasonably high probability that the difference is due more to chance sampling errors

than to any real difference in the populations. On the other hand, if we base a comparison on sample averages, we have no assurance that the difference is not due to chance irregularities in the representation of size classes.

The difficulties discussed in the preceding paragraph can be largely avoided by con-

#### BIVARIATE CHARACTERIZATION

A sample is said to be characterized when morphological features judged to be significant are described for study or publication. Bivariate statistical characterization is based on the fact that pairs of measurements when plotted usually tend to follow a mathematical curve of the form  $y = bx^a$ , where  $y$  and  $x$

TABLE 1  
MEASUREMENTS (IN MILLIMETERS) OF METOPOSAURS FROM THE CHINLE FORMATION NEAR  
LAMY, NEW MEXICO

Sample No.	SL	GW	AL	PL	OW	CL	CW	IW	IL	EL
M.C.Z.										
1	410	400	130	280	—	422	197	386	400	465
1	459	391	157	302	242	300	157	402	437	541
1	483	392	175	308	260	327	185	224	287	350
1	386	343	127	259	215	234	—	380	471	575
1	408	354	127	281	230	294	150	263	343	400
1	352	325	102	250	198	341	170	—	—	—
1	500	355	176	324	255	377	178	—	—	—
1	485	418	175	310	316	297	135	—	—	—
1	—	330	120	—	200	286	149	—	—	—
1	467	440	140	327	304	443	170	—	—	—
1	445	350	135	310	230	339	159	—	—	—
1	—	290	—	—	—	—	—	—	—	—
U.S.N.M.										
1	543	533	170	373	400	410	180	240	285	315
1	504	468	159	345	291	329	163	325	358	390
1	407	351	112	295	238	300	140	329	397	430
1	368	316	117	251	180	270	147	238	—	327
1	498	430	160	338	276	405	179	283	335	380
1	400	366	120	280	240	—	193	—	—	—
1	314	270	76	238	188	—	—	—	—	—
1	474	422	136	338	258	—	—	—	—	—

sidering the relative growth of pairs of unit characters. In statistical terms this constitutes bivariate analysis. Four types of statistical analyses based on patterns of relative growth are employed in this paper: (1) bivariate characterization, (2) bivariate discrimination, (3) estimation of bivariate overlap, and (4) multivariate characterization. The first two methods are adapted from published studies by Teissier (1948), Kermack and Haldane (1950), and Kermack (1954). A condensed and somewhat simplified presentation can be found in Imbrie (1956). The last two methods represent new elaborations of previously published techniques.

are two linear measurements and  $a$  and  $b$  are mathematical parameters taking on various values for different curves. Thus to describe a growth pattern relating two measurements,  $x$  and  $y$ , it is necessary only to specify  $a$  and  $b$  (the growth ratio and the initial growth index, respectively). This system of characterization has the great advantage that the sample is described by a line which is valid over the entire range of observations represented by the sample (and which in some instances can safely be extrapolated beyond the limits of the sample). Consequently the investigator is not called upon to identify any particular growth stage.

TABLE 2

MEASUREMENTS (IN MILLIMETERS) OF METOPOSAURS FROM THE DOCKUM FORMATION IN POTTER  
AND HOWARD COUNTIES AND ADJACENT AREAS, TEXAS

Sample No.	SL	GW	AL	PL	OW	CL	CW	IW	IL	EL
2 <sup>a</sup>	435	370	136	299	200	335	179	430	515	—
2	470	421	140	330	245	345	160	305	340	—
2	395	370	125	270	190	340	162	240	355	—
2	448	400	140	308	220	334	167	300	393	—
2	455	420	138	317	220	375	200	355	490	—
2	432	385	130	302	218	390	172	240	322	363
2	475	470	145	330	274	275	135	308	422	—
2	400	360	125	275	195	324	161	255	321	—
2	510	450	163	357	275	259	112	284	364	—
2	500	550	156	344	300	340	145	262	395	424
2	299	270	96	203	140	270	145	278	336	410
2	372	340	115	257	180	265	115	360	448	—
2	455	424	151	304	246	356	177	359	440	—
2	369	316	121	248	188	366	200	391	339	—
2	374	338	111	263	172	364	179	334	418	510
2	—	—	—	—	—	320	162	320	411	—
2	—	—	—	—	—	384	165	320	397	—
2	—	—	—	—	—	258	135	290	384	—
2	—	—	—	—	—	377	212	315	373	—
2	—	—	—	—	—	289	144	255	341	—
2	—	—	—	—	—	343	168	340	415	—
2	—	—	—	—	—	390	192	310	397	—
2	—	—	—	—	—	362	158	220	285	—
2	—	—	—	—	—	318	153	310	380	—
2	—	—	—	—	—	318	156	367	430	—
2	—	—	—	—	—	341	164	275	312	—
2	—	—	—	—	—	350	168	308	354	415
2	—	—	—	—	—	330	170	289	333	360
2	—	—	—	—	—	319	137	365	415	487
2	—	—	—	—	—	298	142	374	395	—
2	—	—	—	—	—	400	178	280	343	410
2	—	—	—	—	—	290	129	328	375	—
2	—	—	—	—	—	283	134	308	354	—
2	—	—	—	—	—	247	113	—	—	—
2	—	—	—	—	—	268	122	—	—	—
2	—	—	—	—	—	314	168	—	—	—
2	—	—	—	—	—	318	170	—	—	—
2	—	—	—	—	—	354	162	—	—	—
2	—	—	—	—	—	392	170	—	—	—
2	—	—	—	—	—	332	169	—	—	—
2	—	—	—	—	—	297	122	—	—	—
2	—	—	—	—	—	375	184	—	—	—
2	—	—	—	—	—	328	170	—	—	—
2	—	—	—	—	—	323	147	—	—	—
2	—	—	—	—	—	375	192	—	—	—
2	—	—	—	—	—	309	105	—	—	—
2	—	—	—	—	—	322	137	—	—	—
3 <sup>b</sup>	353	321	120	195	200	283	141	247	—	347
3	384	341	120	264	211	343	165	300	—	395
3	409	398	136	273	231	340	185	333	—	443
3	427	391	140	287	245	376	190	371	—	469
3	431	411	143	288	235	349	190	362	—	445

TABLE 2—(continued)

Sample No.	SL	GW	AL	PL	OW	CL	CW	IW	IL	EL
3	432	402	134	298	249	380	202	—	—	—
3	504	—	176	328	—	380	203	—	—	—
4 <sup>c</sup>	151	120	49	102	79	—	—	—	—	—
5 <sup>d</sup>	443	344	168	275	207	—	—	—	—	—
6 <sup>e</sup>	288	232	84	204	140	—	—	—	—	—

<sup>a</sup> From Dockum formation, Potter County, Texas; Panhandle-Plains Museum, Canyon, Texas.

<sup>b</sup> From Dockum formation, Howard County, Texas (Sawin, 1945).

<sup>c</sup> Cast of small skull from Howard County, Texas, in Texas Technological College Museum; original in Austin, Texas.

<sup>d</sup> Type of *Buettneria perfecta*, M.P.U.M. No. 7475.

<sup>e</sup> Type of *Buettneria bakeri*, M.P.U.M. No. 13055.

Whenever the growth ratio ( $a$ ) differs markedly from unity, the growth pattern is strongly curved. If this is the case, it is necessary to transform the original measurements into logarithms and to fit a straight line to the scatter of points representing the transformed data. In dealing with the samples in this paper, however, we found that the samples are small enough and variable enough so that a straight line fits the original data about as well as the transformed data. Lines of relative growth computed for this study are therefore of the linear form  $y = ax + b$ . Here  $a$  represents the slope of the line and  $b$  the value of  $y$  when  $x = 0$ .

Various methods of fitting a line to a scatter of points have been applied to studies of relative growth. The most satisfactory method involves the use of the reduced major axis, a line that minimizes the sum of the products of the distances measured vertically and horizontally from each point

to the line in question. In figure 13A this corresponds to the minimizing of the sum of the products of the distances measured as  $d_x$  and  $d_y$ .

Each sample treated in this paper is characterized in two ways: by a table of original measurements (tables 1–4), and by means of bivariate statistics calculated from the raw data (table 5). For each pair of measurements  $x$  and  $y$ , these statistics include the following:

- $N$  = number of pairs of observations
- $\bar{x}$  = mean of  $x$
- $\bar{y}$  = mean of  $y$
- $s_x$  = standard deviation of  $x$
- $s_y$  = standard deviation of  $y$
- $r$  = correlation coefficient
- $OR_x$  = observed range of  $x$
- $a$  = growth ratio
- $b$  = initial growth index
- $\sigma_a$  = standard error of  $a$

For characters judged to be of special importance, lines of relative growth have

TABLE 3

MEASUREMENTS (IN MILLIMETERS) OF METOPOSAURS FROM THE POPO AGIE FORMATION, WYOMING

Sample No.	SL	GW	AL	PL	OW	CL	CW
7 <sup>a</sup>	448	412	160	288	237	420	280
7 <sup>b</sup>	413	343	154	259	210	—	—
7 <sup>c</sup>	388	312	148	240	192	325	155
7 <sup>d</sup>	540	440	181	359	284	375	200

<sup>a</sup> Type of *Anaschisma browni*.

<sup>b</sup> Type of *Anaschisma brachygnatha*.

<sup>c</sup> Type of *Borborophagus wyomingensis*.

<sup>d</sup> Type of *Koskinonodon princeps*.

TABLE 4  
MEASUREMENTS (IN MILLIMETERS) OF METOPOSAURS FROM ARIZONA

Sample No.	SL	GW	AL	PL	OW
8 <sup>a</sup>	495	467	148	347	244
8 <sup>a</sup>	555	480	175	380	281
8 <sup>a</sup>	606	570	185	421	308
8 <sup>b</sup>	379	330	109	270	211

<sup>a</sup> U.C. locality 7307, Blue Hills, near St. Johns, Arizona.

<sup>b</sup> A.M.N.H. No. 6759 near Cameron, Arizona.

been constructed (figs. 14A, C, 15A, C). Appropriate formulas are given in Kermack and Haldane (1950).

