FAUNA OF UPPER VALE AND CHOZA: 1–5

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INTRODUCTION

A study of the vertebrates of the upper part of the Vale Formation in Knox County and the Choza of Knox and Foard Counties, Texas, has been in progress since 1946 (Olson, 1948). Intensive work for several field seasons has resulted in the accumulation of a large collection of vertebrates, comprising fresh-water fishes, amphibians and reptiles. The complete preparation and study of these materials will occupy a period of several years and it is expected that, in the meantime, additional specimens will be obtained. In view of these circumstances it seems advisable to publish accounts of specimens as their preparation and study have been completed, in order that the information may be generally available. This will be done through a series of articles.

The course of such a program is determined primarily by the order in which materials are prepared and consequently is non-systematic in its organization. Once completed, however, the series will contain information on all the groups of vertebrates that have been discovered in the formation. A final paper of the series will be a comprehensive survey of the geology and fauna of the beds involved, to bring together under a single cover a co-ordinated study of the various contributions made in the earlier articles.

1. A NEW FAMILY OF THE PARAREPTILIA

The specimen that forms the principal basis for the following description was preserved in a nodule that had weathered from a conglomeratic deposit of channel origin. When found, the nodule had suffered considerable spalling, with the result that little of the surface bone of the skull was preserved. The skull was also somewhat crushed and the lower jaws had been forced laterally from their

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life position.   The matrix is hard and the bone soft, so that it has
not been possible to reveal detail in various regions.   So far, this
specimen, a single, isolated vertebra, a maxillary tooth plate, and
two pairs of lower jaws are the only representatives of the genus
that have been definitely recognized.   The collections include some-
what similar smaller jaws, fragmentary palates and various parts
of postcranial skeletons that may prove referable to the genus when
more is known concerning the full skeleton and range of variation.

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Class **REPTILIA**

Subclass **Parareptilia**

Order **Diadecta**

Suborder **Seymouriamorpha?**

Family **Waggoneriidae** fam. nov.

Waggoneria gen. nov.

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Diagnosis.—Maxillary and dentary expanded medially to form
plates bearing several rows of interlocking teeth.   Otic notch open,
with quadrate well forward of posterior termination of dorsal surface
of skull.   Parasphenoidal wings very broad, extending laterally to
quadrate ramus of pterygoid.   Lower jaws deep posteriorly and
heavy throughout.   Articular bone proportionately large.   Centra
of vertebrae amphicoelous posteriorly and opisthocoelous in extreme
anterior part of column.   Neural arches broad and low, neural spines
short.   Articular surfaces of zygapophyses nearly horizontal except
in first two vertebrae.   Interclavicle T-shaped.

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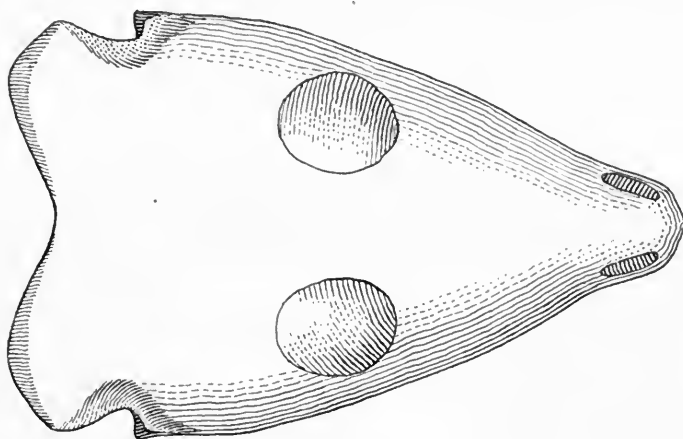**Waggoneria knoxensis[1] sp. nov.**

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Type.—C.N.H.M.-U.R.   14, skull, lower jaws, six anterior
vertebrae and partial shoulder girdle.

Horizon and locality.—Upper part of Vale Formation, Clear Fork
group, Early Permian.   Locality KF (Olson, 1948) at three-channel
hill, approximately seven miles north of Vera, Knox County, Texas.

Diagnosis.—As for the genus.

Skull.—No details of the dorsal surface can be obtained from
the type specimen.   A reconstruction of the probable outlines is

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[1] The generic name is given in recognition of the long-continued aid that has
been given to students of vertebrate paleontology by the Waggoner estate of
Vernon, Texas.   The specific name alludes to the county in which the specimens
were found.
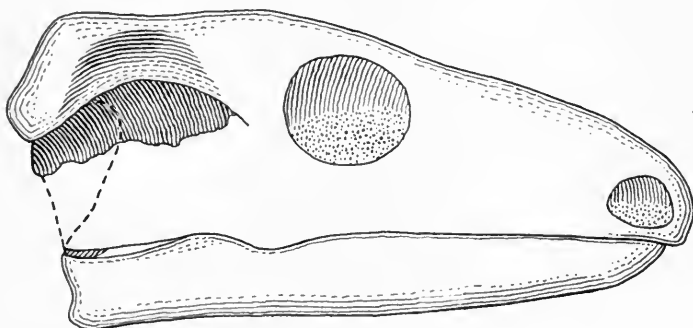
FIG. 38.   Reconstructions of the skull of *Waggoneria knoxensis* gen. and sp. nov.   Based primarily upon type specimen.   A. Dorsal aspect.   B. Lateral aspect. × ⅔.

shown in figure 38, A and B.   The position of the orbits is clear and the general configuration is moderately accurate.   The most interesting features of the skull are the temporal region and the position of the articulation of the lower jaw.   There is no temporal fenestra, but an otic notch is well developed.   This notch appears to have been open broadly, as in *Diadectes* and *Procolophon*.   The articulation of the lower jaws lies at the base of the notch.   The quadrate, which

is poorly preserved, seems to have been similar in general aspects to that of *Diadectes*.

Certain features of interest are revealed in the palatal aspect (fig. 39). The posterior wings of the parasphenoid are present, and the transverse and quadrate processes of the pterygoid are well exposed. No other bones of the palate or of the basicranium are
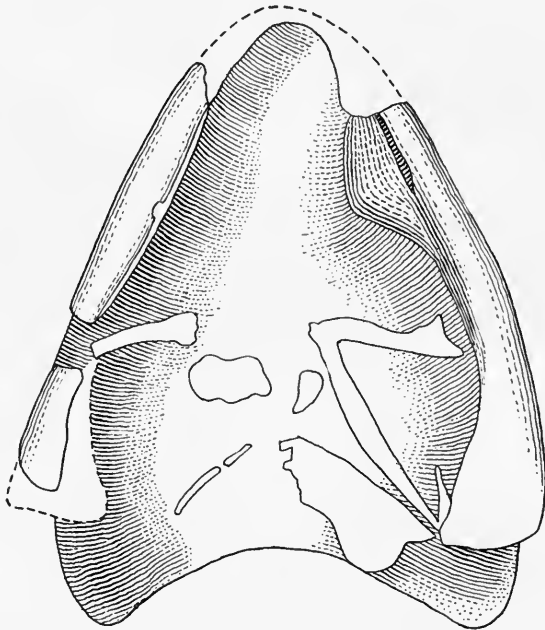

FIG. 39. Ventral aspect of type specimen of *Waggoneria knoxensis* gen. and sp. nov. × ⅔.

revealed except a fragment, which is probably part of the basisphenoid.

The left wing of the parasphenoid is moderately well preserved. It consists of a broad, flat plate that extends laterally to the level of the quadrate ramus of the pterygoid. The anterior margin is curved dorsally. In these respects the parasphenoid is much like that of *Diadectes* and not decidedly different from that of *Seymouria*. Presumably the stapes passed above it from low in the otic notch to the otic region of the brain case. There is a rather slender bone in this area, but it cannot be properly developed without irreparable damage to the parasphenoid and pterygoid.

The preserved parts of the pterygoid show no definitive features. The nature of the cranio-palatal articulation is not revealed.

Dentition and jaws (fig. 40, A, B, C).—Dentary and maxillary teeth are preserved in the type specimen. Each of the tooth-bearing bones is somewhat expanded medially and the shelf-like projections oppose each other when the jaws are closed. The teeth are short,
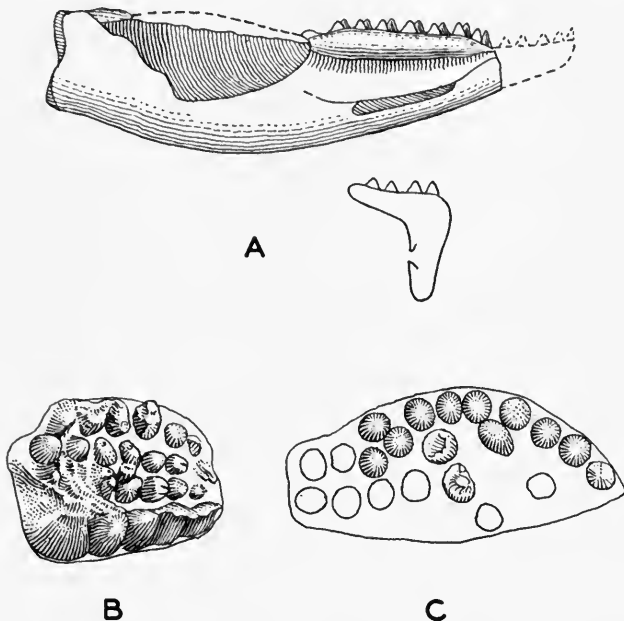

FIG. 40. Jaw and dentition of type specimen of *Waggoneria knoxensis* gen. and sp. nov. A. Inner aspect of lower jaw and cross section at level of expanded dentary. B. Ventral aspect of maxillary dentition of type specimen; drawn from rubber cast. C. Ventral view of maxillary dentition of referred specimen, circles indicating positions of broken teeth. $\times$ ⅔.

slightly bulbous cones. There are four rows of teeth above and at least four below.

The lower jaw is deep relative to its length, presumably in connection with a crushing function of the teeth on the expanded dentary. The articular is a large, strongly ossified bone, and the sheathing dermal bones are thick.

