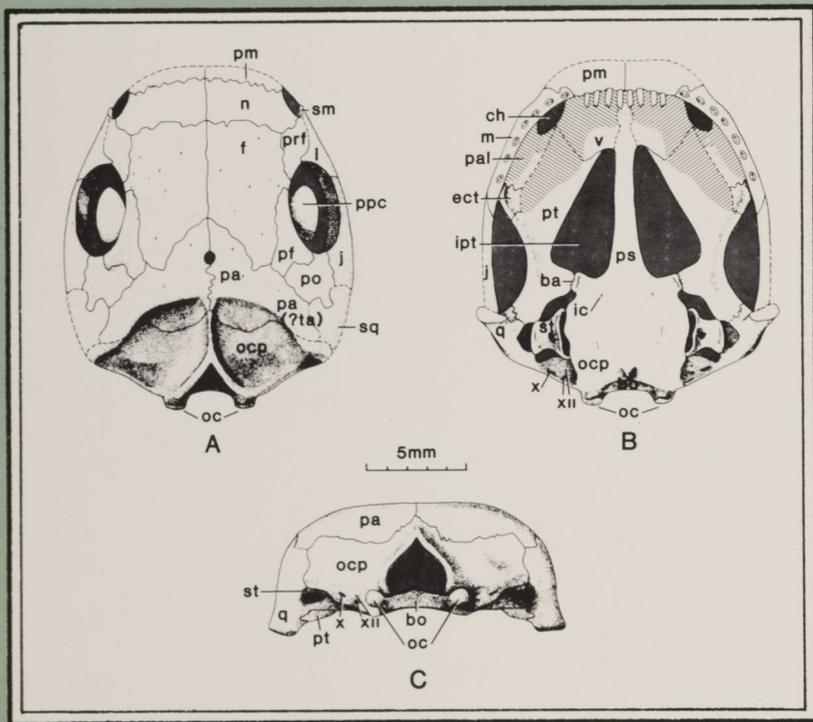


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CARROLLA CRADDOCKI
A New Genus and Species of
Microsaur from the
Lower Permian of Texas

Wann Langston, Jr.
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April 22, 1986
TEXAS MEMORIAL MUSEUM, THE UNIVERSITY OF TEXAS AT AUSTIN

Pearce-Sellards Series

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The Pearce-Sellards Series is an occasional, miscellaneous series of brief reports of Museum and Museum-associated field investigations and other research. All manuscripts are subjected to extramural peer review before being accepted. The series title commemorates the first two directors of Texas Memorial Museum, both now deceased: Dr. J. E. Pearce, Professor of Anthropology, and Dr. E. H. Sellards, Professor of Geology, The University of Texas at Austin.

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ABSTRACT

The specimen, comprising a skull and jaws, is assigned to the suborder Microbrachomorpha and tentatively to the family Brachystelechidae on the basis of the structure of the temporal and occipital regions. It is unique among known microsaur in the possession of marginal teeth with long slender hollow bases and bifurcated crowns and the apparent absence of palatal dentition. *Carrolla craddocki*, new genus and species, from Lower Permian (Wolfcampian) Belle Plains Formation in Archer County, Texas, is described and figured.

If correctly assigned to the Brachystelechidae, *Carrolla* is the first record of the family in North America, but it was probably not equivalent ecologically to the roughly contemporaneous *Brachystelechus* of Europe. *Carrolla* is believed to have been a burrower in hard soils. Its diet may have comprised soft-bodied subterranean invertebrates, but the functional significance of its bicuspidate teeth is obscure. It is one of several unrelated microsaur which developed cryptic behavior under competitive pressures from surface-dwelling reptiles in an increasingly harsh Early Permian environment in North America.

ACKNOWLEDGEMENTS

Science is indebted to Mr. Craddock for placing this and numerous of his other finds in the public trust. We are indebted to Drs. Robert L. Carroll, Donald Baird, and Angela C. and Andrew Milner for their helpful counsel concerning microsaur. The doctors Milner first suggested that the new specimen was a microsaur and Dr. Carroll first noted its resemblance to *Brachystelechus*. Illustrations are by Mr. Michael W. Nickell. Doctors Carroll and John Bolt read early versions of the paper and their counsel is acknowledged with thanks.

Financial support to the senior author from the University of Texas Geology Foundation Owen-Coates Publication Fund is gratefully acknowledged.

INTRODUCTION

The specimen described in this paper consists of the skull and jaw, firmly united. It was collected from the surface in the vicinity of Tit Mountain in northwest Archer County, Texas, by Mr. Kenneth Craddock of Denton, Texas, who has over many years displayed an uncanny ability to ferret out minute specimens from the nodules that so often litter the surface of the Permian outcrops in north central Texas. Mr. Craddock generously donated the specimen to the Texas Memorial Museum on recognition of its considerable scientific significance.

A full review of the Microsauria by Carroll and Gaskill (1978) draws attention to the remarkable diversity of this order of extinct amphibians and obviates any need to review the group in this report. In addition, Schultze and Foreman (1981) have reviewed the tuditanomorph microsaurians and analyzed their relationships cladistically. The new specimen adds one more distinctive genus to the known array, for it is quite unlike any other described genus in many particulars.

Carroll and Gaskill recognized two suborders of Microsauria, Tuditanomorpha and Microbrachomorpha, the former comprising about twenty genera and the latter but four. The new specimen pertains to the Microbrachomorpha, but can only be assigned tentatively to the family Brachysteleschidae among the microbrachomorphs.