#### BIVARIATE DISCRIMINATION TEST

After samples have been characterized according to the scheme outlined above, the investigator normally wishes to know whether or not differences between the growth patterns computed for his samples are great

enough to be considered statistically significant. For any designated pair of samples the hypothesis is set up that the collections were made from identical populations and that (as a consequence) the observed difference in growth pattern is due purely to random sampling errors. If this hypothesis is true, there is no real difference between the samples; if it is false, there is said to be a statistically significant difference between the

TABLE 5  
STATISTICAL CHARACTERIZATION OF SAMPLES OF AMERICAN METOPOSAURS BASED ON MEASUREMENTS IN MILLIMETERS (CALCULATIONS ON GROUPED DATA)

Sample No.	<i>x</i>	<i>y</i>	<i>N</i>	$\bar{x}$	$\bar{y}$	$s_x$	$s_y$	<i>r</i>	<i>OR</i> <sub>2</sub>	<i>a</i>	$\sigma_a$	<i>b</i>
1	AL	SL	18	140	439	28.1	61.6	.933	76-176	2.194	.186	131.8
1	AL	PL	18	140	301	28.4	36.6	.779	76-176	1.292	.191	120.1
1	OW	GW	18	250	381	55.0	63.3	.940	180-400	1.150	.092	93.5
1	SL	GW	18	439	385	61.6	61.9	.854	314-543	1.006	.124	-56.6
1	CW	CL	15	164	343	17.8	55.7	.781	135-197	3.123	.503	-169.2
1	EL	IW	10	420	305	88.1	67.0	.922	315-575	.761	.094	-14.6
2	AL	SL	15	134	427	17.3	58.9	.986	96-163	3.415	.147	-30.6
2	AL	PL	15	134	294	17.6	41.3	.935	96-163	2.346	.215	-20.4
2	OW	GW	15	217	392	44.2	69.1	.971	140-300	1.565	.096	52.4
2	SL	GW	15	427	392	58.9	69.1	.912	299-510	1.173	.124	-108.9
2	CW	CL	47	158	329	24.7	41.4	.813	105-212	1.674	.142	64.5
2	EL	IW	8	425	295	51.0	38.9	.834	360-510	.762	.149	-28.9
3	AL	SL	7	139	420	18.7	47.2	.930	120-176	2.527	.351	68.8
3	AL	PL	7	139	275	18.7	40.0	.747	120-176	2.141	.537	-22.6
3	OW	GW	6	227	380	19.0	36.4	.911	200-249	1.921	.323	-56.10
3	SL	GW	6	406	378	31.9	36.7	.948	353-504	1.150	.150	-88.9
3	CW	CL	7	182	350	21.4	33.6	.950	141-203	1.569	.185	64.40
3	EL	IW	5	419	325	48.8	52.4	.977	347-469	1.075	.103	-125.4
7	AL	SL	4	161	447	15.5	69.5	.996	145-184	4.487	.200	-275.4
7	AL	PL	4	161	285	15.5	49.7	.997	145-184	3.209	.127	-231.7
7	OW	GW	4	235	380	39.7	63.1	.959	190-295	1.589	.226	6.6
7	SL	GW	4	445	380	64.8	60.3	.922	388-540	.930	.180	-33.9
8	AL	SL	4	155	510	33.8	94.7	.996	109-185	2.802	.125	75.7
8	AL	PL	4	155	357	33.8	64.0	.994	109-185	1.893	.104	63.6
8	SL	GW	4	510	465	94.7	99.0	.982	379-606	.957	.090	-23.0



TABLE 6

TEST FOR SIGNIFICANCE OF DIFFERENCE BETWEEN SLOPES OF LINES OF RELATIVE GROWTH RELATING CLAVICLE WIDTH AND CLAVICLE LENGTH FOR METOPOSAUR SAMPLES FROM NEW MEXICO AND FROM POTTER COUNTY, TEXAS (Measurements in millimeters.)

Sample 1 (New Mexico)

$$a_1 = 3.123$$

$$\sigma_{a_1} = 0.503$$

Sample 2 (Potter County, Texas)

$$a_2 = 1.674$$

$$\sigma_{a_2} = 0.142$$

$$z = \frac{|a_1 - a_2|}{\sqrt{\sigma_{a_1}^2 + \sigma_{a_2}^2}} = \frac{1.449}{\sqrt{0.273}} = 2.77$$

Because  $z > 2.58$ ,  $P < 0.01$

samples. In order to treat the two samples as separate taxonomic units it is of course necessary to reject the hypothesis, but in doing so, there will usually be a finite chance that the hypothesis is really true. When a statistic  $z$  is computed, it is possible to determine the probability of making an error of this sort. If this probability ( $P$ ) is greater than 5 per cent, then the observed difference is normally judged not to be significant. On the other hand, if  $P$  is less than 5 per cent, the difference is usually judged to be statistically significant. Details of carrying out

TABLE 7

RESULTS OF TESTS OF SIGNIFICANCE FOR DIFFERENCES IN SLOPE AND POSITION BETWEEN PAIRS OF METOPOSAUR SAMPLES

Sample Pair <sup>a</sup>	Characters	Test	Level of Significance
1-2	CW-CL	Slope	.01
1-3	SL-GW	Position	.01
1-7	AL-PL	Slope	.01
1-8	AL-PL	Slope	.01
2-3	CW-CL	Slope	.01
2-7	AL-PL	Slope	.01
2-8	SL-GW	Position	.02
3-7	SL-GW	Position	.01
3-8	AL-PL	Position	.01
7-8	AL-PL	Position	.01

<sup>a</sup> 1, New Mexico; 2, Potter County, Texas; 3, Howard County, Texas; 7, Wyoming; 8, Arizona.

tests of significance for the slope and position of growth lines are explained in Kermack (1954) and Imbrie (1956). A sample calculation is presented in table 6, and the results of various tests for the material studied in the present paper are given in table 7.

#### ESTIMATION OF BIVARIATE OVERLAP

Whenever morphological differences between two samples are judged to be statistically significant, a problem arises as to the proper taxonomic interpretation of the observed differences. Evaluations of this sort can never be based on biometrical data alone, or indeed on morphological data alone, for of necessity they involve a synthesis of morphologic, stratigraphic, and biogeographic information. Useful guides to the proper interpretation of morphological data may, however, be derived from statistical estimates of the amount of overlap (morphological identity) among the populations from which samples have been drawn.

Univariate statistical techniques for estimating overlap are well known (see Mayr *et. al.*, 1953, pp. 145-147; and Hubbs and Hubbs, 1953). Analogous estimates of overlap in bivariate data have not been widely used but seem to offer a useful approach to the taxonomic interpretation of morphologic data.

Burma (1948, p. 748) has employed a bivariate technique in many respects similar to the one developed below, but his approach is based on regression lines rather than reduced major axes.

Figure 13A represents a sample of six pairs of measurements. A reduced major axis ( $CD$ ) has been computed as a means of describing the average pattern of relative growth. Any point differs from the average condition by an amount  $d_x$  in the  $x$  direction and  $d_y$  in the  $y$  direction. The combined variation may be expressed by the vector sum of  $d_x$  and  $d_y$ , the diagonal  $PP'$  (elsewhere symbolized as  $d$ ). The actual distance from the line is thus  $d/2$  measured at an angle,  $\theta$ , to the  $x$ -axis. The distance from any point to the line can be similarly computed. The entire distribution of these half-diagonal distances ( $d/2$ ) can be treated by normal univariate statistical methods. For example, the standard deviation of these half-diagonal dis-

tances ( $s_{d/2}$ ) will give us a useful measure of dispersion. From Teissier (1948, p. 30) we have

$$s_{d/2} = \sqrt{\frac{(s_x^2 + s_y^2)(1-r)}{2}}.$$

Knowing the standard deviation of the half-diagonal distances ( $s_{d/2}$ ) in the sample, we can estimate the amount of dispersion in the population from which the sample has been taken. Some students prefer to lay off three standard deviations on either side of the line as an estimate of population range, because when a normal distribution is dealt with, such a theoretical range includes on an average 99.73 per cent of the population. Simpson (1941a, p. 797) has noted that this estimate of population range is equivalent to estimating the range of a population of about 442 individuals. The same author gives reasons for preferring range estimates for a population of size 1000, defined as the standard range (SR). This may be computed by laying off 3.2414 standard deviations on either side of the line.

Construction of a bivariate population range diagram will take two forms, depending on whether or not the original data have been transformed into logarithms. If the logarithmic transformation has been made, the amount of dispersion about the line of relative growth normally will be constant over the entire range of observations. This constancy is due to the fact that the amount of dispersion (which is in effect a measure of morphological variation) is ordinarily proportional to absolute size. As the use of logarithms gives equal weight to equal percentage deviations, one can for logarithmic data simply construct two lines parallel to the growth line and each distant from the growth line by an amount  $3.2414 s_{d/2}$ . Where  $\theta$  is the angle made by the growth line with the  $x$ -axis, the distance  $3.2414 s_{d/2}$  should be measured from the growth line at an angle of  $180^\circ - \theta$ .

In the present problem the original data have not been transformed into logarithms, and construction of a population range diagram is based on the assumption that the amount of dispersion about the line of relative growth is approximately proportional to the absolute size of the individual. The

general expression for the computation of the standard range from any point on the line ( $SR_i$ ) will then be given by

$$SR_i = \frac{3.2414 s_{d/2} y_i}{\bar{y}},$$

where

$SR_i$  = standard range at any designated value  
 $s_{d/2}$  = standard deviation of the diagonal distances from the line of relative growth,  
 $y_i$  = any designated value of  $y$ , and  
 $\bar{y}$  = mean of  $y$ .

Note that if  $y_i = 0$ ,  $SR_i = 0$ ; and if  $y_i = \bar{y}$ ,  $SR_i = 3.2414 s_{d/2}$ .

Construction of a bivariate population range diagram for arithmetic data thus proceeds as follows (see fig. 13B and table 8):

STEP 1: Compute  $s_{d/2}$ , according to the formula given above.

STEP 2: Select the lowest observed value of  $y$  (i.e.,  $y_1$ ) and compute the corresponding standard range ( $SR_1$ ) from the general expression given for  $SR_i$ .