Postcranium.—Parts of six vertebrae, clavicles and interclavicle, fragments of the coracoids and part of one rib are preserved in the type specimen. A single, isolated dorsal vertebra, C.N.H.M.-U.R. 15, is all that is known of the remainder of the column. The verte-
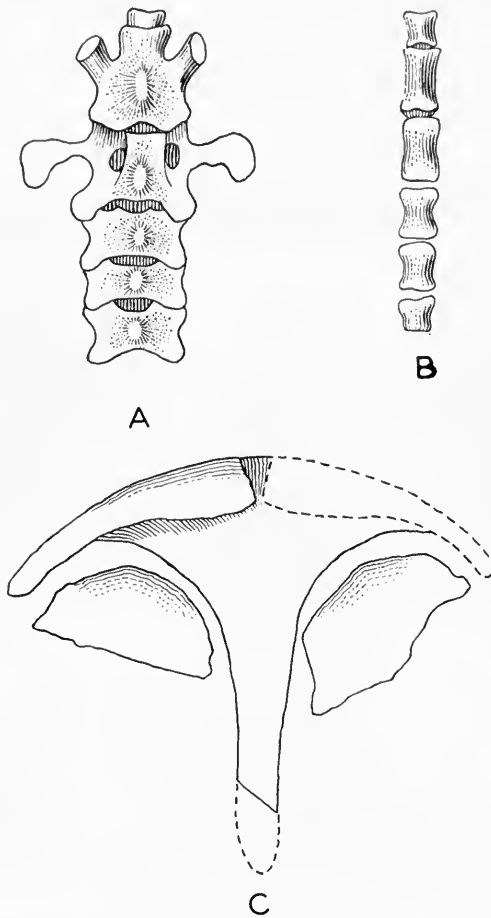
FIG. 41. Vertebrae and shoulder girdle of type specimen of *Waggoneria knoxensis* gen. and sp. nov. A. Dorsal aspect of first six vertebrae. Atlas represented by centrum only. Right side of arches and spines somewhat restored. B. Ventral aspect of centra of first six presacral vertebrae. C. Ventral aspect of interclavicle, clavicles and partial coracoids.

brae of the type specimen (fig. 41, A and B) consist of the first six presacrals. The centra are well preserved but most of the spines, arches and zygapophyses are badly damaged. The centra of vertebrae 3 to 6 are normal for primitive reptiles. A break between the second and third vertebrae reveals the presence of an opisthocoelous articulation of the centra. Neural arches and zygapophyses are fairly well preserved on the left side of the column. The reconstruction in figure 41, A, shows their general condition in dorsal aspect

with the right side and some of the spines restored.   The evidence
for most of the reconstruction is sound but some details may be in
error.   Vertebrae 4, 5, and 6 are alike in general structure and not
greatly different from the more posterior presacrals, as shown by
C.N.H.M.-U.R. 15, except that the zygapophyses and arches are
less broad.   The arches are of the type common to primitive Early
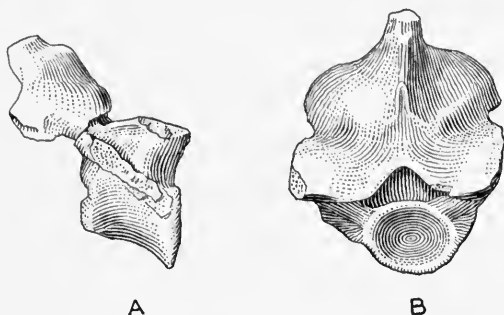Permian reptiles.   They resemble those of *Labidosaurus* most closely

A   B

FIG. 42.   Dorsal vertebrae of *Waggoneria knoxensis* gen. and sp. nov. C.N.
H.M.-U.R. 15.   A. Right lateral aspect.   B. Dorso-anterior aspect.   × 1.

but are considerably more flattened.   Zygapophyses are large, but
proportionately less extensive than those in *Captorhinus*, *Labido-
saurus* or *Diadectes*.   The arch of vertebra 3 is normal, as are the
posterior zygapophyses; the anterior zygapophyses, however, rise
sharply from the level of origin and are expanded medially to form
a secondary junction with the neural arch.   A short, expanded
cervical rib is fused to this vertebra.

The axis is specialized.   It is somewhat distorted and rotated
from its life position but the essential features are clear.   The arch
is very broad, as are the posterior zygapophyses.   The anterior
zygapophyses extend antero-laterally as distinct processes.   Pre-
sumably these articulated with similarly extended processes of the
atlas, but the dorsal part of this vertebra is not preserved.   The
centrum of the axis is specialized in the possession of a sharp ventral
keel.   Between the axis and the atlas there is a small wedge-shaped
intercentrum.   Little can be told about the atlas, since only the
centrum is preserved.   The dorsal parts were lost or, as seems more
probable, were unossified.   The centrum is nearly rectangular in
cross section.   Anterior to the centrum, as seen ventrally, is a bone
that represents either an atlantal intercentrum or the posterior
margin of the occipital condyle, or parts of both.   The articulation

of the vertebra and skull appears to have been single. The only rib preserved is displaced from its natural position. It appears to have been associated with the fifth or sixth presacral vertebra. The rib is holocephalous, has a short shaft and is expanded distally. The transverse process on the only known dorsal vertebra shows that the ribs in this area were holocephalous as well.

MEASUREMENTS   mm.
Length of skull (snout to end of dorsal table)............. 116
Posterior width of skull (maximum)...................... 90
Length of lower jaw (approx.)........................... 108

Anterior dorsal vertebra (based on C.N.H.M.-U.R. 15)

Length of centrum (ventral)............................ 12.5
Height of centrum (anterior)........................... 12.8
Total height of vertebra............................... 30.5
Width of posterior zygapophyses........................ 27.2
Width of anterior zygapophyses......................... 29.5

Relationships.—As yet no genus but *Waggoneria* can be assigned definitely to the new family, Waggoneriidae. Various jaws, parts of postcranial elements, and parts of palates that show some of the characteristics of *Waggoneria* have been found. They differ with respect to size and morphological detail, and some of them may belong to other genera that should be included in the family. Additional collecting and preparation will probably increase the knowledge of the known genus and perhaps bring to light other genera closely related to it.

Broad neural arches, emphasis of the pleurocentral part of the centrum and absence of temporal fenestrae place *Waggoneria* among the primitive reptiles. The open otic notch and broad wings of the parasphenoid indicate that it belongs in the Subclass Parareptilia. Affinities within this subclass are with the Order Diadecta rather than with the Order Chelonia. There are resemblances to the Seymouriamorpha, Diadectomorpha and Procolophonia. The vertebrae of *Waggoneria* resemble those of *Seymouria* more closely than those of genera included in the other two suborders but, as stated, the closest resemblance is to the vertebrae of *Labidosaurus*, a member of the subclass Eureptilia. The temporal and quadrate regions are similar to those of *Diadectes* and *Procolophon* and seem to be structurally somewhat closer to *Procolophon*. The parasphenoid, on the contrary, is more like that of *Diadectes*. It is possible that *Waggoneria* will prove to be a representative of a heretofore unknown suborder of these reptiles, but establishment of such a category must await

more complete evidence; for the present the family is placed very provisionally in the Seymouriamorpha. There is nothing in the known structure of *Waggoneria* that could not have been derived through modifications of *Seymouria*, and some species of this genus might conceivably have been ancestral to it, whereas *Diadectes* is too specialized in a number of respects, the palate, dentition, vertebrae, etc., to be considered as a possible ancestor.

2. A NEW CAPTORINOMORPH REPTILE

Class **REPTILIA**

Subclass **Eureptilia**

Infraclass **Captorhina**

Order **Captorhina**

Suborder **Captorhinomorpha**

Family **Captorhinidae**

Captorhinoides gen. nov.

A number of specimens representing captorhinid reptiles have been obtained from the upper part of the Vale and Choza. At least one is very similar to *Captorhinus isolomus* of the Arroyo. It may be that some of the fragmentary material may be similarly referred, after it has been prepared and studied. In addition, however, there is captorhinid material that does not appear to be referable to the genus *Captorhinus*. Much of it is so fragmentary and so poorly preserved that generic reference will be impossible until much more is known of the Vale and Choza captorhinids from more complete specimens. One skull, however, is complete enough for profitable study and the new genus erected in this section has been based upon it. The specimen was found in a channel conglomerate near the type specimen of *Waggoneria knoxensis*. The bone of the dorsal and lateral surfaces had been destroyed by spalling. The palate, basicranium, stapes and part of the jaws and dentition are well preserved and form the principal basis for the diagnosis.

Diagnosis.—General configuration of skull similar to that of *Captorhinus*. Stapes with broad foot, very large stapedial foramen, and slender, tapering shaft. Basisphenoid-parasphenoid short, with prominent transverse ridge near anterior end. Pterygoid with quadrate process separated into short anterior process and broad posterior plate, the two lacking osseous connection. Epipterygoid with stout, rod-like ascending process and long cylindrical quadrate

process.   Upper and lower jaws with three irregular rows of teeth. Marginal teeth elongated and somewhat recurved anteriorly, gradually diminishing in height posteriorly.   Teeth of inner rows, low, somewhat bulbous cones.

Captorhinoides valensis sp. nov.

Diagnosis.—As for the genus.

Type.—C.N.H.M.-U.R. 13, incomplete skull and jaws.

Horizon and locality.—Upper part of Vale Formation, Clear Fork group, Early Permian.   Locality KF (Olson, 1948), approximately seven miles north of Vera, Knox County, Texas.

Description and comparisons.—Throughout this section the descriptions are augmented by comparisons with members of the genus *Captorhinus*.   Four species of this genus have been described from the North American Permian but the taxonomy is not satisfactory.   It is not certain that the four species are all distinct, and it is possible that certain specimens do not belong to any of the named species.   Falling in this latter category are at least some of the specimens from the Permian fissure fills in the Arbuckle limestone north of Fort Sill, Oklahoma.   Much of the work of Price (1935) was based on material from this locality.   There are moderately great differences in the basicranium, the middle ear and the craniopalatal regions of the various specimens of *Captorhinus* that have been examined, but the skulls do seem to show a continuity of form which indicates that they are variates of a common pattern rather different from that of *Captorhinoides*.   In making comparisons a specimen belonging to the Arroyo species *Captorhinus isolomus* and material of *Captorhinus* sp. from the Oklahoma fissure fills have been used.

THE DORSAL SURFACE (fig. 43, A): Only in the region of the orbit and the right maxillary is bone preserved.   So far as it is possible to tell there are no important differences between the dorsal surfaces of *Captorhinus* and *Captorhinoides*, but it is entirely possible that differences would be evident were the latter better preserved.   The orbits in *Captorhinoides* are large, but this feature is shared with small skulls of *Captorhinus*.   The internal cast of the temporal region has a smooth, uninterrupted surface with no evidence of fenestration.   As in *Captorhinus*, the posterior rim of the dorsal surface of the skull is smoothly rounded and shows no evidence of an otic notch.

JAWS AND DENTITION: Both upper and lower jaws are partially preserved but the sheathing bone is badly damaged or absent, except
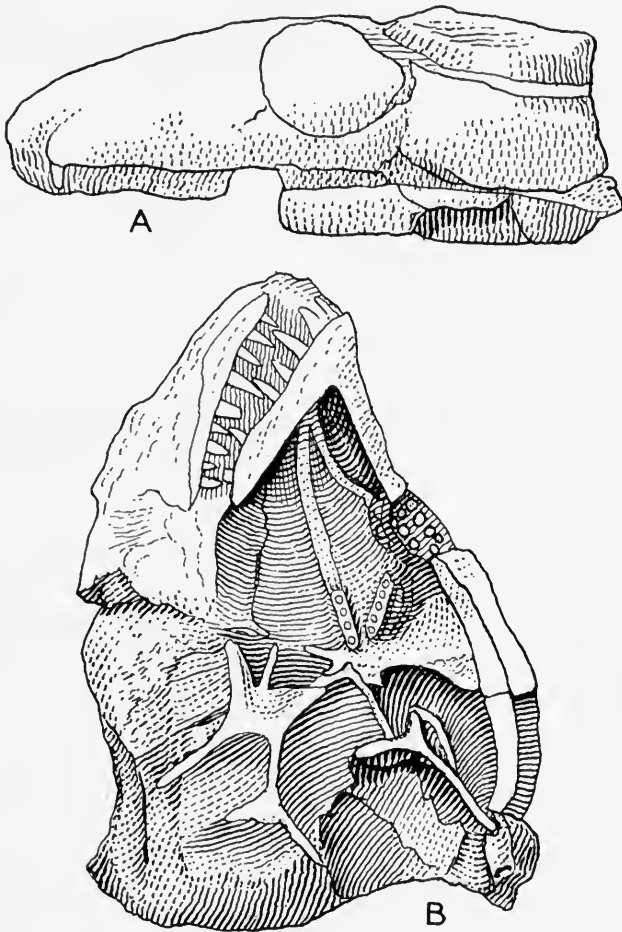
FIG. 43. *Captorhinoides valensis* gen. and sp. nov., type C.N.H.M.-U.R. 13.
A. Lateral aspect of skull.   B. Palatal aspect of skull.   × 2.

anteriorly.   The articulation of the lower jaw and the skull lies at
the extreme posterior end of the skull.   As in *Captorhinus*, there
are multiple rows of teeth on both upper and lower jaws.   A differ-
ence between the two genera exists in the presence of elongated
marginal teeth in the anterior half of the upper jaw of *Captorhinoides*.
This difference can hardly be considered of generic significance but
it may reflect some difference in the dietary habits of the species
of the two genera.   Apparently *Captorhinoides* had recurved pre-

maxillary teeth as did *Captorhinus*, but poor preservation in the area makes the determination uncertain.