TABLE 1

Measurements of the skull and jaws of *Carrollia craddocki*, in millimeters. Measurements are of the specimen as preserved except the width which is an estimate made to correct for the distortion of the left side.

Midline length of skull, basioccipital to snout	15.0
Length of skull from top of foramen magnum to snout	13.0
Width of skull (corrected for distortion)	16.0
Maximum length of orbit	5.0
Maximum height of orbit	4.8
Width of foramen magnum	3.0
Distance between external borders of exoccipital condyles	4.8
Width of occipital plate	12.5
Length of pineal opening	0.7
Length of stapes (foot to head)	2.0
Length of lower jaw	12.0

SYSTEMATICS

ORDER MICROSAURIA

Suborder Microbrachomorpha

Family Brachystelechidae (?)

Carrolla n. gen.

Diagnosis.—Skull length and width approximately equal. Marginal teeth with long hollow bases and enamelled bicuspid crowns with cusps aligned antero-posteriorly. Probably no palatal dentition. Sphenethmoid element ossified. Stapes massive, perforate, and inserting distally into a recess on the medial side of the quadrate.

Carrolla craddocki n. sp.

Holotype.—Skull and attached mandibles. TMM No. 40031-54.

Locality.—Dissected flats about 100 feet above the base of the south side of a butte termed Tit Mountain, about three miles northeast of Dundee, in northwest Archer County, Texas.

Horizon.—Belle Plains Formation, Wolfcampian, Lower Permian.

Etymology.—The genus is named after Dr. Robert L. Carroll whose work with microsauria in collaboration with Pamela Gaskill has greatly facilitated this study. The species is named in honor of Mr. Kenneth Craddock.

Diagnosis.—As for genus. For measurements see Table 1.

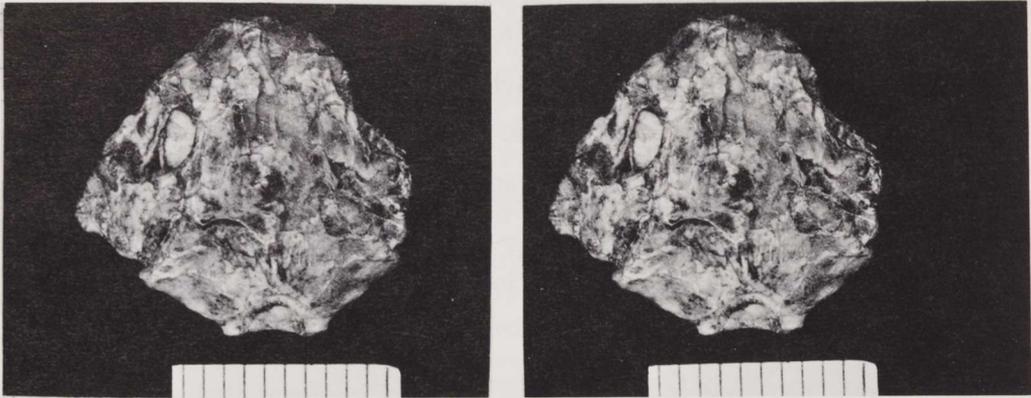
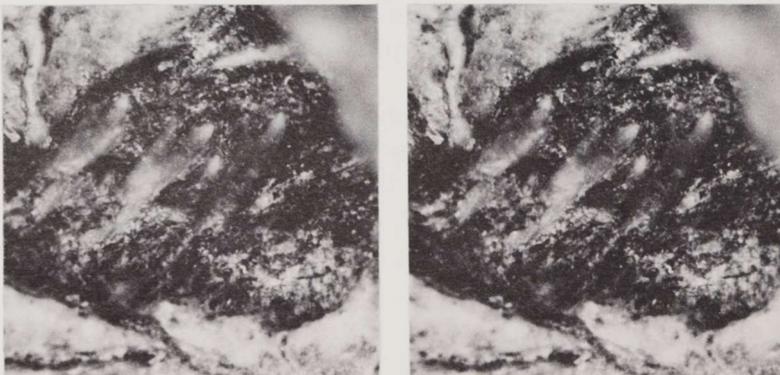
DESCRIPTION

Condition of the Specimen

The general condition of the specimen is shown in Fig. 1. The skull and lower jaws are tightly locked together by matrix. The skull has been flattened somewhat dorso-ventrally, but not to the extreme frequently seen in microsaur specimens. Crushing has skewed the skull to the right so that although the right side is present, it is not visible from above, whereas the left side is more broadly exposed than normal. The occipital plate has been somewhat flattened, which exaggerates the apparent length of the plate. The dorsal surfaces of the lower jaw are obscured, having been forced up underneath the edges of the upper jaw. Excepting a few lower teeth, the dentition is not well preserved.

The surface of the bone has a polished appearance, which suggests some abrasion or weathering. Some of the sutures are distinct, accentuated by a thin layer of red iron oxide between the bones. At places, notably in the palate and the area of the middle ear, separation and displacement of the elements occurred during fossilization. Some of the dermal roofing bones

Fig. 1. *Carrollia craddocki*, n. gen. and sp. TMM 40031-54. Stereograms of A) skull, dorsal view; B) skull, attached lower jaw and stapes, ventral view; C) lower teeth, lingual aspect. C is x 15.