STEP 3: From the point on the growth line

TABLE 8

CALCULATIONS NECESSARY FOR CONSTRUCTION OF  
 POPULATION RANGE DIAGRAM FOR METOPOSAUR  
 SAMPLE FROM POTTER COUNTY, TEXAS

For this sample,

$$\begin{aligned} x &= AL \\ y &= PL \\ s_x &= 17.6 \\ s_y &= 41.3 \\ r &= 0.935 \\ \bar{y} &= 294 \\ a &= 2.346 \end{aligned}$$

$$\begin{aligned} s_{d/2} &= \sqrt{(s_x^2 + s_y^2)(1-r)/2} \\ &= \sqrt{(2015.45)(0.065)/2} \\ &= \sqrt{65.50} = 8.09 \\ SR_i &= \frac{3.2414 s_{d/2} y_i}{\bar{y}} \end{aligned}$$

$$\text{For } y_i = 220, SR = \frac{(3.2414)(8.09)(220)}{294} = 19.6$$

$$\begin{aligned} \text{For } y_i &= 340, SR = 30.3 \\ \theta &= \arctan a \\ \theta &= 67^\circ \\ 180^\circ - \theta &= 113^\circ \end{aligned}$$

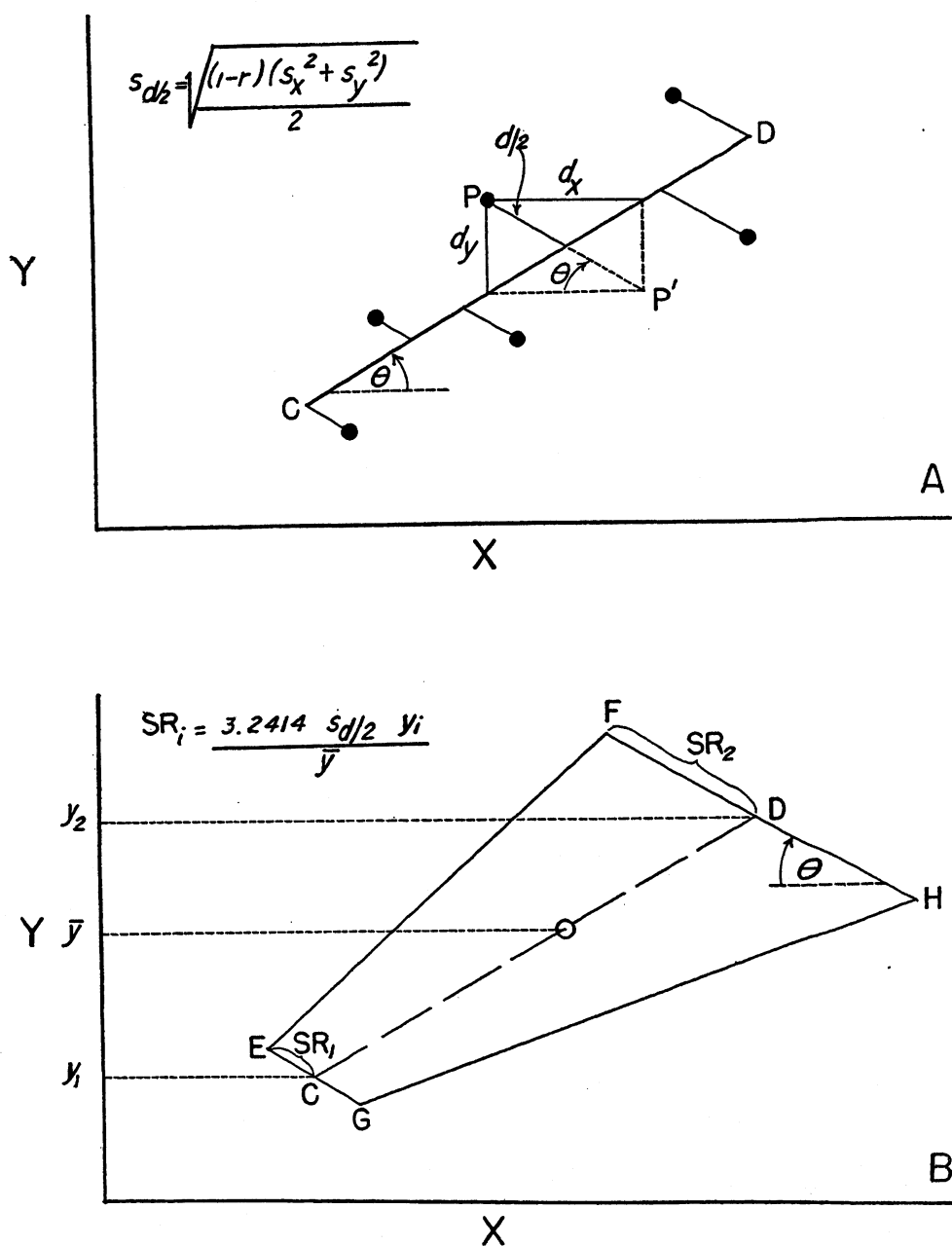


FIG. 13. A. Diagram illustrating reduced major axis ( $CD$ ) as a means of describing the trend of a scatter of points. Dispersion from the line is measured by  $s_{d/2}$ , the standard deviation of half-diagonal distances  $d/2$ . B. Diagram illustrating construction of a bivariate population range diagram ( $EFHG$ ) corresponding to a segment of a reduced major axis ( $CD$ ). For explanation, see text.

corresponding to the lowest observed value of  $y$ , lay off lines  $CE$  and  $CG$ , each equal in length to  $SR_1$ , at an angle  $180^\circ - \theta$ .

STEP 4: Similarly, construct the lines  $DF$  and  $DH$  corresponding to the point  $y_2$ , the largest observed value of  $y$ .

STEP 5: Construct lines  $EF$  and  $GH$ .

The figure  $EGHF$  then represents an estimate of the range of morphological variation that would be encountered in a random sample of 1000 individuals in the size range  $y_1 - y_2$ . This is equivalent to estimating the morphological range of the original population if its total population frequency were 1000. As Simpson has pointed out, if a figure larger than 1000 were designated as standard the increase in estimated morphological range would be negligible.

One limitation of this method (a limitation that does not apply with the same force to logarithmic data) is that extrapolation beyond the limits  $y_1$  and  $y_2$  is not safe. Further, it is clear that the estimate of range given by  $SR_1$  will be slightly higher than the true value for the standard frequency selected, owing to the fact that the standard deviation  $s_{y/2}$  is computed from a slightly heteroscedastic distribution. Neither of these limitations, however, is important enough to impair the utility of the method as a means of visualizing graphically the amount of variation that is to be expected in the population sampled.

By the superposition of two or more range diagrams it is possible to picture the degree of morphological overlap among several populations (see figs. 14B, C, 15B, D). When diagrams are used in this way it must be kept in mind that for each diagram the actual points will tend to concentrate near the growth line and occur with decreasing frequency away from the growth line, in a manner that is approximately described by the normal distribution.

#### MULTIVARIATE CHARACTERIZATION

For purposes of description and analysis it is necessary to treat morphological differences between samples in terms of unit characters such as skull length or skull width. Actual differences in size and form always involve more than one character, so that univariate

analysis gives a very limited picture of the real biological facts. When two variables are treated simultaneously (bivariate analysis), it is possible to arrive at a better characterization of morphological differences. In general, the more characters that are considered together the more satisfactory will be one's statistical view of morphological divergence. Provided that definite growth stages can be recognized, the ratio diagram (Simpson, 1941b) is a convenient means of achieving a multivariate characterization. For our problem, however, we need some multivariate scheme that will take into account differences in size and proportion accompanying growth. One simple method for doing this is to select arbitrary growth stages in some unit character and to estimate for these stages the average values of two ratios. A simple plot of one ratio against another will then provide a graphic record of four unit characters for each designated growth stage.

The necessary calculations are best explained by means of an actual example. Re-

TABLE 9

SKULL PROPORTIONS CALCULATED FOR THEORETICAL AVERAGE METOPOSAUR INDIVIDUALS OF VARIOUS STANDARD ANTORBITAL LENGTHS

Sample	Standard Antorbital Length	AL/PL %	GW/SL %
1	110	42	85
2	110	46	86
3	110	52	89
7	110	91	77
8	110	40	90
1	130	45	87
2	130	46	91
3	130	51	93
7	130	70	82
8	130	42	90.5
1	150	48	88
2	150	45	95
3	150	50	95
7	150	60	84
8	150	43	91
1	170	50	89
2	170	45	98
3	170	50	97
7	170	54	86
8	170	44	91.5

sults of these calculations are entered in table 9 and figure 16.

STEP 1: Select two pairs of characters with one common element (e.g.,  $a/b$  and  $a/c$ ) or two pairs of characters each sharing an element in common with a third pair (e.g.,  $a/b$ ,  $c/d$ , and  $a/c$ ). In this illustration, three pairs of characters are selected:  $GW/SL$ ,  $AL/PL$ , and  $AL/SL$ .

STEP 2: Compute for each pair of characters in each sample the allometric equation relating one unit character to the other. This is normally best done by means of the reduced major axis, as discussed above. For the New Mexico sample, the equations in the form  $y = ax + b$  (see table 5) are

$$SL = 2.194 (AL) + 131.84 \quad (1)$$

$$PL = 1.292 (AL) + 120.12 \quad (2)$$

$$GW = 1.006 (SL) - 56.63 \quad (3)$$

STEP 3: Select one or more growth stages in one unit character to serve as reference standards. In this case stages 110 mm., 130 mm., 150 mm., and 170 mm. in the character  $AL$  were selected. These values represent most of the observed growth range. The steps outlined below will then provide an estimate of the ratios  $GW/SL$  and  $AL/PL$  for average skulls having an antorbital length ( $AL$ ) of the stated standard dimensions.

STEP 4: For growth stage  $AL = 110$ , compute the most likely value of  $SL$  associated with it from equation 1. Thus, for the New Mexico sample,

$$SL = 2.194 (110) + 131.84 = 373.18.$$

STEP 5: For the same growth stage and sample, compute the expected value of  $PL$  from equation 2,

$$PL = 1.292 (110) + 120.12 = 262.24.$$

STEP 6: For the same growth stage and sample, compute  $GW$  from equation 3 and the value of  $SL$  found in step 4,

$$GW = 1.006 (373.18) - 56.63 = 318.79.$$

STEP 7: Compute the desired ratios  $GW/SL$  and  $AL/PL$  and plot the results. In this case,

$$GW/SL = 0.85 \text{ and } AL/PL = 0.42.$$

STEP 8: Proceed similarly for each growth stage and sample. The resulting graph (fig.

16) shows at a glance the changing proportions of the average skull during a portion of the growth of each population. Further, it permits comparison of proportions attained by average individuals at each designated growth stage.

#### SUMMARY OF RESULTS

Four pairs of measurements have been used in our statistical analysis of American metoposaurs: greatest width of the skull versus skull length; postorbital length of the skull versus antorbital skull length; greatest interclavicle width versus extreme interclavicle length; and clavicle length versus clavicle width. Skull measurements are available for the samples from New Mexico; Howard County, Texas; Potter County, Texas; Arizona; and Wyoming. Clavicle and interclavicle measurements are available for all except the Wyoming and Arizona samples.

Lines of relative growth plotted on figures 14A and C and 15A and C indicate the average pattern of growth for the characters designated above. Visual estimate of these growth lines indicates that the five samples exhibit notable average differences in morphology. These differences in growth patterns are shown to be significant (from the statistical point of view) by  $z$  tests for slope and position (table 7). At this point an examination of the bivariate overlap diagrams is enlightening (figs. 14B, D, 15B, D). It is clear that there is a very considerable amount of overlap among the populations. Thus the populations are judged to exhibit significant differences in average patterns of growth, even though containing many individuals that are identical with respect to the morphological features examined.