BASICRANIUM AND PALATE: The most interesting features of the skull occur in these regions. They are shown in figures 43, B, 44, and 45, together with comparative drawings of *Captorhinus isolomus* and *Captorhinus* sp. Figure 44 shows the basisphenoid-parasphenoid in ventral aspect. That of *Captorhinoides* is proportionately short and differs in many details from either of the other two. In the nature of the basipterygoid process of the basisphenoid, *C. isolomus* is more or less intermediate between the extreme conditions shown in *Captorhinus* sp. and *Captorhinoides*. *Captorhinoides* differs markedly from the other two in the presence of a ridge-like cross connection between the latero-ventral flanges of the two sides of the basisphenoid-parasphenoid.

Figure 45 gives comparative illustrations of the cranio-palatal joint and associated osseous elements. Each illustration has been drawn from the specimen, without reconstruction, to show the cranio-palatal joint somewhat open. In life, of course, the basipterygoid process fitted closely into the socket of the pterygoid-epipterygoid complex.

The epipterygoid enters into the joint in each case. In *Captorhinus* it makes up almost the entire articular surface for the palate but in *Captorhinoides* it forms only the dorsal part. The most striking difference, however, lies in the quadrate process of the epipterygoid, which is present in *Captorhinoides* and virtually absent in *Captorhinus*. Whether or not this process actually reached the quadrate or whether it extended only to the posterior plate of the quadrate process of the pterygoid is uncertain. As indicated in the figure, the quadrate process of the pterygoid of *Captorhinoides* has no osseous continuation from the short anterior part, which lies on the posterior margin of the transverse process, to the posterior plate.

This appears to be the condition that occurred during life and not one due to post-mortem damage, since exceedingly delicate features of the stapes are well preserved in the immediate area in which the medial part of the process might be expected. The end of the anterior process seems to have continued as soft tissue for at least a short distance back of its osseous termination, and shows no evidence of having been shortened by breakage. The posterior plate likewise shows no evidence of having been continued anteriorly by bone.
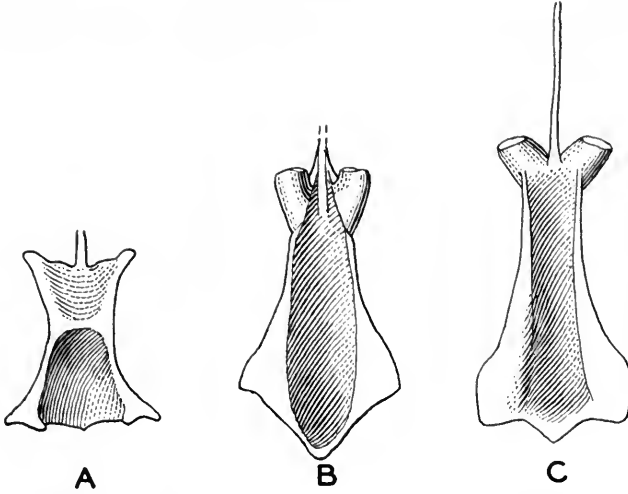
FIG. 44. Basisphenoid-parasphenoid of *Captorhinoides* and *Captorhinus*. A. *Captorhinoides valensis*, C.N.H.M.-U.R. 13; × 2⅔. B. *Captorhinus* sp., M.C.Z. 1198; × 3⅓. C. *Captorhinus isolomus*, C.N.H.M.-U.C. 1702; × 2⅔.

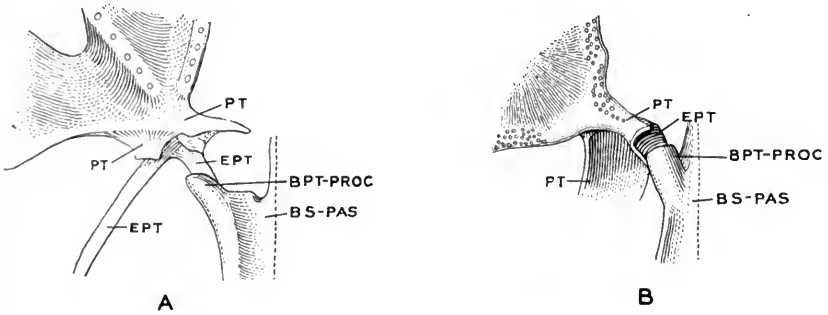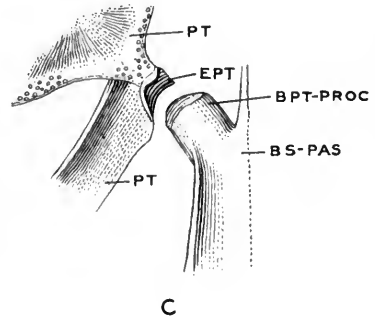FIG. 45. Basicranio-palatal articulation of *Captorhinoides* and *Captorhinus*. A. *Captorhinoides valensis*, C.N.H.M.-U.R. 13; × 4; slightly restored and reversed to correspond in position to B and C. B. *Captorhinus* sp., M.C.Z. 1198; × 4. C. *Captorhinus isolomus*, C.N.H.M.-U.C. 1702; × 4. Abbreviations: BPT-PROC, basipterygoid process; BS-PAS, basisphenoid-parasphenoid; EPT, epipterygoid; PT, pterygoid.

The remaining parts of the palate of *Captorhinoides*, so far as they have been observed, differ only in minor details from those of *Captorhinus* sp. and *Captorhinus isolomus*, and the differences are no greater than those between the described species of *Captorhinus*.

THE STAPES: This bone is well preserved on the left side of the skull in the specimen of *Captorhinoides*. Details of structure in ventral view are shown in figure 46 and the stapes of *Captorhinus isolomus*, which resembles that of *Captorhinus* sp. closely in basic
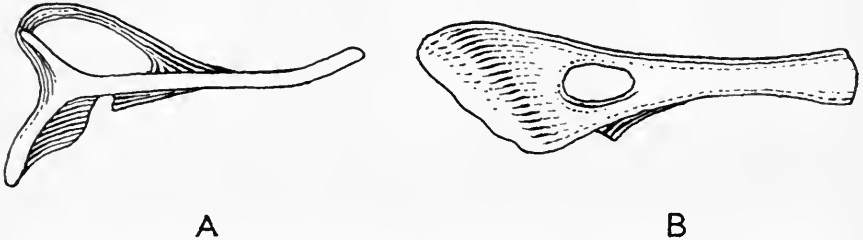

A   B

FIG. 46. Stapes of *Captorhinoides* and *Captorhinus* in ventral aspect. A. *Captorhinoides valensis*, C.N.H.M.-U.R. 13, slightly restored; × 8. B. *Captorhinus isolomus*, C.N.H.M.-U.C. 1702; × 8.

features, is illustrated for comparison. The stapes of *Captorhinoides* differs materially from that of any species of *Captorhinus*. Most striking is the fact that it is much more slender and lightly constructed throughout. That these differences are due neither to age nor size is suggested by the fact that even very small stapes of *Captorhinus* sp. have the characteristic heavy structure.

The stapedial foramen of *Captorhinoides* is very large compared to that of *Captorhinus*. This may have resulted merely from an over-all reduction in the thickness of the various parts of the bone. The dorsal process is slender but distinct, and similar in position and orientation to that of *Captorhinus*.

Discussion.—The skull of *Captorhinoides valensis* has been shown to differ from those of two species of *Captorhinus* in several aspects usually considered to be of fundamental taxonomic significance. On the basis of differences in the basicranium, the cranio-palatal joint, the pterygoid and epipterygoid, and the stapes, the new genus has been established. The striking differences in the stapes would seem, in themselves, to indicate that *Captorhinus* and *Captorhinoides* were markedly divergent. If it may be assumed that the stapes functioned in hearing, it would appear that *Captorhinoides* had a decidedly superior mechanism for transmission of vibrations from the outer to the inner ear. This could be a basic advance of real

significance.   We do not know the total extent of variation of this feature among the species of *Captorhinus* and thus cannot evaluate the full significance of the difference.   To a greater or lesser extent this same difficulty is involved in evaluation of each of the several differences.   In spite of the rather inadequate bases for determining the significance of the differences, they can hardly be of less than generic significance and in some respects they suggest separation at a higher level.

Captorhinoides could have been derived from *Captorhinus*.   If we assume this to be the case, certain of the presumed changes have considerable interest as indicators of trends in evolution of at least one line of the Captorhinomorpha.   The basisphenoid-parasphenoid, being shortened and broadened, approaches the primitive pelycosaur condition more closely than does this region in *Captorhinus*.   Partial exclusion of the epipterygoid from the craniopalatal joint represents a trend toward the condition seen in several reptilian lines, for example certain therapsids.   It is not, however, a change in the direction of primitive Lepidosauria, such as the Eosuchia, which, on the basis of evidence from *Youngoides* (Olson, 1936; Olson and Broom, 1937), have preserved a meniscus that appears to represent the foot of the epipterygoid.   Even in the lacertilians, the meniscus pterygoideus is present as an apparent remnant of participation of the epipterygoid in the joint.   In some diapsids in the archosaurian line, however, the epipterygoid is excluded from the joint.

Ossification of the quadrate process of the epipterygoid, although it is a striking feature in itself, may be of little real significance. A short quadrate process is present in various pelycosaurs and represents merely an ossification of a part of the quadrate process of the palatoquadrate bar; a similar structure may confidently be inferred in *Captorhinus*.   The significance of the structure of this area lies rather in the fact that the epipterygoid appears to replace the quadrate process of the pterygoid functionally in *Captorhinoides*. This specialization shows little morphological convergence to any related group of reptiles.   It is true that the quadrate process of the epipterygoid is prominent in certain therapsids, especially in advanced carnivorous types, and is carried over to mammals (in the equivalent alisphenoid), but the development is actually quite different from that seen in *Captorhinoides*.

The stapes is, as remarked, decidedly reduced.   This trend is one to be anticipated in the ancestry of a number of lines of reptiles.

Even primitive Lepidosauria, for example, appear to have a stapes much reduced over that seen in *Captorhinus*. Marked stapedial reduction occurs among the synapsids but only in the most advanced groups. The stapes is large and heavy in the pelycosaurs and short and stocky in such therapsids as the dicynodonts, gorgonopsians, dinocephalians, and at least primitive therocephalians. Reduction seems to have begun independently within the therapsid lines. There is thus in *Captorhinoides* a general pattern of convergence to two major groups of Eureptilia. Stapedial reduction also occurs in the Parareptilia, as exemplified by the Chelonia.