**A****B****C**

have been damaged and are partly broken away, especially on the right side of the skull roof and in the temporal region. In many places where the bone has been lost, an accurate natural mold of the deep surface is preserved by the matrix. The articular portion of the right mandible is missing.

Remains of a few upper teeth are embedded in the matrix, but most of the teeth have been destroyed. Four lower teeth are exposed deep within the palatal area on the left side, appressed against the underside of the displaced palatal bones.

Dorsal and Lateral Skull Surfaces (Figs. 1A, 2A)

The dermal elements are very thick relative to the size of the skull and in places they are joined by strong sutures with blunt interdigitating tongues and grooves. The skull appears to have been massive, akinetic and capable of withstanding substantial stresses. Some sculpturing is evident on the frontals and on the jugal, beneath the orbit. Small foramina are present in the roofing bones at various places (Fig. 2A).

The gross features of the dermal skull roof are shown in the reconstruction (Fig. 2A) and photographs (Fig. 1A). An effort has been made in preparing the reconstructions to restore the original proportions.

Paired parietals form the posterior part of the skull platform and carry backward onto the sloping occiput, partly covering the unified occipital plate. A strong transverse ridge separates the dorsal platform and occipital surfaces of the parietals. Anterior to this ridge, in the forward half of the parietals, is a well developed pineal foramen. Latero-posteriorly each parietal forms an elongated lappet posterior to the postfrontal and postorbital bones (Fig. 2a, pa(?ta)). This lappet is in the area where a tabular might be expected and although no separation can be found, there is sufficient damage to this part of the specimen that the presence of a tabular cannot be ruled out.

The paired frontals form a broad, largely featureless plate. Laterally, each frontal extends into a narrow contact with the dorsal orbital margin, here separating the post- and prefrontals. The orbit is relatively very large, as is usual in small skulls. Within it lies a single, well preserved palpebral cup (Fig. 2A, ppc) and some fragments of bone which suggest the possible presence of sclerotic plates.

Interpretation of the rather small posterior elements of the skull, exclusive of the occipital area, is uncertain. The squamosal appears to have been relatively large lying largely postero-ventral to the postorbital and making broad contact with the parietal lappet. Its lateral and posterior contacts with the quadrate are, however, largely destroyed. An elongated jugal extends forward from the squamosal to form the lower rim of the orbit, beneath which it exhibits the only distinct sculpture pattern visible on the skull.

Ventral to the jugal and extending to the level of the posterior margin of the orbit is the tooth-bearing maxilla. It is a moderately deep bone which makes contact with the premaxilla at the level of the posterior margin of the external naris, below the septomaxilla.

The anterior margin of the orbit is formed by a moderately large prefrontal and a dorso-ventrally narrow lacrimal. The lacrimal passes forward to the external naris, but is excluded from this opening by the septomaxilla, a tiny cup-shaped bone which forms the posterior margin of the external naris. The ventral and anterior borders of the external naris are formed by a large, tooth-bearing premaxilla. The united premaxillae project forward above the tooth row anteriorly forming a slightly reflected muzzle. Posterior to the premaxillae, and forming the anterior dorsal surface of the skull are the paired nasal bones. Damage and some distortion have made their outlines somewhat uncertain, but the structure and relationships shown in Fig. 2A are probably not seriously in error. These bones are remarkably short and wide.

Oto-occipital and Basicranial Complex (Figs. 2, 3)

The oto-occipital and basicranial complex forms a single structure with the constituent elements indistinguishably fused. Included in this complex and forming much of it, as exposed, is the dermal parasphenoid bone. The occipital portion of the complex forms an "occipital plate" which incorporates the occipital elements and passes laterally into the otic elements, of which the long, posterior portion represents the opisthotic. As preserved, the "occipital plate" makes up about one-third of the total skull length, in dorsal aspect, but this is excessive, it having been exaggerated by crushing. Dorsally the plate is overlapped extensively by the parietal and it extends forward beneath this bone nearly to the level of the pineal foramen.

At the lower corners of the nearly equilateral, triangular foramen magnum lie strongly developed occipital condyles. As preserved, remnants of a thick "odontoid" process of the atlas fill the posterior notch in the basioccipital bone in the fashion characteristic of microsaur. Enough of the condyles can be seen, however, to show that they are joined by a straplike surface of the intervening basioccipital. Lateral to each condyle is a large jugular foramen and medio-ventral to this foramen is a pair of smaller openings. These presumably accommodated nerves IX and X, and XII, respectively. The otic elements of the complex are not recognizable as distinct ossifications, but their general positions are evident. Overlying the broad, lateral expanse of the parasphenoid is the opisthotic part of the periotic and, more anteriorly, what is presumably a prootic is visible. These elements contribute, perhaps with the parasphenoid, to formation of a very large fenestra ovalis into which the expanded foot-plate of the stapes appears to have fitted snugly.