Data plotted on figure 16 enable us to compare simultaneously two significant skull proportions (skull elongation and orbital position) at each of several designated growth stages. It is evident that populations from the southwest (Texas, New Mexico, and Arizona) possess on the average blunter skulls and more anteriorly situated orbits than the Wyoming population. Moreover, the Wyoming population undergoes a much more radical change in orbital position during growth than the southwestern populations. In the light of this analysis it seems clear that the south-

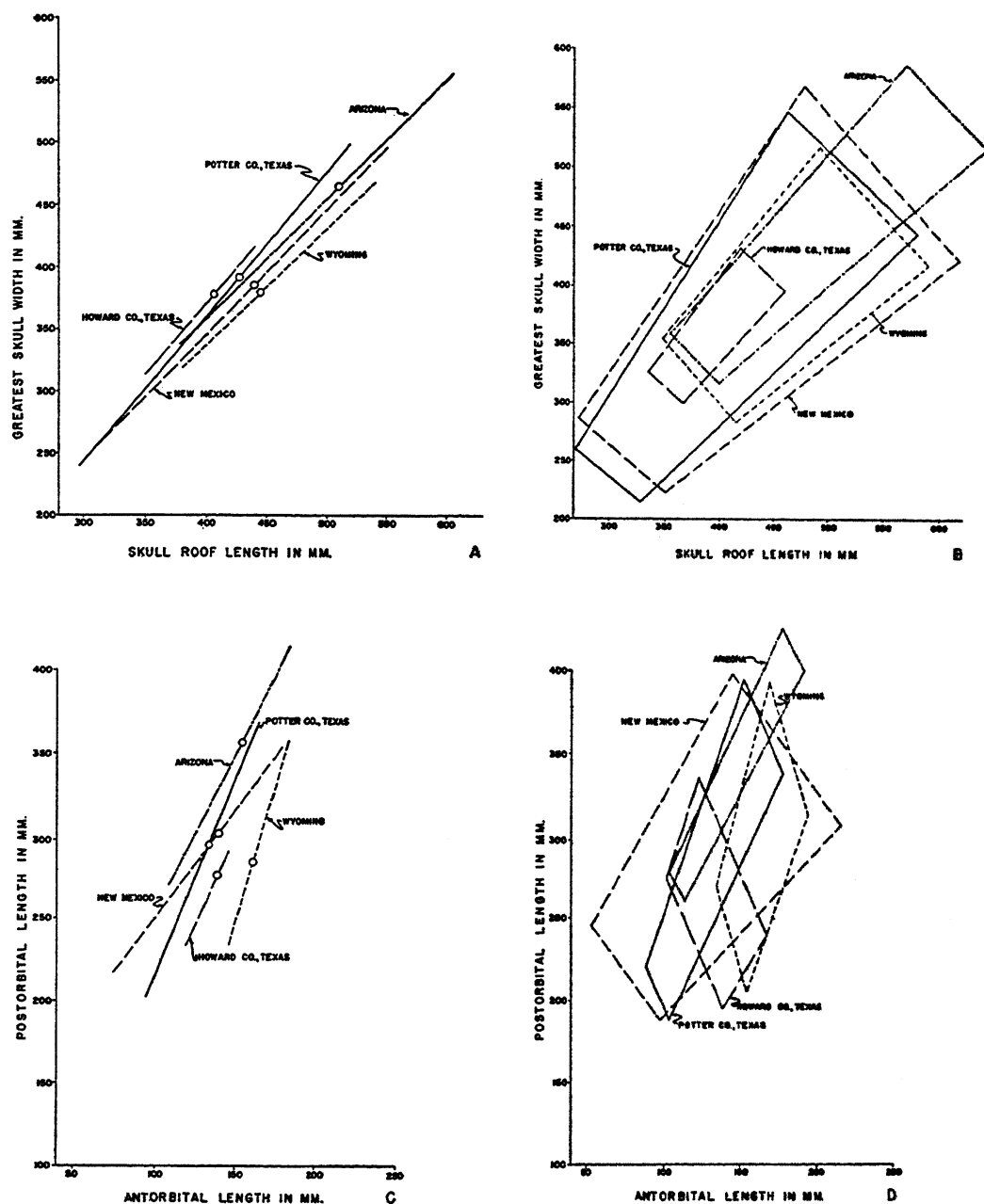


FIG. 14. Reduced major axes and population range diagrams constructed for pairs of skull measurements on five samples of *Eupelorus*. A. Reduced major axes representing average patterns of relative growth of greatest skull width and skull length. B. Population range diagrams corresponding to samples illustrated in A. C. Reduced major axes representing average patterns of relative growth of antorbital length and postorbital length. D. Population range diagrams corresponding to samples illustrated in C.

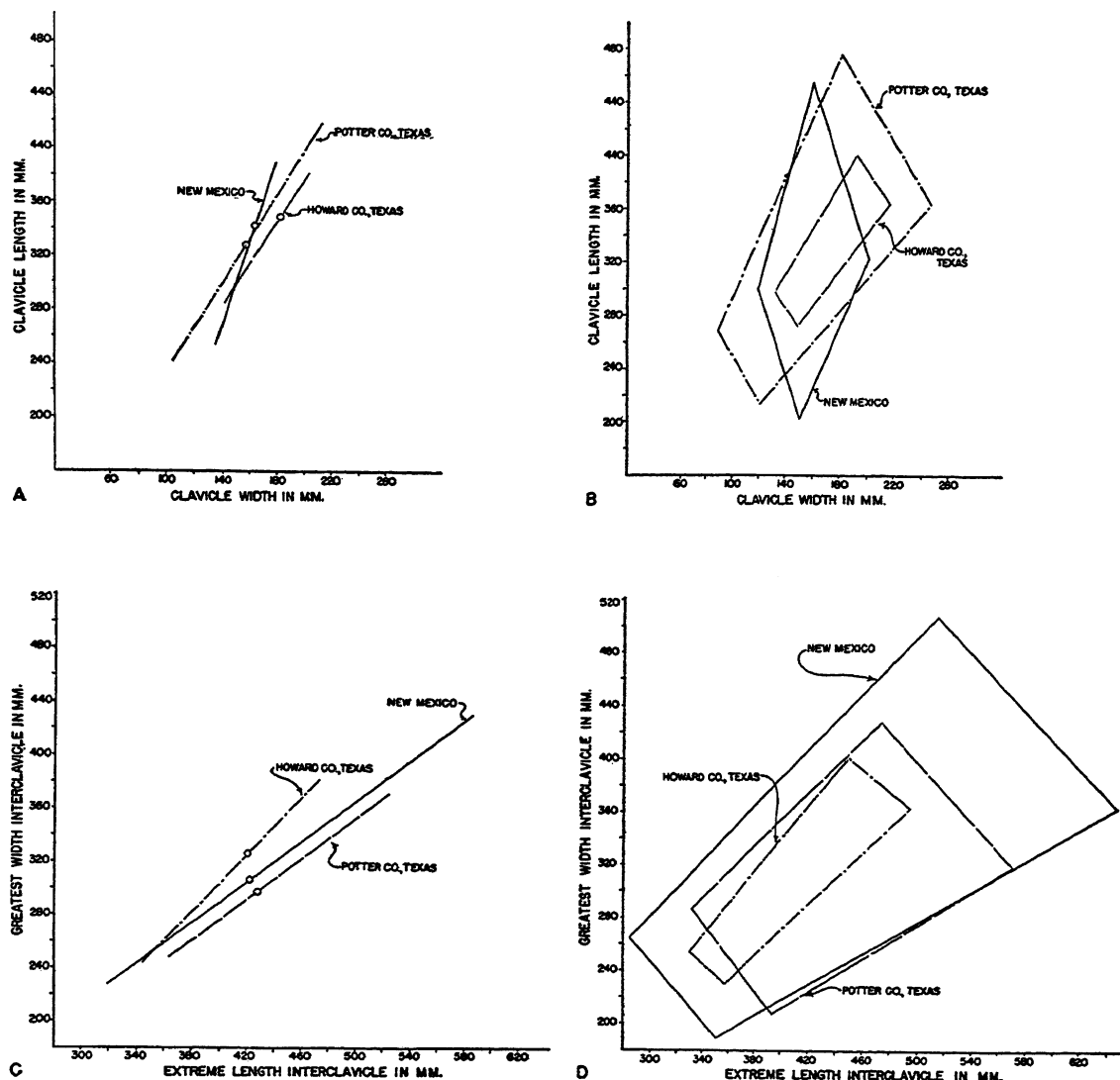
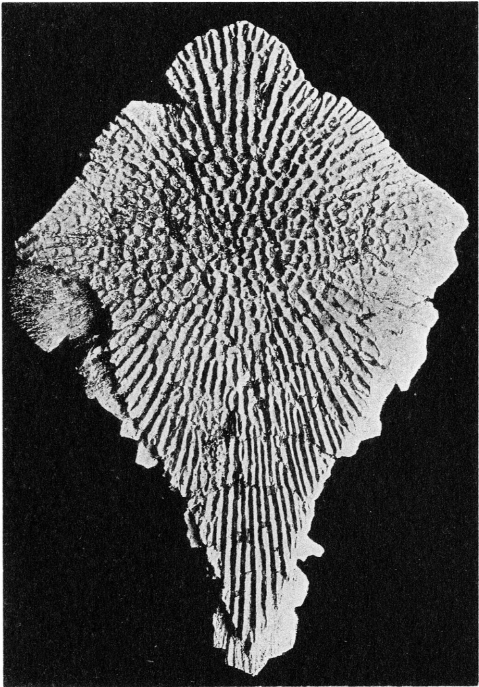