Taken individually, the various changes suggest, in most instances, a trend toward conditions seen in one or more groups of reptiles. Such trends are often, and properly, taken as indications of ancestral-descendant relationships. Inferences of relationships based on single trends are, however, to be regarded with the greatest caution; series of trends are infinitely more reliable. In the present instance, if this philosophy be followed, it is apparent that the series of trends which have been witnessed, when taken together, do not suggest that *Captorhinoides* was evolving toward conditions realized in any one of the major groups of reptiles.

3. LUNG FISH OF THE VALE

GENERAL CONSIDERATIONS

Ten specimens, all from the Vale Formation, have been identified as lung fish. All are isolated teeth or teeth and jaw elements. Five of the specimens were taken from a quarry in fine-grained, green channel deposits in locality KF (Olson, 1948). Remains of fish are abundant in this quarry and it is probable that many of the scattered bones are skeletal elements of lung fish. It may be possible, when the material has been fully prepared, to determine associations and to gain some information concerning the skeletons of these dipnoans. All five specimens from this locality are lower teeth and associated jaw elements. The other five specimens occurred as follows: two large partial lower teeth from coarse channels in locality KF near the quarry; one very small, complete upper tooth from KF at the "three channel hill locality"; a small, nearly complete upper tooth from a conglomerate at locality KI,[1] and a partial large upper tooth from the "boulder locality" of KD.

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[1] Locality KI was investigated for the first time in 1948. It is located on aerial photographs as follows: CGV 5 24, Corners at 1.6–4.5, 1.5–3.3, 2.2–4.5, and 2.2–3.2 (see Olson, 1948, for indexing system).

Teeth of lung fish are abundant at various localities in beds of the Wichita group of the Early Permian in north central Texas but are rare in the Clyde and Arroyo formations of the Clear Fork group. The great majority pertain to the genus *Sagenodus*. *Proceratodus? favosus* is represented by a single specimen from the "Permian of Texas" (Cope, 1884; Hussakof, 1911; Romer and Smith, 1934). *Gnathorhiza* has been found in beds of Wichita and Clear Fork ages, but data on the majority of the specimens known from the Permian are not sufficiently detailed to allow them to be placed stratigraphically with any accuracy. One, an upper tooth collected in Baylor County, Texas, is definitely of Arroyo age (Olson, 1939).

Lung fish are more abundant in the Vale than in the Arroyo, but the abundance by no means approaches that of dipnoans in the Wichita. *Sagenodus*, the common Pennsylvanian and Wichita genus, has not been found in the Arroyo and collecting to date has not revealed its presence in the Vale. All specimens from the Vale may be referred to the genus *Gnathorhiza*. One specimen, C.N.H.M.-U.F. 96, from locality KI, is an upper tooth that differs in no important respect from the specimen from the Arroyo, C.N.H.M.-U.F. 95, and clearly belongs to the same species. The remaining nine specimens, however, are much larger, except for C.N.H.M.-U.F. 88, and differ markedly in a number of features from any heretofore described species of *Gnathorhiza*.

The taxonomy of the genus is rendered difficult by the fact that *Gnathorhiza pusillus* (Cope), from the Pennsylvanian of Illinois, is an upper tooth plate, whereas all others from the Permian beds below the Vale, except for the one from the Arroyo, are lowers. Romer and Smith (1934) have suggested that it is desirable to consider the Permian representatives as specifically different from the Pennsylvanian species, *G. pusillus*, and retain the species *G. serrata* (Cope) rather than recognize only a single species as did Hussakof (1911). Such a differentiation was stratigraphic rather than morphologic, since the only specimens known were the upper tooth from the Pennsylvanian and the lowers from the Permian. The case is somewhat strengthened by the one upper plate from the Arroyo. This tooth differs from the type of *G. pusillus* in the lack of denticulation on the ridges and in the stronger development of the anterior ridge. Also, it is considerably larger, but this may have little real meaning. These two upper plates furnish sufficient morphological evidence for the recognition of two species. The problem of associations still remains, since it cannot be demonstrated that the upper tooth from

the lower Permian actually belongs to the same species as the lowers. The probability that this is the case seems high, however, since all the known lowers are very similar and show no evidence of two species in the pre-Vale Permian. On the basis of this probability, I have followed Romer and Smith in recognizing the Permian species *G. serrata* (Cope) as distinct from the Pennsylvanian species *G. pusillus*.

Romer and Smith (1934) suggest that *Gnathorhiza* is a Permian representative of the family Lepidosirenidae, in opposition to the opinion of Stromer (1910) that the resemblances of the teeth to those of *Lepidosiren* and *Protopterus* are convergent. The many similar features in the dentitions of these three are suggestive of a real relationship. Such similarities, however, might be due to convergence. There is no way of settling this matter from the evidence now available. As will be shown, the lower plates of the Vale specimens show a trend away from rather than toward the condition of the living lepidosirenids but, again, this offers no proof that affinities do not exist. Inasmuch as there are notable resemblances between *Gnathorhiza* and the lepidosirenids and no positive evidence that they are not related, and since there is no other family of the Dipnoi to which *Gnathorhiza* could belong, I have tentatively accepted the placement of the genus in this family.

TAXONOMY

Of the ten identified specimens of dipnoans from the Vale, all of which belong in the genus *Gnathorhiza*, nine belong to one species and one to another. Among the nine are seven lower tooth plates and two uppers. The single representative of the other species consists of an upper tooth plate. So comparisons may be made, the new species, represented by the nine specimens, is considered first.

Class OSTEICHTHYES

Subclass Choanichthyes

Order Dipnoi

Family Lepidosirenidae

Genus Gnathorhiza

Gnathorhiza dikeloda sp. nov.

Type.—C.N.H.M.-U.F. 91. Lower tooth plate and splenial (fig. 47, A and B).

Horizon and locality.—Upper part of Vale Formation, Clear Fork group, Early Permian, locality KF (Olson, 1948), Knox County, Texas, about seven miles north of Vera, Texas.

Referred specimens.—C.N.H.M.-U.F. 87–90, 92–94, C.N.H.M.-U.C. 1668. C.N.H.M.-U.F. 87 from locality KD, remainder from KF.

Diagnosis.—Lower tooth with inner ridge forming narrow, strongly serrated blade. Anterior moiety of blade at least two
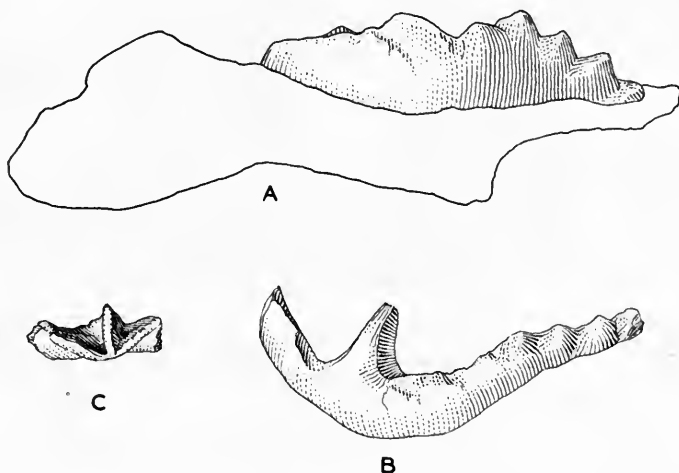

FIG. 47. Lower teeth of *Gnathorhiza*. A. Inner aspect of the type of *G. dikeloda* sp. nov., C.N.H.M.-U.F. 91; × 1½. B. Dorsal aspect of type of *G. dikeloda* sp. nov., C.N.H.M.-U.F. 91; × 1½. C. Dorsal aspect of type of *G. serrata* (Cope), A.M.N.H. 7258 (after Hussakof); × 1½.

times length of posterior moiety, possessing five or six strong denticulations. Single radiating ridge short and serrated on external slope only. Posterior moiety of blade strongly curved laterally and only slightly serrated. Upper tooth with long, compressed inner blade and two short radiating ridges. Inner blade strongly angulated anterior to radiating ridges and bearing three strong denticles. Posterior moiety of inner ridge finely denticulated and uncurved. Radiating ridges with denticulate sloping external margins.

Description and discussion.—Adults of the species are much larger than those of *G. serrata* or *G. pusillus*, as shown in Table 1. The shearing function of the blades of the teeth are even more highly developed than in the other species by virtue of the elongation of the anterior moieties of the inner ridges of both the upper and lower

tooth plates. This difference is clearly shown in the LAM/LPM column in Table 1.

Each of the differences is of such a high order that there is no need to demonstrate its validity by statistical analysis.

TABLE 1.—COMPARISON OF MEASUREMENTS OF
GNATHORHIZA DIKELODA AND G. SERRATA

	Total length[1]	Length of anterior moiety	Length of posterior moiety	Length of radiating ridge	LAM[2] LPM
		G. dikeloda			
C.N.H.M.-U.F. 90....	28.0	21.5	9.0	5.2	2.4
C.N.H.M.-U.F. 94....	27.0	20.0	9.0	4.8	2.2
C.N.H.M.-U.F. 93....	30.0	24.0	10.0	...	2.4
C.N.H.M.-U.F. 92....	....	....	8.8	5.2	...
C.N.H.M.-U.F. 91....	30.5	25.2	10.2	6.0	2.4
		G. serrata			
A.M.N.H. 7258.......	10.8	6.2	4.7	...	1.3
A.M.N.H. 8014.......	12.2	8.2	5.3	...	1.5

TABLE 2.—PARAMETERS OF SAMPLE OF
GNATHORHIZA DIKELODA

Measurements	N	M	s
Total length........................	4	28.9 ± 0.81	1.65 ± 0.59
Length of anterior moiety...........	4	22.7 ± 1.17	2.35 ± 0.83
Length of posterior moiety..........	5	9.4 ± 0.25	0.65 ± 0.21

The nature of the upper teeth in *G. dikeloda* is less readily determined. The only adult tooth is C.N.H.M.-U.F. 87 and this is only a small part of the inner ridge and of the two radiating ridges (fig. 48). The short portion of the inner ridge that is present is somewhat straighter than that in *G. serrata*. More information is provided by a very small tooth, C.N.H.M.-U.F. 88, whose total length is only 8.9 mm. The tooth appears to be an unerupted plate of an immature individual. The general characteristics show, with little doubt, that this was the type associated with the lowers of the adults. This belief is strengthened by the fact that the preserved parts of

[1] Measurements in millimeters, taken as follows: Total length equals distance from the anterior extremity of the tooth to the posterior extremity measured along a line parallel to the longitudinal axis of the jaw. Length of anterior moiety equals the distance from the position of intersection of the radiating ridge and the inner ridge to the anterior extremity of the tooth in a direct, straight line. Length of posterior moiety equals the distance from the point marked by the intersection of the radiating ridge and the inner blade to the posterior extremity of the tooth in direct, straight line. Length of radiating ridge is the distance from the intersection as above to the lateral extremity of the ridge.

[2] LAM, length of anterior moiety; LPM, length of posterior moiety.

the large upper are identical with those in the complete small tooth in every way except size. The principal features of this upper tooth and comparisons with upper teeth of *G. serrata* are shown in figure 48.