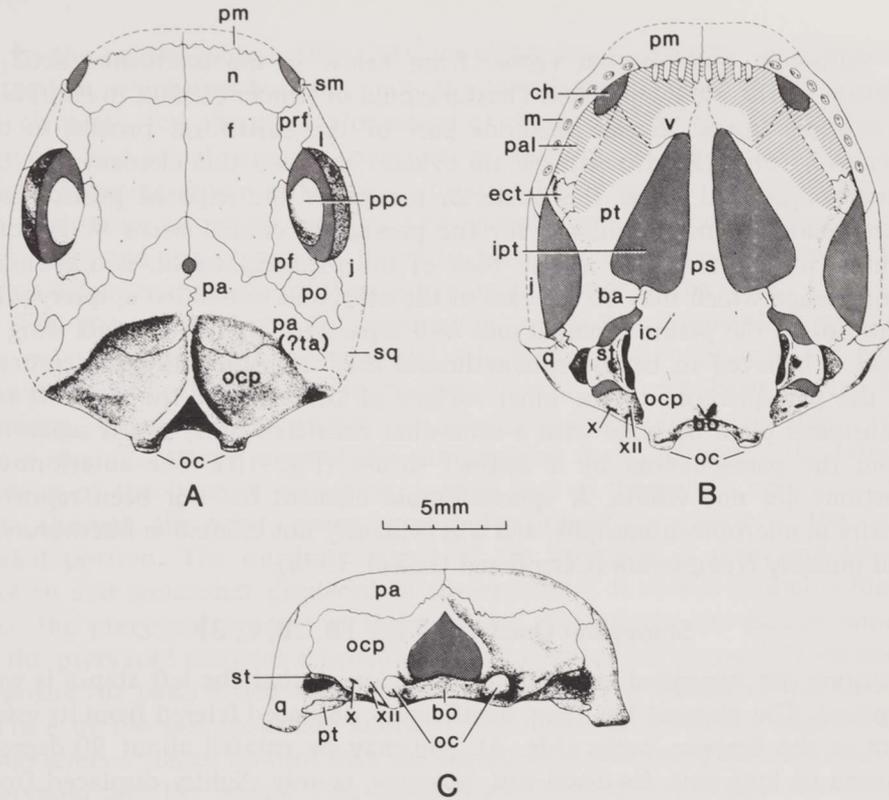


Fig. 2. *Carrolia craddocki*, n. gen. and sp. TMM 40031-54. Reconstruction of skull A) dorsal view; B) ventral view; C) posterior view. Location of some features in C is somewhat conjectural; the articular surfaces of the occipital condyles are not visible in the specimen. Crosshatched areas are obscured in the specimen.

The parasphenoid dominates the complex ventrally and coossification with the other elements makes precise demarcation of the elements impossible. The broad posterior plate of the parasphenoid passes anteriorly into a long cultriform process whose anterior end is concealed by the tightly appressed lower jaws. Near the anterior margin of the plate, to each side of the midline, is a small foramen for the internal carotid artery, a feature present in some but not all microsaur. Lateral to the foramen the parasphenoid forms the ventral surface of the broad basiptyergoid process. Dorsal to this extension and evidently solidly fused to it, the partially ossified basisphenoid contributes to the articular surface of the process. The basicranial articulation lies essentially in a horizontal plane and was a freely movable joint in life.

Although possibly not visible from below in the uncrushed skull, a portion of the pleurosphenoid [basisphenoid of Romer (1950), in *Pantylus*] is exposed dorsal to the posterior part of the cultriform process in the specimen (Fig. 1B). No sutures are evident between this element and the para-basisphenoid. Near the posterior margin of the exposed portion is a prominent foramen, probably for the passage of cranial nerve V. Anteroventral to the foramen, at the base of the pleurosphenoid, is a rounded prominence which may be the base of the otherwise unossified epipterygoid. Anterior to the pleurosphenoid and well separated from it, the left wing of what is believed to be the sphenethmoid rises from the cultriform process of the parasphenoid to the inner surface of the vault of the skull. It is a featureless plate of bone with a somewhat restricted base, and is separated from the parasphenoid by a distinct suture (Fig. 1B). The anteriormost portions are not visible. A sphenethmoid element has not been reported before in microbrachiomorphs, and was evidently not ossified in *Microbrachis* and possibly *Hyloplezion* (Carroll and Gaskill, 1978).

Stapes and Quadrate (Figs. 1B, 2B, C, 3)

Crushing has expanded the middle ear region so that the left stapes is well exposed. The element has been significantly displaced laterad from its insertion in the fenestra ovalis (Fig. 3), and may be rotated about 90 degrees around its long axis. Its distal end, however, is only slightly displaced from its lodgement in the quadrate. The stapes is a stout bone with a broadly expanded, somewhat rectangular footplate, a short, thick shaft and a rounded, slightly expanded distal end, which in life rested freely in a well-formed stapedia recess of the quadrate. As preserved, a large stapedia foramen is visible near the ventral margin.

The quadrate is a large bone with a strong ascending process. The pterygoid process is short and massive, and is joined sutured to the quadrate ramus of the pterygoid. Above it is the specialized triangular recess into which fitted the distal end of the stapes. The articular condyle of the quadrate is a simple anteroposteriorly rounded hinge that, as preserved, lies in the transverse plane of the skull. Its transverse diameter is about seven times its anteroposterior diameter (Fig. 1B).

Palate (Figs. 1B, 2B)

The paired bones of the palate are exposed on the left side of the skull. They are slightly broken and somewhat displaced. The lower jaw and some matrix, which cannot be removed, obscure the lateral edges of the pterygoid, palatine and vomer, but some additional details can be observed dorsally through the orbit. The parasphenoid is in natural position, but the other bones have been displaced upwards.

In the reconstruction (Fig. 2B), an effort has been made to eliminate distortion, which involved not only the lateral and dorsal displacement of the elements, but also some elongation of the occiput which has tended to shift the basicranial complex somewhat posteriorly. The arrangement of the palatal bones as shown in the reconstruction conforms for the most part to the customary microsauro pattern. The interpterygoidal vacuity, however, is very large and the pterygoids failed to meet anteriorly, so that the vomer forms the anterior border of the vacuity on either side of the skull.