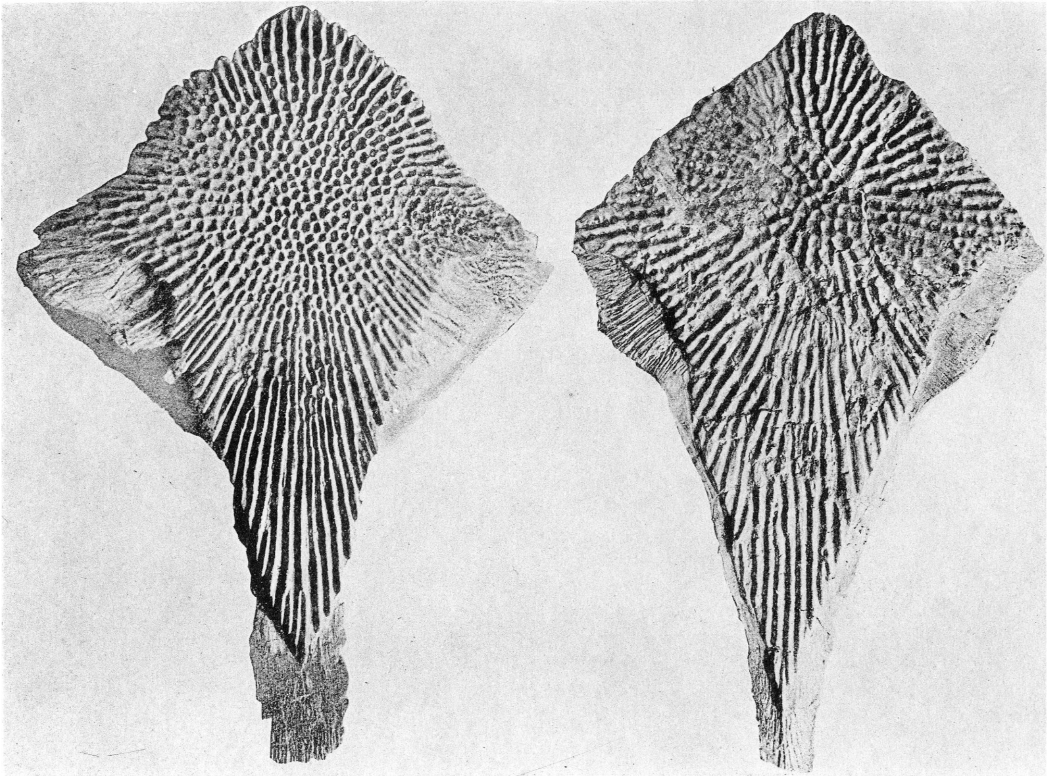
FIG. 15. Reduced major axes and population range diagrams constructed for pairs of postcranial measurements on three samples of *Eupelor*. A. Reduced major axes representing average patterns of relative growth of clavicle width and clavicle length. B. Population range diagrams corresponding to samples illustrated in A. C. Reduced major axes representing average patterns of relative growth of interclavicle width and extreme interclavicle length. D. Population range diagrams corresponding to samples illustrated in C.

#### PLATE 27

1. Interclavicle of *Eupelor fraasi fraasi*. This is the type of *Metoposaurus fraasi* Lucas.  $\times \frac{1}{3}$ . From Lucas, 1904.
- 2, 3. Interclavicles of *Eupelor fraasi jonesi*. These are paratypes of *Buettneria perfecta* Case. 2.  $\times \frac{1}{3}$ . 3.  $\times \frac{1}{3}$ . From Case, 1922.



1



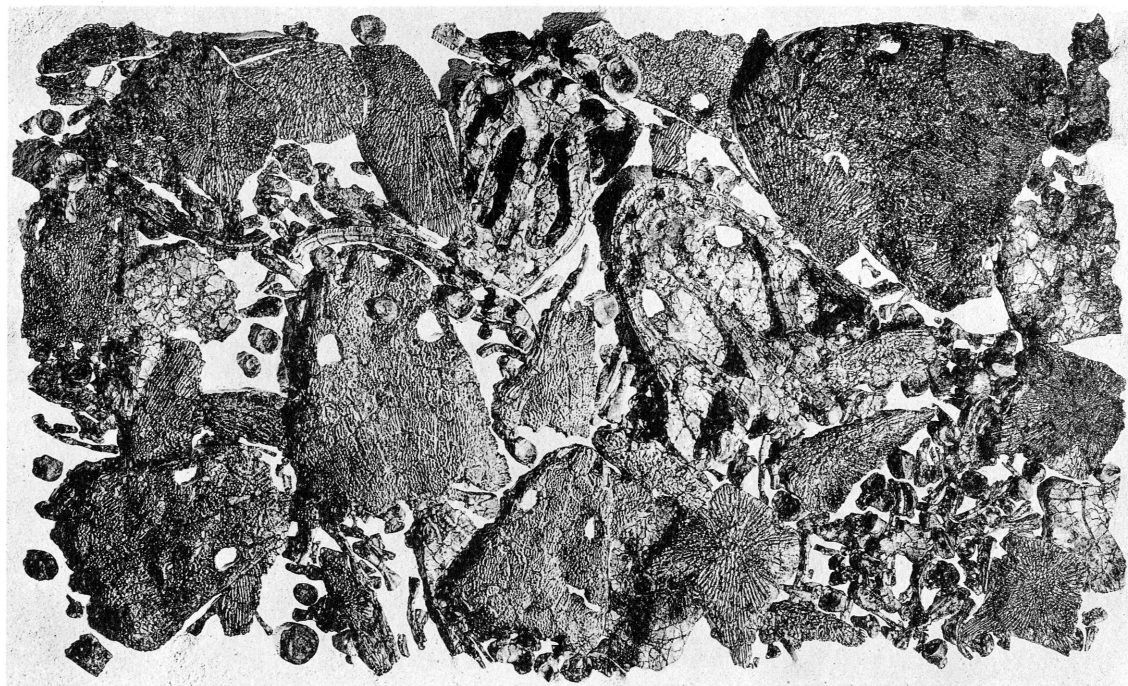
2

3





1



2

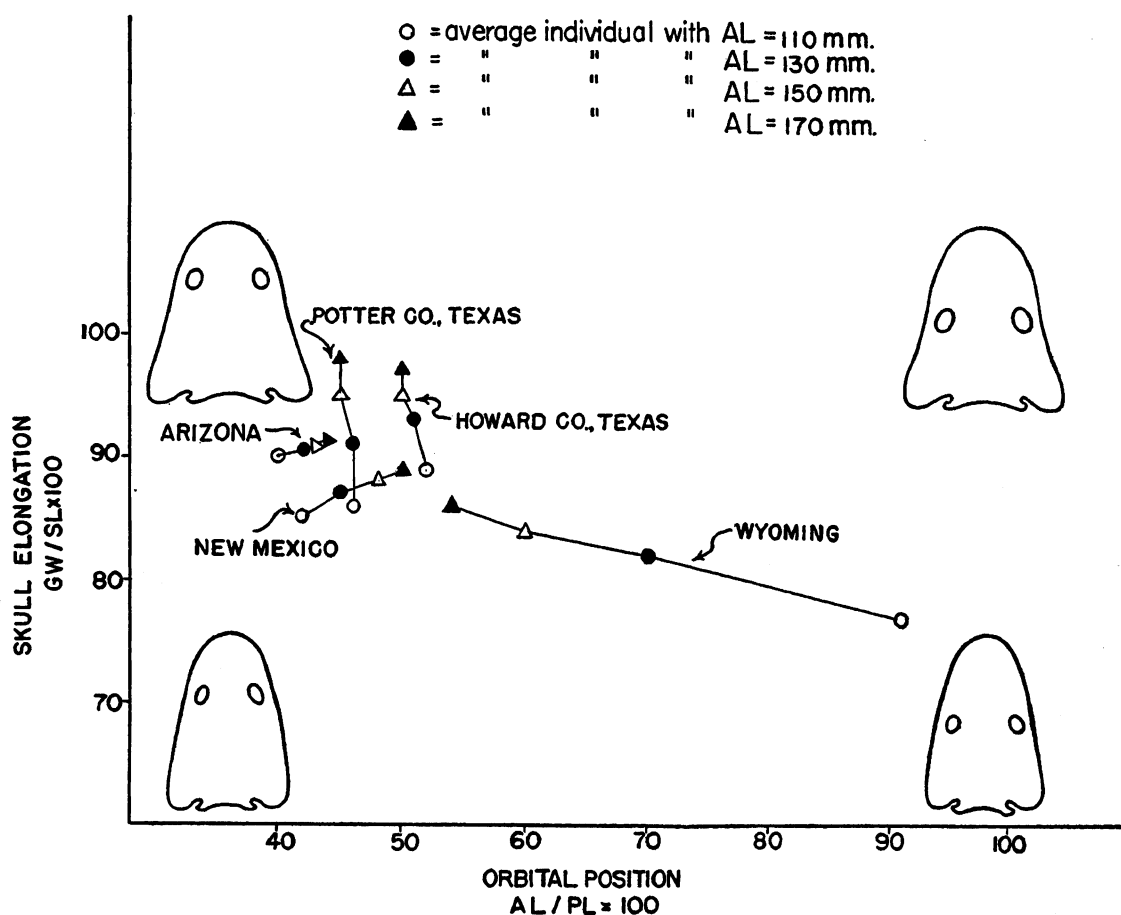


FIG. 16. Diagram illustrating skull proportions of theoretical average individuals having antorbital lengths equal to 110, 130, 150, and 170 mm. Skull outlines picture theoretical individuals corresponding to corners of variation field included in diagram. For detailed explanation, see text.

western samples form a compact group quite distinct (on the basis of average morphology) from the Wyoming specimens.

Turning to the points on figure 16 representing the four southwestern populations, we see that there is a difference between the populations from Texas and those from New Mexico and Arizona. Both of the Texas samples tend with increasing size to develop a slightly shorter antorbital distance. The Arizona and New Mexico specimens, on the

other hand, tend to develop a relatively longer antorbital distance during growth. Each of these groups, then, may be characterized in terms of a distinctive growth pattern.

A study of Colbert and Hooijer (1953, pp. 21-24) on the degree of osteological differences to be found among certain species and subspecies of modern mammals provides some basis for judging the taxonomic significance of the differences documented in the

#### PLATE 28

1. Slab containing skulls, jaws, and elements of the postcranial skeleton of the New Mexico population of *Eupelor fraasi fraasi*. Exhibited in the Museum of Comparative Zoölogy, Harvard College. Photograph by courtesy of the Director of the Museum of Comparative Zoölogy.

2. Similar slab of the same population exhibited in the United States National Museum. Photograph by courtesy of the Director of the United States National Museum.