Gnathorhiza serrata (Cope)

A single tooth, C.N.H.M.-U.F. 96, from the Vale is referred to this species. This tooth (fig. 48, B) is identical, except for a slight
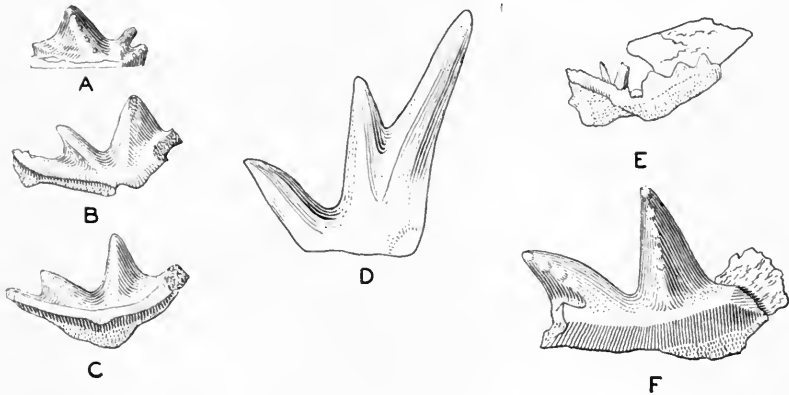

Fig. 48. Upper teeth of *Gnathorhiza*. A. *G. pusillus* (Cope), type, C.N.H.M.-U.C. 6508; × 2½. B. *G. serrata* (Cope) from the Vale, C.N.H.M.-U.F. 96; × 2½. C. *G. serrata* (Cope) from the Arroyo, C.N.H.M.-U.F. 95; × 2½. D. *Lepidosiren;* × 2½. E. *G. dikeloda* sp. nov., immature individual, C.N.H.M.-U.F. 88; × 2½. F. *G. dikeloda* sp. nov., C.N.H.M.-U.F. 87; × 2½.

size difference, with the upper tooth of *G. serrata* from the Arroyo. It was found at locality KI. So far as can be told, the horizon is essentially the same as that from which the five specimens of *G. dikeloda* were obtained in locality KF. In this single tooth there is evidence that the species known from the Arroyo continued unchanged into the Vale.

4. THE SKULL OF GNATHORHIZA DIKELODA OLSON

It was stated above (p. 105) that teeth of the dipnoan *Gnathorhiza* occur in beds of Late Pennsylvanian and Early Permian age, extending to the top of the Vale Formation of the Clear Fork group. Recent work has shown their presence in the Choza beds, as well. Three species have been recognized from teeth, *G. pusillus* from the Pennsylvanian, *G. serrata* from the Arroyo and Vale formations of the Early Permian Clear Fork and apparently from the Wichita
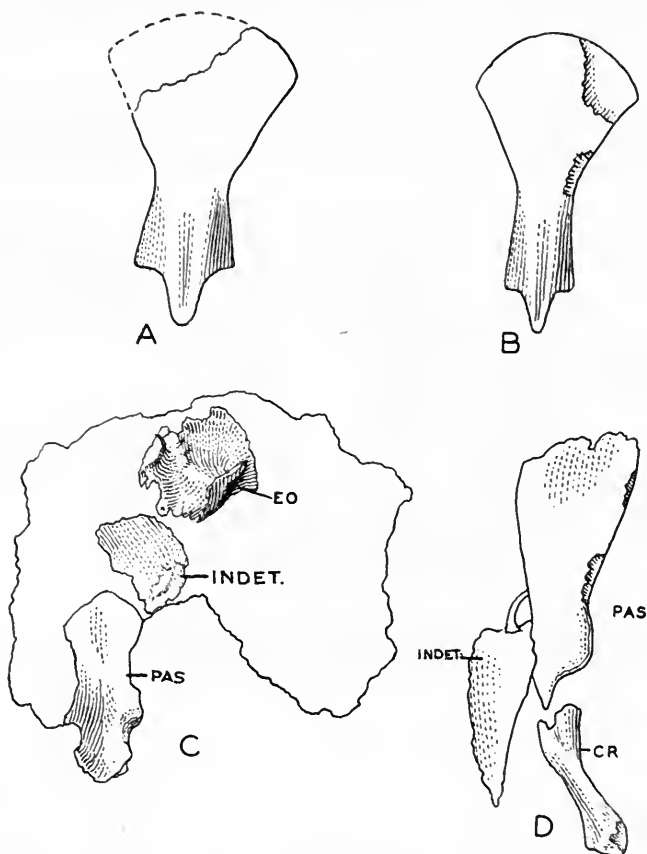
Fig. 49. Parasphenoid and associated elements of *G. dikeloda*. A. C.N.H.M.-U.F. 175, ventral aspect. B. C.N.H.M.-U.F. 168, ventral aspect. C. C.N.H.M.-U.F. 171, dorsal aspect, showing inverted plate *B* with exoccipital process. D. C.N.H.M.-U.F. 182, ventral aspect, showing cranial rib. CR, cranial rib; EO, exoccipital; PAS, parasphenoid. All × ⅔.

group as well, and *G. dikeloda* from the Vale and Choza. The last-named species, described on page 107, was founded on a lower tooth and jaw. Disarticulated skull plates were abundant in the deposits from which the type and referred specimens were obtained and many of these pertained to *G. dikeloda*. Using these elements I have attempted to reconstruct the skull of *G. dikeloda* and to use the skull as a means of determining the taxonomic and phylogenetic position of the genus. Skull parts of the other species are not known.

About 200 individual skull elements have been studied. Those that have contributed most to the interpretation are illustrated

in figures 49 to 52.   In only three instances has any articulated material been found and this has not been particularly instructive. All the plates, however, have been obtained from fine-grained channel deposits in locality FK (Olson, 1948) in Knox County, Texas.   Mixed with the bones of the lung fish are jaws, skull plates,
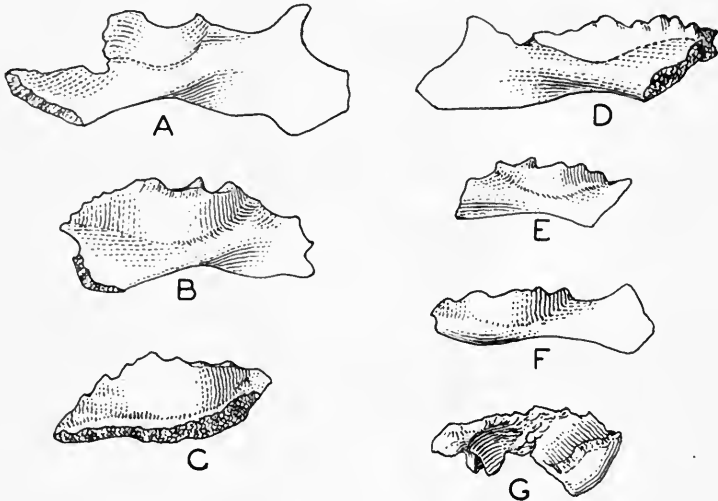

FIG. 50.   Jaws of *G. dikeloda*.   A–F.   Lower jaws in medial aspect.   G. Upper jaw in lateral aspect.   A, C.N.H.M.-U.F. 197; B, C.N.H.M.-U.F. 198; C, C.N.H.M.-U.F. 196; D, C.N.H.M.-U.F. 91, type of species; E, C.N.H.M.-U.F. 118; F, C.N.H.M.-U.F. 169; G, C.N.H.M.-U.F. 204.   All × ⅔.

girdle elements and limb bones of trimerorhachid amphibians and vertebrae of *Dimetrodon* and *Waggoneria.*

With one exception every type of dipnoan bone that has been observed has a frequency of 4 or more, and it seems safe to assume that all ossified parts of the skull, with the possible exception of very small bones, have been found.   The size of the various elements is such that the bones could not have come from the small species, *G. serrata*, which does occur in the Vale.   Furthermore, no teeth of this species have been found at locality KF.   There is little doubt that all of the elements belong to the single species *G. dikeloda.*

In a study based on fragmentary materials such as those available for this work, the probability of errors is always high—errors of both major and minor proportions.   It is almost certain that some modifications in the reconstructed skull pattern will be necessary in the
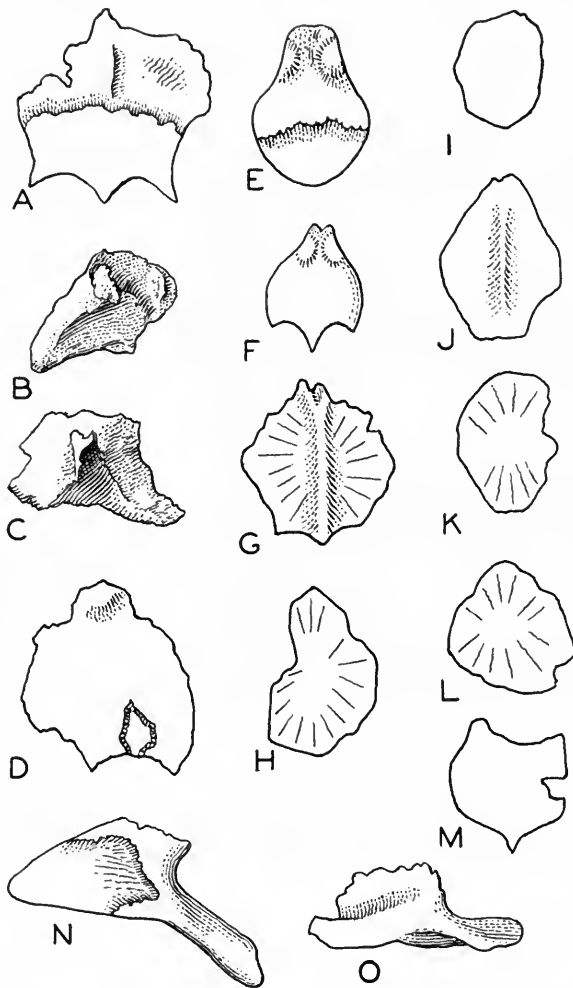
FIG. 51. Skull elements of *G. dikeloda*. A–M. Median elements, oriented with anterior ends toward top. N–O. Lateral element Y1+Y2. A, C.N.H.M-U.F. 203, plate *B* in dorsal aspect; B, C.N.H.M.-U.F. 175, plate *B* in ventral aspect, showing exoccipital; C, C.N.H.M.-U.F. 175, plate *B* in ventral aspect, showing exoccipital; D, C.N.H.M.-U.F. 185, plate *B* in dorsal aspect; E, C.N.H.M.-U.F. 171, plate *F* in dorsal aspect; F, C.N.H.M.-U.F. 173, plate *F* in dorsal aspect; G–M, plate *D* in dorsal aspect, C.N.H.M.-U.F. 178, U.F. 166, U.F. 187, U.F. 174, U.F. 165 and U.F. 164, respectively; N and O, plate *Y1+Y2* in lateral aspect with anterior end to the right, C.N.H.M.-U.F. 205 and U.F. 199 respectively. All × ⅔.