The parasphenoid was described earlier and is the dominant element of the palatal complex. The pterygoid, which was not fused with the basicranium, has been removed from contact with the para-basisphenoid by crushing. As in other microsaur, the pterygoid lacks a transverse flange and has a smooth margin around the subtemporal fossa. Although the lateral portion of the bone is concealed, a small part of the palatal ramus can be seen through the orbit, giving some indication of the nature of the concealed portion. The quadrate ramus of the pterygoid is short and stout, broken and somewhat displaced in the specimen. It makes sutural contact with the pterygoid process of the quadrate. Posteriorly, the palatal ramus of the pterygoid contains a broadly vaulted longitudinal channel which ends opposite the basal articulation. A notch occurs in the margin of the palatal surface of the pterygoid and lateral to the notch the posterior edge of the bone sends a flange upward into the matrix that fills the space between the pterygoid and the stapes. This flange is confluent with the quadrate ramus of the pterygoid and likely formed the osseous antero-lateral wall of whatever middle ear chamber was present (a middle ear cavity may, in fact, have been absent, as in apodans and salamanders [Carroll, pers. comm.]).

A well developed ectopterygoid is present. It is quadrilateral in form and somewhat wider than long. It is displaced in the specimen to lie over part of the pterygoid. The postero-lateral edge is turned down and may have formed the anterior edge of the subtemporal fossa as the medial edge of the pterygoid is similarly deflected. Anteriorly, the ectopterygoid appears to have been inserted into a groove on the ventral surface of the palatine and, as seen from above, through the orbit, it appears to have lacked contact with the maxilla.

The palatine is partially hidden by the lower jaw. As exposed, it has a subtriangular outline, and is broken anteriorly. How it relates to the internal naris is uncertain as this structure is not visible in the specimen. The ventral surface of the palatine was partly covered by the ectopterygoid, as noted in the preceding paragraph.

Little can be said about the vomer other than that it was a plate-like bone which had a long contact with the anterior edge of the palatal ramus of the pterygoid. The preserved portion of the medial edge is curved dorsally, suggesting that it abutted against the anterior portion of the cultriform process of the parasphenoid, but this cannot be confirmed in the specimen.

Mandible (Figs. 1B, 3, 4A)

Although much of the lower jaw is preserved, it is not well exposed (Fig. 4A). It is about two-thirds as long as the skull. The symphysis is thick and the dentary must be deep to accommodate the long roots of the teeth. At least one splenial was present and like other bones in the skull and jaw it is remarkably thick for its size. The angular projects backward beneath the articular, but there is no retroarticular process. The submeckelian foramen is evidently surrounded by the angular. The prearticular is a triangular bone on the medial side of the jaw. Its superior edge is exceptionally elevated, so that in medial aspect its dorsal outline resembles that of the lateral edge of the adductor fossa in other microsaur. Anteriorly, however, the superior edge of the bone is seen to pass medial to the tooth row so there can be little doubt that it is the prearticular.

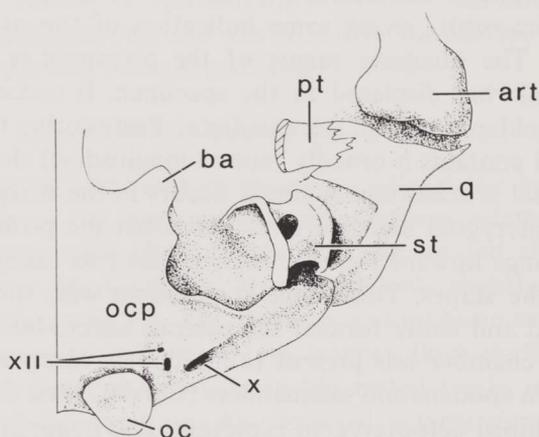


Fig. 3. *Carrollia craddocki*, n. gen. and sp. TMM 40031-54. Right postero-lateral part of skull, lower jaw and stapes as preserved, ventral view. Approximately x 6.

Dentition (Figs. 1C, 4A, B)

No dentition is present on the exposed elements of the palate. Comparable areas are consistently denticulate in other microsaur, excepting possibly *Goniorhynchus*. It is, of course, possible that teeth or a shagreen of denticles is present on the concealed portions of one or more of the palatal bones as in *Goniorhynchus*, but even in this unlikely event the absence of any sort of dentition on the major parts of the palatal bones is unique among microsaur. That some sort of shagreen existed in the roof of the mouth but was unattached to the bone is also possible, but we believe highly unlikely. Such a condition has been reported in *Crinodon limnophyes* by Carroll and Gaskill (1978), however.

The marginal dentition of *Carrolla* is also unique within this group of animals. It comprises closely spaced, slender teeth with enamelled bifurcated crowns (Fig. 4A, B). The dental formula is not determinable, but at least the following teeth are present: Pmx 4 + Max 6 or 7/Dent. >4. Of the upper teeth only a few damaged crowns are seen, but three teeth are completely exposed on the lingual surface of the left dentary, owing to loss of the splenial bone (Figs. 1C, 4A). The crown of a fourth tooth is also present. The hollow pulp cavities of some of the bases have been exposed accidentally during preparation. The teeth have long bases and are attached to the dentary in acrodont or possibly pleurodont fashion. The bases are cylindrical toward the bottom, but toward the crowns they become somewhat flattened transversely, thus producing a spatulate appearance.