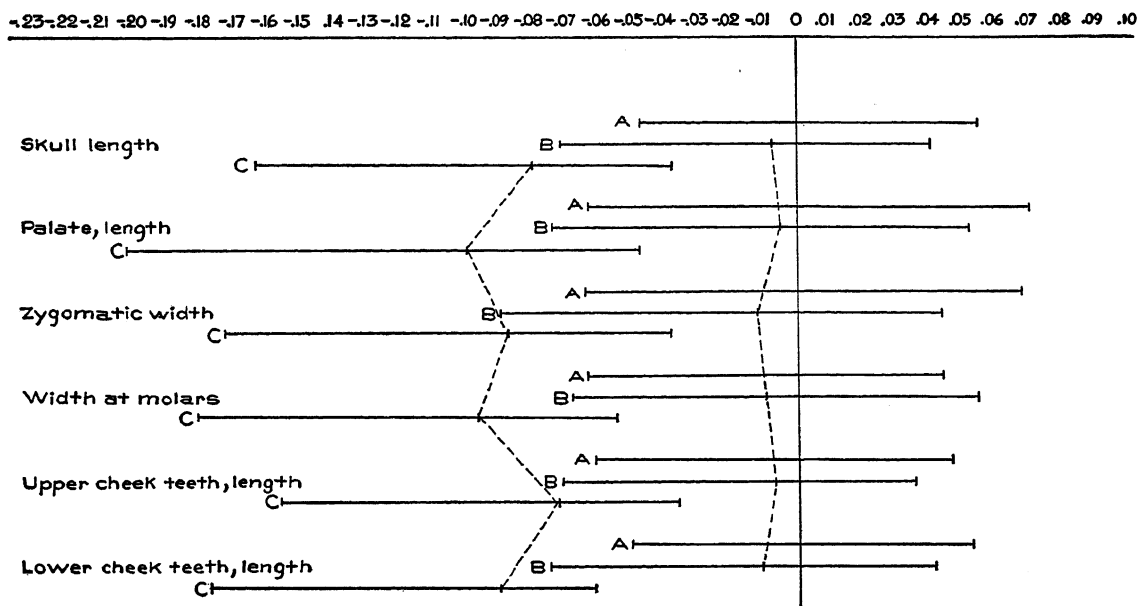


FIG. 17. Ratio diagram showing comparison of certain osteological characters in two species of *Mustela* and two subspecies of *Mustela sibirica*. The latter show a strong overlap of the characters measured, whereas the two species of *Mustela* show little overlap in these same characters. A. *Mustela sibirica fontanierii*, six males, four females. B. *Mustela sibirica davidiana*, six males, three females. C. *Mustela altaica kathiah*, four males, three females, one indeterminate. Data from Allen, 1938. From Colbert and Hooijer, 1953.

present paper. Figure 17, for example, illustrates by means of a ratio diagram the degree of overlap among three small samples of *Mustela*. Between subspecies there is a very considerable degree of overlap. Overlap between species, while less marked, is still quite noticeable in spite of the small sample size. If these data were treated by estimating the standard range of a population of 1000, the degree of overlap would, of course, be greatly increased.

Essential features of this biometric study may be summarized as follows:

1. The five samples of American meto-

posaurus treated here differ significantly in average growth patterns that relate at least four osteological dimensions.

2. A considerable degree of morphological overlap exists in the five populations sampled.

3. Simultaneous analyses of two significant skull proportions ( $GW/SL$  and  $AL/PL$ ) reveal degrees of morphological divergence which seem to reflect geographic differences.

4. The degree of morphological overlap estimated for populations of metoposaurus is roughly comparable to the degree of overlap found in species and subspecies of certain modern mammals.

## THE GENERA AND SPECIES OF METOPOSAURS

### DISCUSSION

WE ARE FACED with the problem of trying to evaluate the data that are set forth in the preceding pages of the present paper. It is shown, first, that the known metoposaurs of late Triassic age that are found in Eurasia and North America have been assigned by various students to a considerable number of genera and species. Some among the numerous names that have been given to upper Triassic metoposaurs have been based on very poor materials—materials so fragmentary as to give very little if any validity to the names for which they form the tangible evidence. Other names have been based on adequate materials, yet without any clear indications as to how the proposed new genus or species is truly distinct from some previously described form.

The review of the metoposaurs above shows that, treated quite objectively, these fossils are remarkably similar to one another. The differences are not nearly so great as had been supposed by the original describers of the various genera and species. Indeed, many of the differences on which taxonomic definitions have been based are no more impressive than individual variations seen in other animals.

Therefore it is evident that the number of named categories for upper Triassic metoposaurs should be greatly reduced, if our logic is to follow the results of our biometric analyses. The problem is how great the reduction of names should be and how it should be brought about.

The first metoposaur to be described was *Metopias diagnosticus*, named by von Meyer in 1842. Subsequently Lydekker substituted the name *Metoposaurus* for *Metopias*, this latter name having been preoccupied. *Metoposaurus diagnosticus* is obviously a valid name, and fortunately this species was based on some very good materials. Of the other described Eurasiatic metoposaurs, *Metoposaurus stuttgartiensis* was described on the basis of some ribs and vertebrae that are difficult to evaluate; *Metoposaurus santacrucis* was founded on a fragmentary skull that is in no way unusual and appears to represent a young individual of *Metoposaurus*

*diagnosticus*; *Trigonosternum latum* was based on a portion of an interclavicle that shows no truly distinctive features; while *Metoposaurus heimi* was based on a rather complete skull. It seems logical to consider all these names as probably synonymous with *Metoposaurus diagnosticus*. The one possible exception is *Metoposaurus heimi*, which may represent a distinct species of the genus. The proportions of the skull in *Metoposaurus heimi* are somewhat different from those of the original species; it is shorter and broader than the skull of *Metoposaurus diagnosticus*. Viewed in the light of our population analysis of American metoposaurs, these differences are judged to be of probable infraspecific rank. Therefore it is here proposed to regard all the Old World forms so far described as belonging to a single species.

The first metoposaur to be described from North America was *Dictyocephalus elegans*, named from a fragmentary skull roof of a very small individual. It is quite possible that this may represent a very young animal belonging to the same genus and species as one of the other North American metoposaurs, of which adult skulls are known. But as there is no way to prove this, and as a satisfactory evaluation of the type specimen cannot be attempted because of its fragmentary nature, it seems best to regard the name as valid, with a realization that comparisons of subsequently described forms to this type are all but impossible. In other words, there are no common grounds for referring other American metoposaurs back to *Dictyocephalus elegans*.

This brings us to the next described North American form, *Eupelorus durus*. The type materials are not so comprehensive as might be desired. Nevertheless some good fossils are preserved in the lot from Phoenixville, Pennsylvania, collected by Wheatley, which include the major portion of a clavicle, part of a interclavicle, and other fragments. These bones indicate a large metoposaur of the usual type.

The clavicle of *Eupelorus durus*, the one bone that is complete enough for an analysis of characters, shows a comparatively large area of rounded or roughly hexagonal sculp-

tured depressions on its surface, which may be contrasted with the comparatively small area of such depressions that characterized the sculpturing in *Metoposaurus*. As is indicated above, this difference in sculpture is one of the few qualitative differences to be seen between the Eurasiatic and North American metoposaurs. Together with other characters of the skull and postcranial skeleton we regard this as indicative of a generic distinction between the Old World and New World forms. Therefore we consider *Eupelor durus* to be a valid genus and species.

The next North American metoposaurus to be described was the single interclavicle from near Cameron, Arizona, named *Metoposaurus fraasi* by Lucas. The bone clearly is not to be referred to the genus *Metoposaurus* because of its shape and also because of the large area of rounded, sculptured pits at the center of the bone. Its surface is similar to that part of the interclavicle of *Eupelor durus* preserved in the type materials. Therefore it is logical to regard the Arizona specimen as belonging to the genus *Eupelor*, or to a closely related genus.

Should the interclavicle from Arizona, described by Lucas, be placed in a genus other than *Eupelor*? It might be argued that interclavicles of metoposaurs are poor criteria on which to base taxonomic judgments. But the uncomfortable fact is that we must here use an interclavicle in coming to a decision, because this is the only bone available. Of course it might be said that the interclavicles of two genera of metoposaurs could be so much alike that generic distinctions might not show up in these bones. Yet the comparison of *Metoposaurus* from Europe with the North American metoposaurs seems to indicate qualitative distinctions between genera that are visible in the interclavicle. Because the interclavicle described by Lucas is generally similar to what we know of the interclavicle of *Eupelor*, we believe that the chances are strongly in favor of a generic identity between the two.

The next question is, Should the interclavicle (*M. fraasi*) be referred to *Eupelor durus* or should it be placed in a separate species, *Eupelor fraasi*? There is no truly objective way to answer this question, with

the type materials that are available. On the basis of the probabilities involved we are suggesting that the form from Arizona may be regarded as taxonomically distinct from the eastern form. The two are separated by a distance of 2000 miles, and among modern amphibians and reptiles such geographic separation is frequently quite sufficient to be marked by taxonomic differences of either specific or subspecific magnitude.

Suppose for the moment that we consider the first described metoposaurus from western North America to be specifically distinct from the Newark form. This means that the name of the western form should be *Eupelor fraasi*. There seem to be no good reasons for regarding the various described species of metoposaurs from the southwest as taxonomically distinct from one another. As is shown by the biometric study, the populations that were analyzed all come within the limits of specific identity, and such differences as do appear can very logically be attributed to variation within the species. We are therefore proposing that all the metoposaurs from Texas, New Mexico, Arizona, and southern Utah should be regarded as of a single species. Consequently the forms described as *Metoposaurus jonesi*, *Buettneria perfecta*, *Buettneria major*, *Kalamoiskelor pinkleyi*, *Buettneria bakeri*, and *Buettneria howardensis* become synonyms of *Eupelor fraasi*.

We regret having to make this decision, because it eliminates the genus *Buettneria* which is well established in the literature. Yet there seems to us no other course possible if we are to place any confidence in the reality or the reliability of our biometric study. In this connection it might be well to say that, even if the southwestern metoposaurs are regarded as generically distinct from those of eastern North America, *Buettneria* would still probably have to be abandoned in favor of *Anaschisma*, first described from the Triassic of Wyoming, some 17 years before the description of *Buettneria*.

This brings us to a consideration of the metoposaurs of Wyoming, originally described as four distinct species contained in three genera, namely, *Anaschisma browni* and *brachygnatha*, *Borborophagus wyomingensis*,

and *Koskinonodon princeps*. The biometric analyses indicate that the known specimens described from the Popo Agie formation of Wyoming form a growth series similar to the series in the populations of *Eupelor fraasi* from Texas and New Mexico (see fig. 18). Therefore it seems proper to regard the metoposaurs from Wyoming as belonging to a single genus and species.

As for the genus, all the evidence indicates differences of less than generic grade between the metoposaurs from Wyoming and those of the southwest (see figs. 14B, D, and 15B, D, especially). Because the southwestern metoposaurs are here regarded as belonging to the genus *Eupelor*, those from Wyoming must also be considered as of this genus.

The problem of the species is more difficult. The first metoposaur to be described from Wyoming was *Anaschisma browni*. Therefore it might be logical to designate the Popo Agie metoposaurs as *Eupelor browni*. About the only good distinctions that can be seen between the metoposaurs from the two areas are those of certain proportions. On the average, the Wyoming forms have the orbit set slightly farther back in the skull than do those of the southwestern states; in other words the Popo Agie metoposaurs have a slightly greater antorbital length than the Chinle and Dockum metoposaurs. In addition, the postparietal bones of the Wyoming metoposaurs appear to be consistently shorter than those in the Chinle and Dockum metoposaurs.