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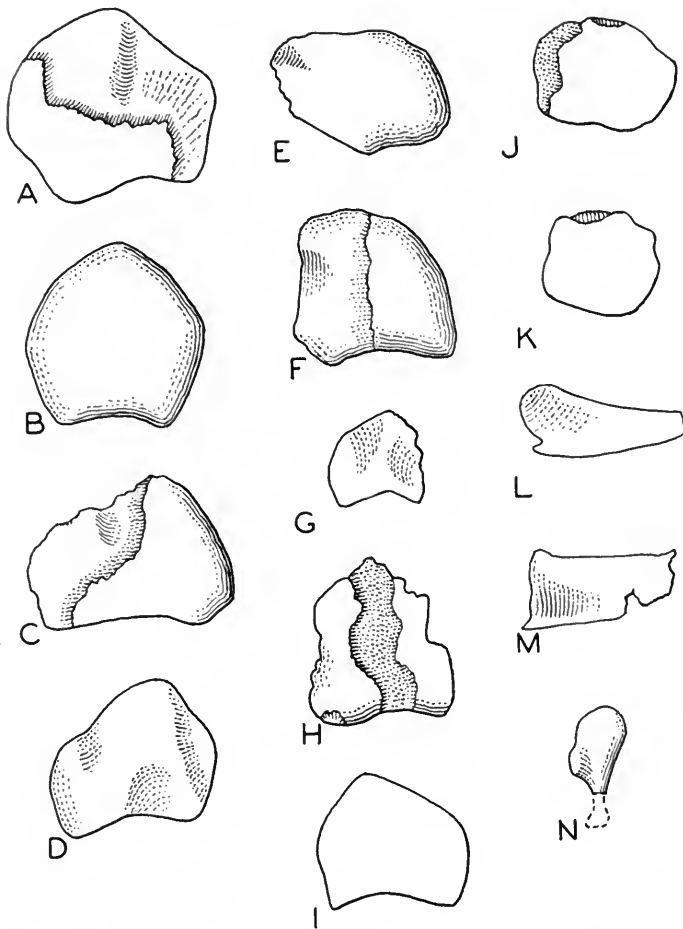
FIG. 52. Lateral skull elements of *G. dikeloda.* A–I, plate $M+L1+L2+K$ with orbital margin toward bottom, C.N.H.M.-U.F. 179, U.F. 176, U.F. 176, U.F. 183, U.F. 204, U.F. 173, U.F. 177, U.F. 181, U.F. 183, respectively. J and K, plate *J* with ventral margin in upper right hand corner, C.N.H.M.-U.F. 191, U.F. 204, respectively; L and M, plate *I* with anterior end to right and dorso-medial toward top, C.N.H.M.-U.F. 175, U.F. 181, respectively; N, C.N.H.M.-U.F. 184, "squamosal" element in lateral aspect with dorso-posterior portion toward top (dotted outline reconstructed from rather poor impression in matrix). All × ⅔.

event that articulated skulls are found. So far as field investigations have progressed, however, the chances of finding articulated materials seem to be poor and an attempt to understand the skull, even though the restorations may be inaccurate in some parts, seems justified
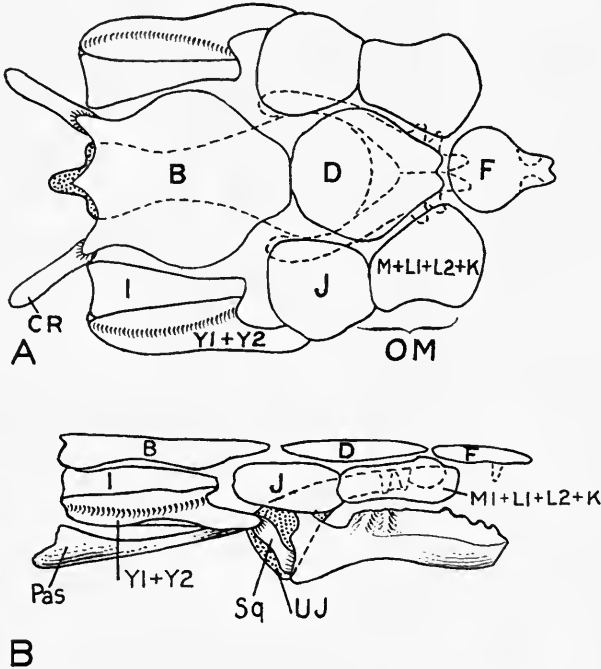
Fig. 53. Reconstructions of skull of *G. dikeloda*. Solid lines represent visible bones, broken lines those concealed by the surface of the skull. A. Dorsal aspect. B. Lateral aspect. Approximately × ⅔ of adult skull. Lettered bones based on system of Westoll (1949). CR, cranial rib; OM, orbital margin; PAS, parasphenoid; Sq, "squamosal;" UJ, upper jaw.

in view of the information that such a study can yield. Every effort has been made to avoid errors and the more questionable parts of the restorations are documented in the text. The comments on taxonomy and phylogeny on pages 120–124 are, of course, only as valid as the interpretations of the identities and positions of the bones.

THE SKULL ELEMENTS AND THE RESTORATIONS

In the following paragraphs the bones of the various series are described in some detail and their probable positions in the skull are given. The reader may best maintain his orientation by reference

to the reconstructions (fig. 53), but he should consult figures 49 to 52 for an evaluation of the evidence. The terminology of Westoll (1949) has been adopted so far as it is applicable to the elements described. The fossils offer little evidence on homologies of the various bones so that these have been taken from various sources as noted in the text. For the reconstructions, an effort has been made to approximate the mean sizes of the different bones in the hope that this would produce a reasonably integrated whole.

Palate, jaws and teeth (figs. 49 and 50).—The parasphenoid and the upper jaw, usually called pterygo-palatine, make up the palate, as in most dipnoans. The principal features of the parasphenoid are well shown in figure 49, A and B, and need little additional comment. The basal, posterior spur is constant in the species, and the posterior part of the dorsal surface is deeply grooved to receive a large noto-chord. The parasphenoid is typically dipnoan and presents no unusual major features. Three well-preserved and seven partial parasphenoids have been found. There is some variation in length and width and considerable variation in thickness.

Only two tooth-bearing upper jaws have been found, which is in rather odd contrast to the dozen lowers. The single element of the upper jaw corresponds closely to that of other lung fish. It is proportionately broader and shorter than that in *Protopterus* and *Lepidosiren* but otherwise much the same. There is no reason to doubt that the upper jaw was associated with the expanded anterior end of the parasphenoid in typical dipnoan fashion. There was a moderately strong antero-median symphysis between the right and left jaws.

Several fairly well-preserved lower jaws and teeth have been recovered, plus some fragmentary remains, to make a total of twelve specimens. Best preserved is the lower jaw and tooth described above (p. 107) and designated as the type of the species, C.N.H.M.-U.F. 91 (fig. 50, D). Specimens obtained since the time that the description was written have added little to what was then known. Only a single lower jaw element has been identified, that called splenial or coronoid by various workers on modern lung fish. Anteriorly, this element carries the very long, sectorial lower tooth and medial to the anterior margin of this tooth it forms a strong symphysis with the opposite jaw. Posterior to the tooth, the jaw thins rapidly and is projected dorsally into a thin "coronoid process." The general pattern is much the same as that in *Protopterus*, *Lepido-siren* and *Epiceratodus*, but the posterior ramus is proportionately

thinner in *Gnathorhiza* and there is no evidence of a Meckelian orifice such as is found in recent genera. It would appear that the inner margin of the basal part of the ramus had degenerated to a greater degree than is the case in living lung fish. No small element is to be found below the splenial. This element is set in a deep notch in *Lepidosiren* and *Protopterus*. No such notch occurs in *Gnathorhiza*. As in modern dipnoans, the articular part of the lower jaws appears to have been an unossified portion of Meckel's cartilage.

A somewhat puzzling relationship exists between the upper and lower teeth. Lower teeth have an exceedingly long, serrate, anterior blade. Large upper teeth do not show any such development. If the lower and upper jaws are placed in the position consistent with the condition in *Protopterus* and *Lepidosiren*, which seems logical in view of the morphological similarities of the teeth and jaws in the three genera, the long lower blade projects far beyond the anterior limit of the upper tooth. A very small upper tooth, described above (p. 108), has a long anterior blade that would occlude with the anterior part of the lower blade, but no large upper tooth shows this structure. The anterior margin of two well-preserved upper teeth seems to be smooth. Whether the small tooth does not actually pertain to this species or whether the anterior blade and any support-ing structure that it may have had were lost by wear cannot be determined from the material at hand. In all respects, except size and the long blade, the large and small upper teeth are similar. The problem appears to be insoluble at present but, in any event, it is evident that in the adult the anterior part of the lower tooth did not meet an opposing blade of the upper. It may, however, oppose the "vomerine" teeth, whose position may be inferred from tubercles observed on the ventral surface of the most anterior element of the median series of dermal roofing bones.

Median dorsal series (fig. 51, A–M).—Three types of median plates have been observed, each represented by several specimens. Their median position has been inferred from their bilateral sym-metry and from the presence of longitudinal structures that pre-sumably lay along the midline. Representatives of each type are shown (fig. 51) and their positions in restoration (fig. 53). Two of the three median elements have distinctive features that define their positions clearly. A number of plates (fig. 51, B and C; also fig. 49, C, *EO*) possess a ventral process that corresponds very closely to the exoccipital in *Protopterus*. In no single plate in which the ventral side is exposed have both exoccipital processes been

preserved, but right and left exoccipitals have been observed on different plates. Two plates that carry this process have a curving posterior distal margin and one has a posterior median projection. This permits association of these plates with another (fig. 51, A) that shows the full posterior margin in dorsal aspect, as well as much of the outline of the lateral margin of the plate. It seems evident from the presence of the exoccipitals and the configuration of the posterior margin of the plates that this median plate lay at the back of the skull in the position indicated in the restorations. It corresponds to plate *B* of Westoll (1949).

Two complete plates and several fragments represent another type of median plate (fig. 51, E and F). The outline in dorsal and ventral aspect is roughly flask-shaped and corresponds closely to the outline of the rostral plate, dermo-ethmoid of Bridge (1898) and others, in *Protopterus* and *Lepidosiren*. The posterior margin of the smaller plate (fig. 51, F) is emarginated, presumably as the result of incomplete ossification. The ventral surface carries a pair of strong, rounded tubercles that probably mark the positions of a pair of vomerine teeth. These are an integral part of the plate with no evidence of separate origin. That these plates represent anterior members of the median series seems certain and, as such, they correspond to plate *F* of Westoll (1949).

There is little definitive about the third type of median plate (fig. 51, G–M). These plates are thin and in most instances poorly ossified. The edges are feathered and irregular. A rough diamond shape is characteristic. The end interpreted as posterior is somewhat flattened and, in some instances, seems to carry a short posterior spur that presumably passed under the more posterior median element (fig. 51, M). The anterior margin normally has a slight, posteriorly directed emargination. Since this type of plate is clearly median, there seems no alternative to the conclusion that it lay on the dorsal midline of the skull between plates *B* and *F*, and thus is comparable to plate *D* of Westoll (1949).

G. dikeloda appears to have had a midline series of three plates. This is in contrast to *Epiceratodus*, *Lepidosiren* and *Protopterus*, which have but two, but very similar to *Ceratodus sturii* Teller (interpretation of Westoll, 1949, fig. 9) and, in some respects to *Sagenodus*.

Lateral plates (fig. 51, N and O; fig. 52).—Interpretation of the lateral plates has been more difficult and conclusions are less certain than in the cases of the palate, jaws, and median plates. The

reconstructions, of course, show the plates with definite outlines and in definite positions, but it must be realized that the certainty is not as great in some instances as figure 53 might indicate. The probabilities of accuracy for each set of plates are considered in the following paragraphs.

Two types of nearly flat plates, somewhat rounded in outline, have been found, each represented by a considerable number of specimens. Both types are asymmetrical and cannot have lain in the midline. The configuration of the larger series of plates is shown in figure 52, A–I. One margin of this type of plate is smoothly finished along a slightly asymmetrical, concave surface. The asymmetrical triangular apex of the opposite side may be fitted nicely into the recess created by the margins of median plates *F* and *D* (see fig. 53, A). In this position the curved margin lies in the vicinity of the orbit and appears to constitute the dorsal orbital rim. This type of plate can be placed in position with considerable confidence.