The crowns of the teeth are distinguished from the bases by a subtle color difference which probably signals a change in density and the presence of enamel. The crown forms about one-fourth of the total height of the tooth (Fig. 4B). There is no evidence of pedicellate structure. The crowns are divided into anterior and posterior cusps, which vaguely resemble the forked tongue of a serpent. The posterior cusp is always smaller than the anterior one and is bent a little backward near the tip. There is some variation in the degree of forking, and the disparity in the size of the anterior and posterior cusps is greater in the upper teeth than in the mandibular teeth. Presumably the bases of the upper teeth are shorter than those of the lower teeth inasmuch as the dentigerous bones are narrower dorso-ventrally than the dentary.

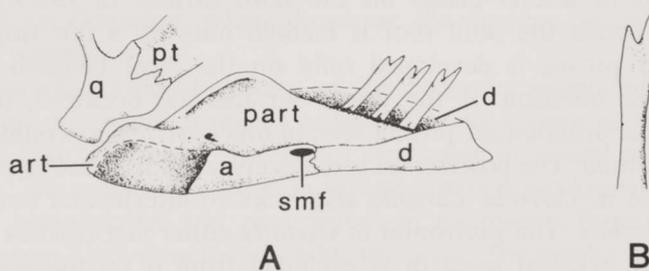


Fig. 4. *Carrolla craddocki*, n. gen. and sp. TMM 40031-54. A) Reconstruction of left mandibular ramus, lingual view. Approximately x 6. B) Composite drawing of the presumed lingual surface of a lower tooth. The larger cusp is anterior. Greatly enlarged.

RELATIONSHIPS

Carrolla craddocki is assigned to the Microsauria on the basis of its temporal region, which lacks supratemporal and intertemporal bones, and probably also the tabular (whose presence or absence does not affect the assignment), its basioccipital-exoccipital complex, which evidently forms a broad cranio-cervical articular surface of the type described as "strap-shaped" by Carroll and Gaskill (1978), and the absence of an otic notch.

Assignment to the Microbrachomorpha is based upon the presence of a broad parietal-postorbital contact, which would exclude any connection between the tabular (if present) and the postfrontal. The absence of a separate postparietal is also suggestive, in view of the absence of this bone in *Brachystelechus* and its small size in the other genera of the suborder. In many particulars, however, including the presence of an ossified sphenethmoid, *Carrolla* differs from the four other known members of the Microbrachomorpha, suggesting, as Carroll and Gaskill (1978) noted, that this suborder may not, in fact, be a natural group (*i.e.*, not monophyletic).

Carrolla is more similar to *Brachystelechus* than to other microsaurians in the general proportions of the skull and the configuration of the postorbital region, in particular, the shape and relationships to adjacent elements of the parietal lappet and the absence of a postparietal. It must be stressed, however, that the skull of *Brachystelechus* is very incomplete. The upper and lower jaws, and the dentition, the palate and some of the marginal elements of the skull are missing, and the braincase is unknown. Thus, although the bifurcated marginal teeth and very large interpterygoidal vacuities of *Carrolla* are not known elsewhere among microsaurians, the possibility exists that such may occur in *Brachystelechus*.

Several clear-cut differences between the two genera do exist. Massive pitting occurs in several places on the skull surface of *Brachystelechus*, whereas in *Carrolla* the skull roof is marked only by a few tiny pore-like foramina and pitting is developed only on the jugal beneath the orbit. Although some abrasion of the dorsal surfaces has occurred, it does not appear that the pronounced pitting seen in *Brachystelechus* could have been present in *Carrolla*. The postfrontal is relatively small in *Brachystelechus* and relatively large in *Carrolla*. *Carrolla* also lacks an interfrontal bone, present in *Brachystelechus*. The prefrontal in *Carrolla* either just reaches the posterior tip of the external nares or is excluded from it by the septomaxilla, whereas in *Brachystelechus* it enters broadly into the narial border.

Like other microsaurians *Carrolla* exhibits a large suite of characters, one or another of which occurs in other genera, but which is not duplicated *in extenso* in any of them. Two cladistic analyses published by Schultze and Foreman (1981) show this general pattern as well. One analysis is of the families of Tuditanomorpha. In it, the common familial features are pre-

dominantly plesiomorphs, several autapomorphies occur in the familial lineages, and only four clusters of two or more synapomorphies are defined, these being common to the families Gymnarthridae and Goniiorhynchidae. A total of 23 characters was used in this analysis. Among the Gymnarthridae, in the second analysis which employs a larger array of characters, synapomorphies unite only the four species of *Euryodus*. The distribution of characters emphasizes the great variety of microsaur stressed by Carroll and Gaskill (1978) and also, of course, renders many of them useless for taxonomic purposes, given the current state of knowledge. Some examples in *Carrolla* are as follows:

1. The ectopterygoid in *Carrolla* does not appear to make contact with the maxilla as it does in most microsaur. This condition, however, is also found in *Hyloplecion*.

2. Limited bilateral contact of the frontal with the dorsal border of the orbit occurs in *Carrolla*, *Saxonerpeton* and *Hapsidopareion*. Limited contact on one side but not on both, as figured by Carroll and Gaskill (1978), occurs in known individuals belonging to *Hyloplecion* and *Odontopteron* and broad contact is present in *Llistrophus* and *Brachystelechus*. In most microsaur, however, no frontal-orbital contact occurs.