These are real differences, but the problem is how much value they should be given. Do they represent specific or subspecific differences? On the basis of the analysis, it might be logical to recognize them as either of subspecific or of specific grade. On the basis of our knowledge of differences in the skulls of distinct species of modern reptiles, for instance, there is justification for regarding the differences in the metoposaur skulls from Wyoming and the southwest as of specific importance.

Several possibilities exist with regard to the taxonomy of North American metoposaurs. If we consider the metoposaurs from Wyoming as specifically separable from those of the southwestern states, then the large meto-

posours of North America may be assigned to three species, as follows:

*Eupelor durus*; Newark group, eastern North America  
*Eupelor fraasi*; Chinle and Dockum formations, southwestern United States  
*Eupelor browni*; Popo Agie formation, Wyoming

As a sidelight on this problem it may be helpful to compare the known distribution of North American metoposaurs with the distribution of some recent North American reptiles.

A parallel to the possibility of three distinct species is to be seen in the North American distribution of certain species of skinks belonging to the genus *Eumeces*, as mapped by Hobart M. Smith (1946). In eastern North America there is a widely distributed species that ranges from southern Pennsylvania to the tip of Florida and westward to southern Missouri, Arkansas, and eastern Texas; this is *Eumeces laticeps*. Separated from this range by a considerable geographical gap is the range of *Eumeces multivirgatus*, which occupies an area that runs through central New Mexico and Arizona, northward through eastern Colorado, and into Nebraska, South Dakota, and Wyoming. Another species, *Eumeces brevilineatus*, occupies a range in southern Texas and northern Mexico that in a general way is between the ranges of *Eumeces laticeps* and *Eumeces multivirgatus* (fig. 19B). There are various other species of *Eumeces* in North America in addition to the ones cited above, but these three show how three distinct modern species are distributed over an area that corresponds in a general way to the area in which the various fossil metoposaurs have been found.

If, on the other hand, the metoposaurs from Wyoming are regarded as only subspecifically separable from those of the southwestern states, the large metoposaurs of North America would be assigned to two species, one of which would contain two subspecies:

*Eupelor durus*  
*Eupelor fraasi fraasi*  
*Eupelor fraasi browni*

In this connection, a parallel to the possibility of two species with subspecies for the

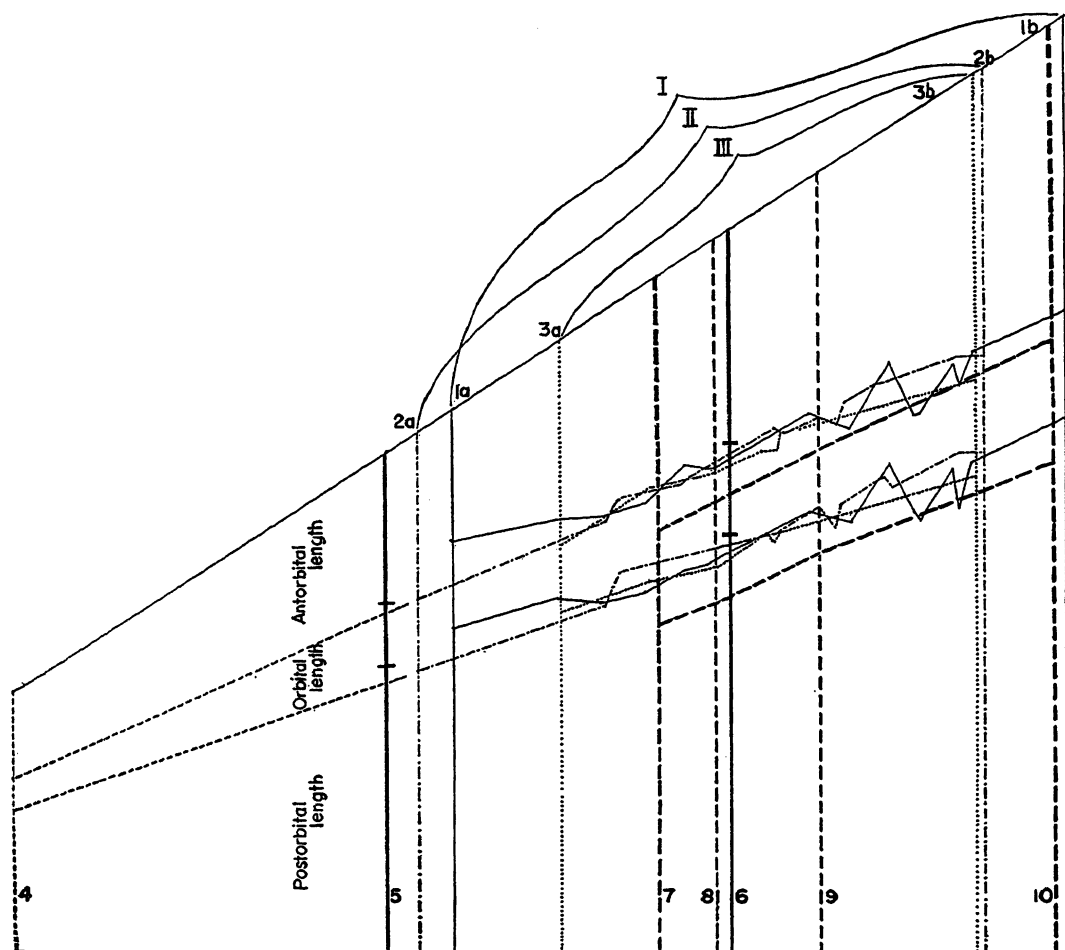


FIG. 18. Diagram showing comparisons between skull roof length, antorbital length, orbital length, and postorbital length in metoposaurs of western North America. Total length of vertical lines indicates skull roof lengths. Upper diagonal connects smallest and largest skull roof lengths; the other skull roof lengths are arranged along this diagonal at points where their total lengths intersect diagonal. Several pairs of diagonal lines that run more or less parallel indicate front and back borders of orbits in various metoposaur populations. Orbital limits indicated in 5 and 6 by simple cross bars. 1a, 1b. Smallest and largest skulls of New Mexico population of *Eupelor fraasi fraasi*, with connecting lines showing orbital limits. 2a, 2b. Smallest and largest skulls of Potter County, Texas, population of *Eupelor fraasi jonesi*, with orbital limits indicated. 3a, 3b. Smallest and largest skulls of Howard County, Texas, population of *Eupelor fraasi jonesi* with orbital limits indicated. 4. Skull of *Eupelor fraasi jonesi*, originally described as *Buettneria bakeri*. Diagonals drawn from orbital limits of this skull to those of next smallest *Eupelor* skull from Texas. 5. Skull of *Eupelor fraasi jonesi*, originally described as type of *Buettneria bakeri*. 6. Skull of *Eupelor fraasi jonesi*, originally described as type of *Buettneria perfecta*. 7-10. Four skulls of *Eupelor browni* from Wyoming, treated in same way as Texas and New Mexico populations. Note that diagonals connecting orbital borders of Wyoming skulls are offset from comparable lines for Texas populations. This diagram shows that metoposaur skulls from western North America, originally described under various generic and specific names, exhibit similar patterns of relative growth.



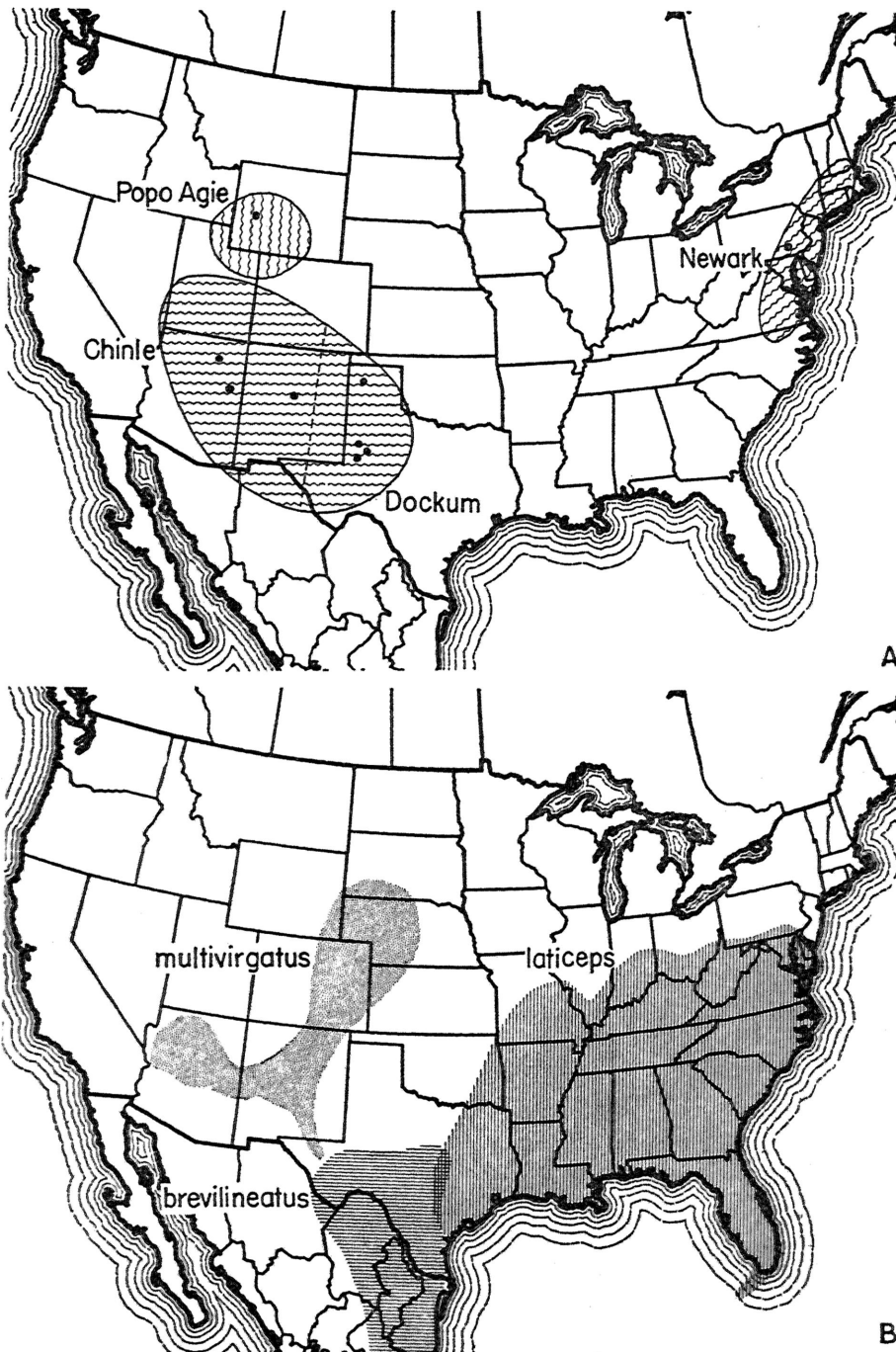


FIG. 19. A. Localities at which metoposaurus have been found in North America. Dots show actual fossil localities; patterns indicate general ranges (very conservatively estimated) possibly occupied by several populations during late Triassic times. In east is Newark population, here designated as *Eupelor durus*. In Wyoming area is Popo Agie population, designated as *Eupelor browni*. In southwest are Chinle and Dockum populations, the first designated as *Eupelor fraasi fraasi*, the second as *Eupelor fraasi jonesi*. B. Ranges of three modern species of the skink, *Eumeces*, in North America.