The smaller rounded plates (fig. 52, J and K) have fewer definitive characters. The shape is moderately constant and two small features aid in placement. On one margin there is a projecting shelf that must have passed beneath an adjacent element. Flanking this shelf is a short, smoothly finished margin much like the orbital margin of the larger plates. If the small plate is placed so that the smooth margin forms a posterior continuation of the orbital margin, the projecting shelf then articulates with the larger more anterior plate and a reasonable relationship to plate *D* exists. A space is left in the area created by the tapering margins of plates *D* and *B* but this is explained, perhaps, by the fact that the adjacent margin of the small plate tapers to a poorly defined, feathered edge that suggests incomplete ossification. The same type of edge occurs on plate *D*, whereas the margins of *B* are reasonably well developed.

The position of the two rounded plates seems fairly well established. The precise locations may be slightly in error but the general area can hardly be incorrect. It is difficult to be certain of homologies but the positions strongly suggest that the larger plates correspond to Westoll's $M+L2+L1+K$ and the smaller to his plate *J*.

Another type of lateral plate occurs in the deposits, a long, thin, wedge-shaped bone with a strong spur at one corner of the border (fig. 52, L and M). The position of this plate is by no means certain but it may at least be placed in a reasonable position. There is, of course, the possibility that it does not belong to *Gnathorhiza* at all,

but it certainly finds no reasonable place in the skulls or postcrania of any other animal known from the deposits, and the structure of the bone is the same as that of other skull plates of *Gnathorhiza*. One margin of this plate fits moderately well against the lateral margin of median plate *B*, if the broader end, which is well finished, is considered to be posterior. One surface of this plate, presumably ventral, gives the appearance of having received a flat spur from a bone that lay latero-ventral to it. Such a spur occurs on an element, described below, that is labeled *Y1+Y2* in figure 53 and located with some confidence. At the postero-lateral margin of the lateral plate under discussion, as oriented, occurs the strong spur that projects ventrally and seems to fit into the notch created by a posterior process of *Y1+Y2*. These features, taken together with the fact that there is no other plausible place where the bone might lie in the skull, have been the basis of its placement. In this position it would, presumably, be equivalent to element *I* of Westoll.

Four fairly well-preserved specimens and some fragments give evidence of the rather complex bone that is thought to have lain latero-ventral to element *I*. The bone is best understood by reference to figure 51, N and O. In the orientation indicated in the restoration (fig. 53, B), this bone consists of an anterior ventral process, a broad dorsal plate and a short posterior spur. The ventral edge is rounded and well finished, as if it marked part of the skull margin. The crescentic recess above the anterior process has a very thin, knife-like edge unlike that found in the orbital margin. This, among other things, makes it improbable that this bone was associated with the orbit, as its shape might otherwise suggest. If the bone did not lie in the orbital region, the indicated position must be correct. There are several details that point in this direction. The dorsal plate is very thin and irregularly grooved as if it inserted under an adjacent bone. It will be recalled that the under surface of element *I* gave indication of carrying such a bone. The posterior spur is well suited to articulate with the ventral spur of *I*. The anterior process could well be a quadrate process and in the orientation suggested it passes to the proper area. A well-defined groove passes anteriorly and curves slightly dorsally from the posterior end of the base of the dorsal plate to the anterior crescentic incisure. This appears to show the course of a latero-sensory canal which corresponds closely to that on *Y1+Y2* of various late Paleozoic dipnoans (see, for example, Westoll, 1949, fig. 8).

One other feature of importance in the placement of this element is the nature of the inner surface of the anterior quadrate process.

Since the importance of this feature becomes apparent only when its probable relationship to a bone so far undescribed is recognized, a digression to consider the latter is in order. In recent lung fish, of which *Protopterus* may be taken as an example, the articulation of the jaws is accomplished by cartilage, Meckel's cartilage in the lower jaw and the quadrate cartilage in the skull. Lying lateral to the quadrate cartilage is a thin, spatulate, dermal bone that overlies a descending process of the large posterior roofing element of the skull. The ventro-anterior end of the spatulate element is expanded into a thin but deep condyloid process that, capped by cartilage, aids in the jaw articulation. The homology of this element has been variously interpreted, perhaps the most logical interpretation being that it is squamosal. A similar element, known from only one specimen (fig. 52, N), has been found in the *Gnathorhiza*-bearing sediments. The condylar part is damaged but the remainder is very like the "squamosal" of *Protopterus*. If this element lay in a position similar to that in *Protopterus*, it would pass to the anterior process of the bone discussed in the preceding paragraph and identified as $Y1+Y2$. The inner surface of the anterior process of the latter is strongly concave, opening ventro-medially, precisely as would be the case had it received that dorso-posterior end of the small "squamosal" element. This is believed to have been the case.

DISCUSSION

It was hoped when this study was undertaken that positive evidence concerning the position of *Gnathorhiza* with respect to the living Lepidosirenidae might be forthcoming. Although results have been unsatisfactory in this regard, a number of interesting items that have come to light may be considered briefly. Romer and Smith (1934) suggested an early separation of the Ceratodontidae and Lepidosirenidae, recognizing a Pennsylvanian proceratodont and referring *Gnathorhiza* to the family Lepidosirenidae. Stromer (1910, 1936 and 1938) has argued strongly that the lepidosirenids, excluding *Gnathorhiza* from the group, originated from the ceratodontids late in the Mesozoic and that the resemblances in dentition between *Gnathorhiza* and *Protopterus* and *Lepidosiren* were the result of convergence. Dollo (1896) and Agar (1906) imply a similar relationship among living lung fish, with *Epiceratodus* the most advanced. The problem involved is clear cut and simple, namely, whether the differentiation was pre-Triassic, presumably

in the Permo-Carboniferous, or whether it was post-Triassic, presumably in the Cretaceous. Solution is not an easy matter.

Until now, only teeth of *Gnathorhiza* have been available for study. The work of Westoll (1949) has greatly amplified our knowledge of the patterns of skull evolution in the dipnoans of the Paleozoic. Evidence concerning skull evolution in the Mesozoic is scant. Both Westoll (1949) and Stromer (1938) have discussed the evidence, the latter in some detail, and both have concluded that the case for late origin of the lepidosirenids from a ceratodont stock is to be preferred. It would appear that the principal basis for such a conclusion, as both writers suggest, is the absence of any remains of lepidosirenids from the Mesozoic, coupled with the facts that the morphological pattern of the lepidosirenids could have been derived from that of the ceratodontids and that late Mesozoic teeth are highly variable.

Now that many details of the skull of *G. dikeloda* are available, it is possible to study the resemblance of this skull to those of other Paleozoic lung fish, and to *Protopterus* and *Lepidosiren*. A consideration of the possible Paleozoic ancestors shows that the most probable source of *Gnathorhiza* is the genus *Sagenodus*. *Gnathorhiza* could have been derived from this genus both from the aspects of time and morphology, and in view of the resemblances of plates B and D in the median series and I, J, and $M+L2+L1+K$ in the lateral series and the fact that the necessary dental modifications, while striking, would not have been prohibitively drastic, *Sagenodus* may well have occupied the ancestral position. Assuming this to have been the case, the following changes would appear to have occurred. Element D of the median series expanded at the expense of the paired element E, which is lost in *Gnathorhiza*. F has enlarged. Q and N, plus the circumorbital bones 2, 3 and probably 4, are gone, and the orbital margin is formed by $M+L2+L1+K$ and J. There is no element X in *Gnathorhiza* so far as known. $Y1$ and $Y2$ have fused and H is absent. I has become longer and narrower but has maintained its position. $Y1+Y2$ have developed a strong quadrate process that appears to have overlain the "squamosal."

The dermal bones appear to have become more deeply set so that there is no trace of grooves for the latero-sensory organs except on $Y1+Y2$. Most skull bones have lost intimate articulation with their neighbors and, except adjacent to such structures as the orbits and skull margins, tend to "feather out" toward the edges. Elements D and J are very thin but the others have maintained considerable

thickness. The parasphenoid and jaws have changed little but the dentition has modified to a strictly sectorial type. The only bone remaining in the brain case is the exoccipital element. A strong cranial rib is present.

As a result of these changes, *Gnathorhiza* approaches rather closely the patterns seen in *Protopterus* and *Lepidosiren*. Assuming for the moment that *Gnathorhiza* may be considered ancestral to the living lepidosirenids, additional changes necessary to produce *Protopterus* or *Lepidosiren* would not be great and would seem to represent a continuation of some of the trends established in *Gnathorhiza*. Continued loss of bone would account for disappearance of the already thin elements D and J. Element I would have disappeared, and $Y1+Y2$ and B would have continued to sink deeper below the surface. $M+L1+L+K$ would be most drastically modified of any of the elements that did not disappear, remaining for the most part superficial but being elongated into the rather remarkable processes found in the two living genera. Jaws and dentition would have undergone only slight modifications. Such changes are certainly plausible.

With this evidence alone the case seems fairly strong. The changes from *Sagenodus* to *Epiceratodus*, however, are different only in a few points. Westoll's circumorbital bone 4, bone X and bone I are present in *Epiceratodus*. All are small and, although only I has been identified in *Gnathorhiza*, the others might have been present but small and hence not found. None of these are found in the lepidosirenids. D and J are found in *Gnathorhiza* and not in *Epiceratodus*, but *Ceratodus sturii* Teller, from the Triassic, has D strongly developed. This form, in some respects, appears to be intermediate between *Sagenodus* and *Epiceratodus*. Unlike *Gnathorhiza*, *C. sturii* lacks J and I, and $M+L2+L1+K$ is elongated. The circumorbital series, as interpreted, is complete in contrast to that inferred in *Gnathorhiza*. If the changes from *Sagenodus* to *Epiceratodus* are carried through the *C. sturii* stage, a reasonable point of departure for the lepidosirenid type is reached at about the *Epiceratodus* stage.

There is apparent in evolution, in these lines as in so many others, a pattern of comparable changes and similar trends in series that are at least ordinally related. Striking, in the genera under consideration, is the fact that *Gnathorhiza* has become highly modified in the Early Permian, whereas the first record of important modification in the ceratodontid line is in the Triassic. This may,

of course, be due to the scantness of the record, for no skulls or teeth that can be referred with certainty to this line are known in the Paleozoic. Romer and Smith (1934), it is true, have noted teeth with a *Ceratodus*-like pattern from the Carboniferous and it is possible that these specimens actually represent ancestral forms. None are known from the Early Permian, however. If the negative evidence of the lack of ancestral lepidosirenids in the Mesozoic is to be considered an important item in the suggested derivation of the lepidosirenids from the ceratodonts, some consideration must be given to the fact that no protoceratodonts occur in the Permian and no *Sagenodus* types have been found above beds of Wichita age, although dipnoans of the *Gnathorhiza* type have now proven to be abundant in the Vale of Clear Fork age. By application of the same sort of evidence and the same type of reasoning as used in the case for relationship of the ceratodontids and lepidosirenids, it might be concluded that *Gnathorhiza*, not an impossible ancestor for *Ceratodus* morphologically, is to be considered ancestral to both the ceratodont and lepidosirenid lines.

Phyletic inter-relationships appear to be highly complex as a result of the tendency for independent developments of similar modifications in related lines. It seems equally possible from the morphological standpoint for the lepidosirenids to have arisen from either the *Gnathorhiza* stock or from the ceratodontid stock, and it is not impossible, although the dentition may make it improbable, that the ceratodontid stock might have arisen from *Gnathorhiza*. Thus, as things now stand, the morphological evidence must be considered as inadequate to solve the problem of relationships.