3. The septomaxilla is moderately small and forms the posterior rim of the external naris in *Carrolla*. In most microsaur the bone is relatively larger and is incorporated into the narial opening, but *Carrolla* and *Crinodon* are similar. The condition in *Brachystelechus* is unknown.

4. The pineal foramen is large and lies in the anterior half of the parietal in *Carrolla*. The foramen is absent in some microsaur, small in others, and large in a few. Its position relative to the anterior margin of the parietal varies. Its size and position in *Carrolla* is comparable to that in *Hyloplecion*, *Brachystelechus* and *Hapsidopareion*. The size of the foramen in *Carrolla* is comparable to *Crinodon*, where, however, the opening lies in the posterior half of the parietal.

5. A dorsally directed process of the posterior margin of the palatine ramus of the pterygoid forms an anterior dermal margin of the middle ear in *Carrolla* and *Microbates*, but is not developed in several other genera of microsaur. The precise condition in several genera is not known.

6. The basioccipital and exoccipitals in microsaur form a continuous articular "strap-like" structure met by the atlas. The precise structure varies widely among the genera. The general structure of *Carrolla* is similar to that found in *Hapsidopareion* and *Rhynchonkos* (*Goniiorhynchus* in Carroll and Gaskill, 1978, *Rhynchonkos*, Schultze and Foreman, 1981) in which the exoccipitals form a strong "double" condyle, but with the basioccipital still forming a part of the articular surface. This appears to be a derived condition among the microsaur.

7. The stapes, both in form and relative size, varies remarkably among the microsaur. A large, oval footplate and a slender stem that projects laterally, or somewhat ventrally from it, represent the most common structure. The stem may or may not be perforate. In some genera, such as *Pantylus* there are well developed dorsal and ventral processes. An accessory vertical structure is found in both *Pantylus* and *Rhynchonkos*. The footplate in some genera is angular and in *Pelodosotis* complexly irregular. The stapes of *Carrolla* does not fit well into any of the general patterns. The subrectangular foot is rather like that of *Microbrachis*, but the more lateral portions are thick and the stout shaft has a large stapedia foramen, whereas in *Microbrachis* the stem is slender and the foramen is very small. This element, as much as any, indicates the immense variation within the order and the difficulties of systematic assessments.

HABITS

That *Carrolla* was an ecological "equivalent" to *Brachystelechus* from roughly contemporaneous deposits in Europe seems unlikely. Carroll and Gaskill seem ambivalent about the habitat of *Brachystelechus*, stating that it, "...may have been equally at home in the water as on the bank." (Carroll and Gaskill, 1978:201). Familial relationship in this instance is no bar to widely different habits, because the respective localities were on opposite sides of a massive land barrier, were at least 5,000 kilometers apart, and the difference in geological age of the deposits may be several million years, correlations between the Rotliegende and the Wichita Group being somewhat imprecise.

Absence of lateral line canals in *Carrolla*, while not conclusive, suggests terrestrial habits. The massive construction of the little skull, the thick and broad palpebral bones, the broad occipital surface (for attachment of powerful neck muscles) and the inferred blunt and protruding rostrum may be evidence for burrowing habits in *Carrolla*. Burrowing habits have been imputed to *Ostodolepis* and *Pelodosotis* because of their wedge-shaped rostra, among other things. Gans (1974) illustrates a variety of head shapes encountered in amphisbaenians which not only resemble *Ostodolepis*, but also come close to the profile inferred for *Carrolla*. The widely dispersed "nutrient" foramina in the dermal skull roof of *Carrolla* may be related to a thick integument that might also be expected in a burrower (Gans, 1974). The Lower Permian redbeds in northcentral Texas contain buried soil horizons and remnants of ancient duricrust zones which could have presented difficulties to such small burrowing vertebrates as *Carrolla*. Perhaps in these situations the exceptionally massive stapes with its well developed quadrate articulation added to the strength of the head as a unit. It should, coincidentally, have functioned more efficiently as a hearing mechanism by way of bone conduction in a subterranean environment than in the air.

The very limited fossil record of microsaur can be interpreted as reflecting an evolutionary tendency within some groups to move from a predominantly aquatic, to a more terrestrial, reptilomorph, and burrowing anguiform habitus. (The Gymnarthridae, on the other hand, are believed to have become more aquatic during their evolutionary history, according to Carroll and Gaskill, 1978). Selection for increasingly cryptic behavior and, in the case of the Gymnarthridae, more aquatic habits, might have resulted from competition with surface-living reptiles toward the end of micro-saur existence.

The unique dentition of *Carrolla* seems suitable only for tender food, probably some soft-bodied subterranean invertebrates. The anteroposteriorly bicuspid teeth double the number of effective tooth crowns in the short jaws. Bolt (pers. comm.) has pointed out that under certain conditions occlusion of these crowns should produce an efficient shearing action, but nothing is known about the actual pattern of occlusion in the present instance. Bicuspid teeth are present in some Pennsylvanian and Permian labyrinthodonts, but as in lissamphibians, the cusps in these animals are arranged normal to the long axis of the tooth row (Bolt, 1967, 1977, 1979). Larsen and Guthrie (1975) observed that in the existing tiger salamander (*Ambystoma tigrinum*) the teeth pierce prey only to the level of the largely horizontal lingual cusps. This prevents the prey from being too securely impaled and permits the clean release of the food for transfer toward the throat. "Thus the teeth, although part of a kinetic-inertial feeding system . . . exert static pressures and function largely to retain rather than to maim" (Larsen & Guthrie, 1975:146). The cusps in *Carrolla*, however, are relatively larger and less divergent than in the salamander, so Larsen and Guthrie's explanation seems unlikely for the micro-saur.