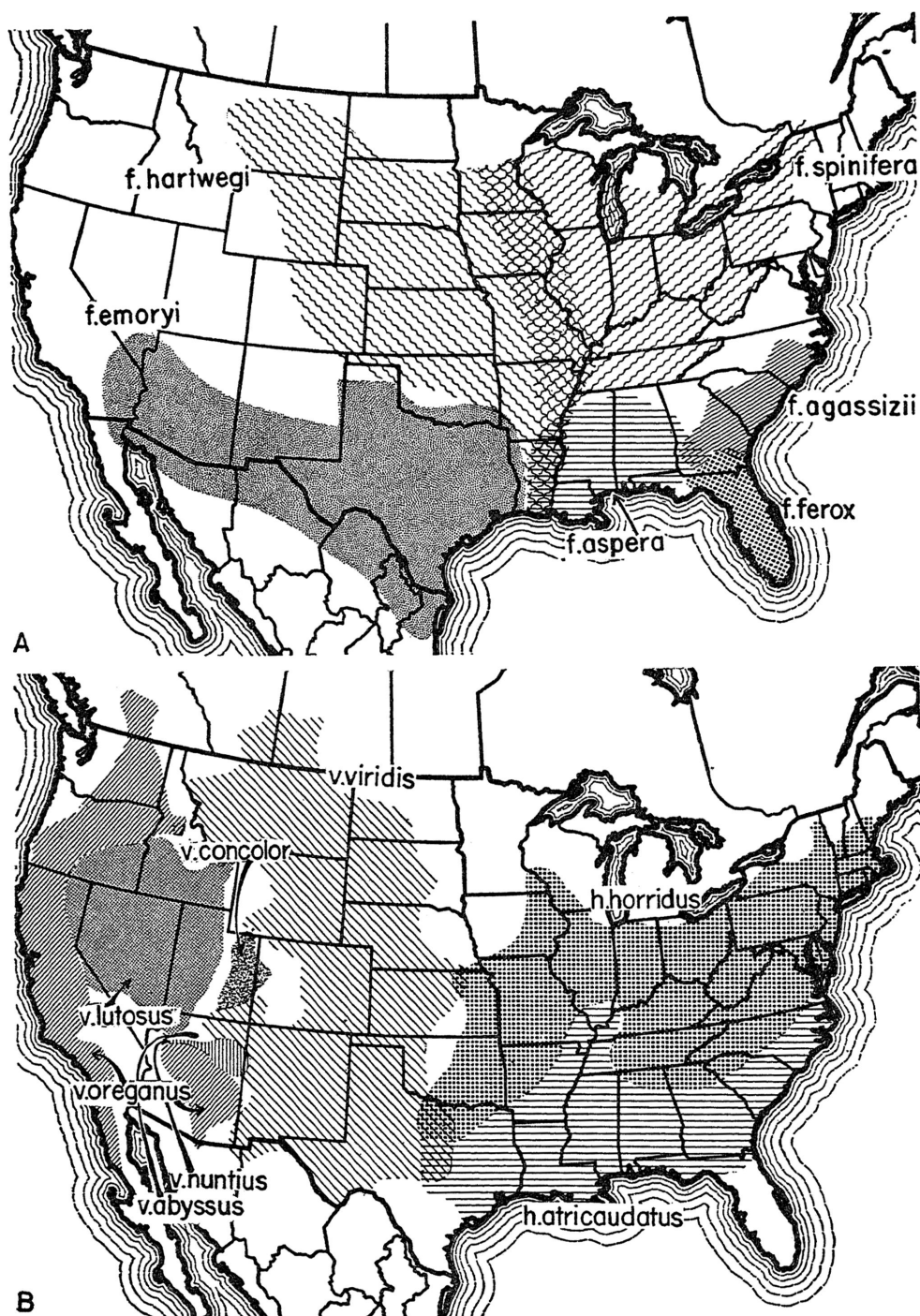


FIG. 20. A. Ranges of subspecies of modern soft-shelled turtle, *Amyda ferox*, in North America. B. Ranges of subspecies of two species of modern rattlesnakes, *Crotalus horridus* and *Crotalus viridis*, in North America.

metoposaurs is to be found in the distribution of some North American rattlesnakes of the genus *Crotalus*, as mapped by Schmidt and Davis (1941). In eastern North America are the rattlesnakes belonging to the species *Crotalus horridus*, ranging along the Atlantic coast from Maine to Florida and inland, south of the Great Lakes, to Iowa, Kansas, Oklahoma, and Texas. This species is subdivided into two subspecies, *Crotalus horridus horridus* to the north and *Crotalus horridus atricaudatus* to the south.

In western North America is the species *Crotalus viridis*, which in turn may be subdivided into several subspecies, as can be seen in figure 20B. There is a fairly distinct separation between the eastern and the western species along the line where the lowlands of the middle western region give way to the high plains of the west.

If the distribution of the metoposaurs during the Triassic was similar to the modern distribution of these two species of rattlesnakes, we might then postulate an eastern species, *Eupelor durus*, and a western species *Eupelor fraasi*, each with one or more subspecies. On the basis of the known record no subdivision of the eastern form is apparent, while in the western area there might be two subspecies, *Eupelor fraasi fraasi* and *Eupelor fraasi browni*.

Of course there is a third possibility, namely, to think of the large metoposaurs of North America as belonging to a single species, with three subspecies. In this case the nomenclature would be as follows:

*Eupelor durus durus*  
*Eupelor durus fraasi*  
*Eupelor durus browni*

Here there is a parallel among modern reptiles of the possibility of a single North American species subdivided into several subspecies—in the distribution of subspecies of the soft-shelled turtle *Amyda*, as mapped by Carr (1952). In this case all the subspecies belong to a single species, *Amyda ferox*. There are four eastern subspecies of *Amyda ferox* that range from the Atlantic coast to about the Mississippi River (fig. 20A). One could imagine that during Triassic times some subspecies of metoposaurs in eastern and western

North America showed somewhat analogous patterns of distribution.

In this connection it might be well to point out the fact that the habits and the habitat of the Triassic metoposaurs very probably were more nearly similar to those of the soft-shelled turtle than to those of the snake or of the lizard cited above. The ancient amphibians and the modern turtle were and are inhabitants of streams and ponds, but whether this argument is to be given much weight in coming to conclusions as to the taxonomy of the North American metoposaurs is, of course, problematical. After all, these are analogies only—a comparison of ancient amphibians with modern reptiles.

Finally, there is still another possibility, which is to regard the Newark and the Popo Agie metoposaurs as belonging to two distinct species and the Chinle and Dockum metoposaurs as subspecies of still another species. This is a refinement of the first possibility, mentioned above. The biometric data (especially fig. 16) indicate lesser differences between the Texas and the New Mexico-Arizona populations than between the southwestern populations as a whole and the Wyoming forms, and this evidence gives weight to the present possibility. If such be the case, as we believe is the most probable of the outlined possibilities, the nomenclature would be as follows:

*Eupelor durus*; Newark group, eastern North America  
*Eupelor fraasi fraasi*; Chinle formation, New Mexico and Arizona  
*Eupelor fraasi jonesi*; Dockum formation, Texas  
*Eupelor browni*; Popo Agie formation, Wyoming

#### CONCLUSIONS

The comparisons that have been made between some distributions of modern reptiles and what we know of the geographic range of Triassic metoposaurs in North America indicate on the one hand the several possibilities from which a choice can be made. On the other hand, it seems to us that the biometric analysis indicates to some degree just what direction the choice should take. It is our opinion, based on the biometric analyses as seen against the background of comparisons with modern distributions as well as on

comparisons with what we know about species and subspecies overlap among some modern vertebrates, that, aside from the problematical *Dictyocephalus elegans*, the North American metoposaurs should be regarded as belonging to three species. One of these is found in eastern North America and two are found in the west. Furthermore, it is our opinion that one of the western

species, namely, the one found in the southwestern states, may be divided into two subspecies—one from Texas, the other from New Mexico and Arizona. Finally, it is our opinion that on the basis of present knowledge the European metoposaurs should be placed in a single species. In the light of these conclusions, the taxonomy of the metoposaurs can be indicated in the following way:

*Metoposaurus* Lydekker, 1890.

*Metoposaurus diagnosticus* (Meyer), 1842, Keuper, central Europe

Synonyms: *Metoposaurus stuttgartiensis* Fraas, 1913

*Metoposaurus santaecrucis* (Koken), 1913

*Trigonosternum latum* Schmidt, 1931

*Metoposaurus heimi* Kuhn, 1932

*Dictyocephalus* Leidy, 1856

*Dictyocephalus elegans* Leidy, 1856, Newark group, North Carolina

*Eupelor* Cope, 1868

*Eupelor durus* (Cope), 1866, Newark group, Pennsylvania, New Jersey

Probable synonym: *Calamops paludosus* Sinclair, 1917

*Eupelor fraasi fraasi* (Lucas), 1904, Chinle formation, Arizona, New Mexico, Utah

Synonyms: *Buettneria major* Branson and Mehl, 1929

*Kalamoiketor pinkleyi* Branson and Mehl, 1929

*Eupelor fraasi jonesi* (Case), 1922, Dockum formation, Texas

Synonyms: *Buettneria perfecta* Case, 1922

*Buettneria bakeri* Case, 1931

*Buettneria howardensis* Sawin, 1945.

*Eupelor browni* (Branson), 1905, Popo Agie formation, Wyoming

Synonyms: *Anaschisma brachygnatha* Branson, 1905

*Borborophagus wyomingensis* Branson and Nehl, 1929

*Koskinonodon princeps* Branson and Mehl, 1929

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