The stratigraphic evidence is of little more help. Great gaps in the paleontological record have existed in the past. Some have been filled while others still remain. Some, such as the lack of evidence of coelacanth fish in the Tertiary, are explainable on environmental bases; others, such as the lack of late Paleozoic, Mesozoic and Cenozoic ancestors for the lampreys and hagfish, can be explained by the absence of hard parts; still others, such as the absence of known ancestors for the Chelonia of the Triassic, have, at present, no explanation that is not purely conjectural. It thus becomes very unsafe to assume that the lack of evidence of lepidosirenids in the Mesozoic is strong evidence that they did not come into existence prior to the late Mesozoic and thus must have been derived from the ceratodontids. Perhaps, if such Mesozoic ancestors existed, they lived under circumstances where preservation was improbable;

perhaps their range was restricted, as in the case of the two genera of today. Any one of many explanations might be possible.

Every argument that may be advanced can be countered by one equally plausible and we are forced, if we wish to classify, to use a classification that has no sound basis of phylogenetic probability. Such a classification, then, must be a categorization that is arbitrary and practical, that introduces as little confusion as possible into nomenclature, and that impedes and restricts our patterns of thought no more than is necessary. Of the several possibilities in the present situation, each may do violence to actuality. It seems more practical at present to include *Gnathorhiza* with the forms that it resembles most closely, as a genus under the Family Lepidosirenidae, than to erect a new family for it, which would be necessary under any other scheme.

5. AN ERYOPID AMPHIBIAN

GENERAL CONSIDERATIONS

One moderately well-preserved skull, a small part of the sculptured dorsal surface of another skull, and a few skull roof fragments, of uncertain affinities, are the only remains of large, labyrinthodont amphibians that have been found to date in the upper beds of the Vale. The first two may definitely be assigned to the genus *Eryops*. It was reported earlier (1948) that this genus had not been discovered in two seasons of collecting and that the failure to find any traces of such a large animal might indicate that it did not exist in the vicinity during the time of deposition of the beds. This, of course, is now known to be incorrect, but the absence of limb bones, vertebrae and other skeletal parts from the channel deposits, which carry most of the specimens in the area, has yet to be explained. Although the fragment of sculptured dorsal surface of the skull was found in a channel conglomerate, it was not until production was obtained from clay deposits that any well-preserved remains were obtained.

Only the skull, C.N.H.M.-U.R. 23, is preserved well enough to permit specific identification. This skull, although fractured into a mosaic of small bone fragments, has preserved the original shape with but little crushing. No sutures can be distinguished. It was found with the palatal surface exposed and the lower jaws and ventral margins of the skull were somewhat damaged by weathering. Only the dorsal surface has been prepared, since this is sufficient for identification and the skull was too fragile for further preparation.

The skull resembles that of the type of *Eryops megacephalus* Cope in virtually all features that can be studied, except that it is somewhat smaller. Measurements are given in Table 3 along with measurements of the type (taken from Case, 1911). The difference in size and slight differences in proportions cannot be considered significant taxonomically, for a much greater range of variation is seen among specimens of this species from earlier Permian beds. The exact horizon from which the type of *E. megacephalus* came is not known, but quite certainly the species occurs throughout much of the Wichita and in the Clyde, Arroyo and Vale Formations of the Clear Fork. The species persisted over a relatively long period of time, longer, apparently, than did most species of Early Permian tetrapods.

OCCURRENCE AND FAUNAL RELATIONSHIPS OF
ERYOPS IN THE VALE

Until 1948, vertebrates of late Vale age were known only from beds of moderate to coarse conglomerates that originated as stream deposits. During 1948, however, several occurrences in fine, green channel sediments, red channel sands and clays of non-channel origin were discovered. Two localities in the Vale and one in the Choza where production may be obtained from clays are now known, as follows:

1. "Clay Hill" in KH at CGV 4 41, 2.6–3.3, Vale.

2. "Chocolate Clay Locality" in KH at CGV 5 26, 6.3–4.95, Vale.

3. Locality FA,[1] Choza.

The skull of *Eryops megacephalus*, C.N.H.M.-U.R. 23, was found at the first listed locality. The layer in which it occurred is exposed around the margin of Clay Hill, a rounded prominence about 40 feet high and 150 feet in diameter, about 15 feet above the base of the hill. The northern and western exposures of the bed consist of about six feet of sandy, purplish-red clay. They grade into a more

[1] See Olson, 1948, for index system. Locality FA was discovered and explored in 1948–1950. It lies just north of the North Fork of the Wichita River in Foard County, Texas, approximately north of Vera, Texas. It is shown on aerial photograph CZW 1C 59 and has irregular boundaries that may be limited as follows: NE corner at 1.3–3.9, N 60° E to 3.5–3.3, along margin of exposures to 3.7–2.4, thence to 4.95–3.2, and SE and SW along margin of exposures to corner on river at 4.3–1.5, W and slightly N along margin of open breaks to tank at 1.6–2.75, along margin of exposures to NE corner of area.

sandy, somewhat thicker phase exposed at the southern margin of the hill. This extremity contains layers and lenses of fine conglomerate. Much of the clay is rich in compressed plant remains, which impart the purplish cast to the rock and give it a finely laminated appearance. The clay deposit does not occur in the adjacent hills to the north, east or west, but is continued in a sandy, conglomeratic phase in a hill about fifty yards to the south of Clay Hill. This deposit in turn is continuous to the south with a conglomerate formed in a stream channel. It appears that the clay was laid down in a pond of no more than a hundred yards in diameter with an inlet to the south. Overlying the clay bed are deposits of clay and sandstone capped by a conglomerate. All of these appear to be of flood-plain origin.

In addition to the skull of *Eryops*, fragments of small amphibians, two sets of vertebral spines of small dimetrodonts, jaws of *Trimerorhachis*, and many teeth and pieces of calcified cartilage of xenacanth sharks have been found in the clay. This assemblage, except for the dimetrodonts, which quite certainly came to the ponds for watering or, perhaps, feeding, may well typify the life assemblage that was characteristic of open and moderately persistent ponds of the time. A deposit very similar to the one described above, so far as the physical constituents are concerned, was found in locality FA, but no plant or vertebrate assemblage was found in it.

It is possibly significant that *Eryops*, except for fragments, has not been found in the many channel deposits that have been studied. It may have been restricted in habitat to ponds and absent from the streams and stream margins. The absence of *Diplocaulus* in fine-grained deposits, in which its presence has not been noted, may also be noteworthy in suggesting that this aquatic amphibian, abundant where it does occur, existed in late Vale times in running water only and was not associated with *Eryops*. This is in marked contrast to the conditions in the Arroyo, in which *D. magnicornis* was predominantly a pond dweller and in which association with *Eryops* is not infrequent. In this regard, it is of interest to note that one fair specimen and several fragments of *Diplocaulus* were found in the sandy-conglomeratic phase of the deposit in the exposures to the south of Clay Hill. It is inevitable that such suggestions concerning ecological relationships in part depend upon the fragile web of negative evidence. Through many such analyses, correcting misinterpretations as more evidence appears, we may hope eventually, however, to obtain a reasonably clear idea of environmental

conditions and faunal and floral relationships and associations throughout short spans of time even in periods as remote as the Permian.

TABLE 3.—MEASUREMENTS OF ERYOPS MEGACEPHALUS
(*In millimeters*)

Specimen	Skl (g)[1]	Skl (m)	Skw (dp)	Iow	Orw	Orl
A.M.N.H. 4189.......... 433		335	118	86	57	48
(type)						
C.N.H.M.-U.R. 23........ 360		310	120	60	55	55
(Vale)						

[1] Abbreviations: *Skl(g)*, greatest skull length, snout to level of posterior termination of quadrate; *Skl(m)*, skull length along dorsal midline; *Skw(dp)*, skull width at posterior end of dorsal platform; *Iow*, interorbital width, minimum; *Orw*, orbital width, maximum normal to midline; *Orl*, orbital length, maximum parallel to midline.

ADDENDUM

As the result of unexpected delay in publication of this series of papers, certain family, generic and specific names established herein inadvertently appeared in an earlier paper (Olson, E. C. 1951, Vertebrates from the Choza Formation, Permian of Texas. Jour. Geol., **59**, pp. 178–181). The names are as follows: Family Waggoneridae, genus and species *Waggoneria knoxensis*, species *Gnathorhiza dikeloda*.

REFERENCES

AGAR, W. E.
    1906. The development of the skull and visceral arches in *Lepidosiren* and *Protopterus*. Trans. Roy. Soc. Edinb., **45**, pp. 49–64, 3 pls.

BRIDGE, T. W.
    1898. On the morphology of the skull in the Paraguayan *Lepidosiren* and in other dipnoids. Trans. Zool. Soc. London, **14**, pp. 325–376, 2 pls.

CASE, E. C.
    1911. Revision of the Amphibia and Pisces of the Permian of North America. Carnegie Inst. Wash., Pub. 146, pp. i–vii+1–148, 25 pls., 51 figs.

COPE, E. D.
    1884. Fifth contribution to the knowledge of the fauna of the Permian Formation of Texas and the Indian Territory. Proc. Amer. Phil. Soc., **22**, pp. 28–47, 1 pl.

DOLLO, L.
    1896. Sur la phylogenie des Dipneustes. Bull. Soc. Belge Geol., Paleont., Hydrol., **9**, pp. 79–128, 5 pls.

HUSSAKOF, L.
  1911. The Permian fishes of North America. Carnegie Inst. Wash., Pub. 146, pp. 155–175, 7 pls., 4 figs.

OLSON, E. C.
  1936. Notes on the skull structure of *Youngina capensis* Broom. Jour. Geol., 44, pp. 523–533, fig. 1.
  1939. The fauna of the *Lysorophus* Pockets in the Clear Fork Permian, Baylor County, Texas. Jour. Geol., 47, pp. 389–397, 2 figs., 1 pl.
  1948. A preliminary report on vertebrates from the Permian Vale formation of Texas. Jour. Geol., 65, pp. 186–198, 2 pls., 2 figs.

OLSON, E. C. and BROOM, R.
  1937. New genera and species of tetrapods from the Karroo beds of South Africa. Jour. Paleont., 11, pp. 613–619, 7 figs.

PRICE, L. I.
  1935. Notes on the brain case of *Captorhinus*. Proc. Boston Soc. Nat. Hist., 40, pp. 377–386, 4 pls.

ROMER, A. S. and SMITH, H. J.
  1934. American Carboniferous dipnoans. Jour. Geol., 42, pp. 700–719, 7 figs.

STROMER, E.
  1910. Ueber das Gebiss der Leposirenidae und die Verbreitung tertiärer und mesozoischer Lungenfische. R. Hertwig Festschrift, 2, pp. 613–624 .
  1936. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Egyptens. VII. Baharije-Kessel und -Stufe met deren Fauna und Flora. Abh. Bayer. Akad. Wiss. Math.-Naturw., Abt. N. F., 33, pp. 1–102, 21 figs., 1 pl.
  1938. Die Wüstenfisch *Ceratodus*, Ag. 1833 und siene mezo- und känozoischen Verwandten. Neues Jahrb. Min., Geol., Pal., Beil.-Bd. 80, Abt. B, pp. 248–263, 1 fig.

WESTOLL, T. S.
  1949. Evolution of the Dipnoi. Genetics, Paleontology and Evolution. Princeton Univ. Press, pp. 121–184, figs. 1–11.