The bicuspid teeth in *Amphibamus grandiceps* from Mazon Creek were interpreted as a juvenile dissorophid character by Bolt (1979). The possibility that *Carrolla* represents a larval phase of some other micro-saur is diminished, however, if it was a terrestrial form. In any event, if microsaur had a complex life cycle, as is postulated for dissorophid labyrinthodonts by Bolt (1977), or if the larval and adult stages were as morphologically disparate as they are in lissamphibians, it is doubtful that the adult form could be identified from a larval specimen.

Carroll and Currie (1975) have pointed out a number of resemblances between the skulls of microsaur, in particular *Goniorhynchus*, and the living apodans. In *Carrolla*, absence of postparietals, if confirmed, and fusion of the otico-occipital components into an os basale are reminiscent of apodans, which also share with *Carrolla* a hypertrophy of the cranial roofing bones and a posterior location of the cranio-cervical joint relative to the quadrate. The strong articulation between stapes and quadrate is a further similarity to most apodans.

On the other hand, the bones of the skull of *Carrolla* display interrelationships and details characteristic of microsaur and other Paleozoic amphibians, there being no obvious fusion of elements in the cheek region and no evidence of the apodan specialization of the lacrimal. Pedicellate teeth, present in all apodans according to Carroll and Currie, are lacking in *Carrolla*. Thus, as with other microsaur, *Carrolla* exhibits some close parallels to the Apoda, but until more conclusive evidence is obtained to support a close microsaur-apodan relationship, *e.g.*, an apodan fossil record, the resemblances noted above may be interpreted conservatively as parallel developments between animals with somewhat similar habits.

GEOGRAPHIC DISTRIBUTION

To judge from what is clearly a fragmentary fossil record of microsaur, tuditanomorphs were more diverse than microbrachomorphs which until now have comprised only four monotypic families. Of these four, the Odonterpetontidae and, questionably, the Hyloplesiontidae have been reported from North America. *Carrolla* represents a third microbrachomorph in North America and, if correctly assigned to the Brachystelechidae, it is the first North American record of that family.

The geographic distribution of microsaur is spotty (Carroll and Gaskill, 1978), conforming to the Laurasian Permo-Carboniferous distribution of coal-swamp and redbeds vertebrates in general (Panchen, 1977). Milner and Panchen (1973) and Panchen (1977) argue convincingly that distribution of Permo-Carboniferous tetrapods was strongly influenced by upland topography attending the Appalachian and Hercynian orogenies. Terrestrial animals were evidently better able to disperse between the European area southeast of the barrier and the American side on the northwest than the aquatic fauna which was apparently restricted by the barrier.

Although the vagaries of discovery are ever present (Panchen, 1973), it is interesting that all microsaur finds are within about three degrees of the Westphalian to Lower Permian paleoequators (Scotese, Bambach, *et al.*, 1979). If the known distribution of microsaur on both sides of the highland "barrier" bears any resemblance to their actual ranges, it is arguable that this is as much a reflection, initially, of climatic zonation, because early occurrences lie well within the late Carboniferous tropical rainy zone predicted by Ziegler, Scotese, *et al.* (1979). It is well to bear in mind that development of the Appalachian and Hercynian orogenies was not a sudden event.

Such North American Permian microsaur as *Carrolla*, *Pantylus*, *Microroter*, *Ostodolepis*, etc., like many other redbeds tetrapods, may be viewed as specialized survivors adapted to the harsher environments that succeeded Late Carboniferous equability in the tropics (Ziegler, Bambach, *et al.*, 1981).

CONCLUSION

The small microsaur skull described in this paper reveals many structural details. Although somewhat distorted and damaged, it is in general among the best preserved examples of this group. The small size of most microsaurians and the diversity of known forms suggests that many new taxa remain to be discovered. As it now stands, *Carrollia* adds one more distinctive genus to this confusing group. Perhaps, as more representatives are reported, consistent suits of characters will be found to unite the genera into readily defined families and higher taxonomic units. The work of Romer (1950), Carroll and Gaskill (1978), and the recent analysis by Schultze and Foreman (1981), have aided greatly in bringing order in the form of a functional classification. Nevertheless, the full diversity of the order Microsauria and its relationships to other orders of amphibians remains largely obscure.

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ABBREVIATIONS

a	angular
art	articular
ba	basicranial articulation
bo	basioccipital area
ch	choana
d	dentary
ect	ectopterygoid
f	frontal
ic	foramen for internal carotid artery
ipt	interpterygoid vacuity
j	jugal
l	lacrimal
m	maxilla
n	nasal
oc	occipital condyle (exoccipital)
ocp	oto-occipital-parasphenoid complex
pa	parietal
pa(?ta)	parietal lappet, possibly including tabular
pal	palatine
part	prearticular
ps	parasphenoid
pm	premaxilla
po	postorbital
pf	postfrontal
prf	prefrontal
ppc	palpebral bone
pt	pterygoid
q	quadrate
sm	septomaxilla
smf	submeckelian foramen
sp	splénial
sq	squamosal
st	stapes
v	vomer
x	foramen for 10th cranial nerve (jugular foramen)
xii	foramina for xii (?xi) cranial nerve

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