CHENOPROSOPUS LEWISI, A NEW COCHLEOSAURID AMPHIBIAN (AMPHIBIA: TEMNOSPONDYLI) FROM THE PERMO-CARBONIFEROUS OF NORTH-CENTRAL TEXAS

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ABSTRACT

A unique specimen from the Permo-Carboniferous of north-central Texas represents a new species of cochleosaurid temnospondyl, *Chenoprosopus lewisi,* and the first occurrence of the genus outside the Lower Permian of New Mexico. The new material consists of a virtually complete skull with attached mandible and associated postcranial remains, including partial pectoral and pelvic girdles, femora, and a few vertebrae. Although the skull is only half the size of the smallest individual of the genoholotypic species *C. milleri,* the degree of ossification and development of dermal sculpture indicate an adult form. The genus is differentiated from other cochleosaurids by its more narrow and acuminate snout, little to no septomaxilla-lacrimal contact, a jugal-lacrimal contact that is equal to or shorter than the jugal-prefrontal contact, and a choana with a round anteromedial margin. Three derived characters unite the family Cochleosauridae: an elaborate jugal-pterygoid suture that excludes the maxilla and ectopterygoid from the subtemporal fossa, vomers that are elongated anterior to choanae, and choanae that are elongate and wide anteriorly. Despite similarities between *Chenoprosopus* and *Edops,* the conventional assignment of cochleosaurids to the Edopoidea is supported by only one derived character, an elongate premaxilla that borders a small, inset external naris. Archegosaurid temnospondyls resemble cochleosaurids in the possession of elongate premaxillae and vomers but lack small, posteriorly positioned external nares. If cochleosaurids and archegosaurids prove to be closely related, several characters regarded presently as derived for eryopoid-grade temnospondyls were developed independently from a cochleosaurid stock.

INTRODUCTION

The higher level taxonomy of the large and complex amphibian order Temnospondyli bears a strong historical influence of fossils from the Lower Permian of north-central Texas. More than half of the commonly recognized temnospondyl superfamilies (Trimerorhachoidea, Edopoidea, Dissorophoidea, and Eryopoidea), as well as many families within these groups, derive from Texas specimens. Cochleosaurids, however, have not been reported from this region despite their occurrence in the Lower Permian of New Mexico. A new species of the cochleosaurid *Chenoprosopus* is described here on the basis of a unique specimen discovered recently in Texas.

Within the Lower Permian of north-central Texas, the majority of tetrapod material has come from four "redbed" formations—the Archer City, Nocona, Petrolia, and Arroyo—that range in age from middle Wolfcampian (Asselian) to middle Leonardian (Artinskian). The new specimen, however, was found in the Markley Formation, a coal-bearing, terrigenous clastic unit that straddles the Virgilian–Wolfcampian (Carboniferous–Permian) boundary (DiMichele et al., 1991). Whereas vertebrate remains collected previously from this interval are few and fragmentary (Romer, 1935; Hook, 1989), the new specimen includes a virtually complete skull and several postcranial elements.

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The genus *Chenoprosopus* was established by Mehl (1913) on the basis of a partial skull collected near Arroyo de Agua, New Mexico, by Paul C. Miller. A second partial skull, also collected by Miller from the same deposit, was described briefly by Williston (1918). Although these specimens indicated an alligator-like skull of general temnospondyl design, the cochleosaurid affinities of *Chenoprosopus milleri* became clear only after two more-complete skulls were discovered in the Arroyo de Agua area (Langston, 1953). These four specimens are of intermediate size (approximate skull lengths range from 190 to 300 mm) and are from Lower Permian rocks that are said to Wolfcampian in age. Though well ossified, the new Texas specimen is only about half the size of the smallest skull from New Mexico.

Abbreviations used for collection repositories are: AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; UCMP, University of California Museum of Paleontology, Berkeley; and USNM, National Museum of Natural History, Washington, D.C. Anatomical abbreviations used in the figures: a, angular; art, articular; c, clavicle; ct, cultriform process; d, dentary; dp, dermal plates; eo, exoccipital; f, frontal; fe, femur; i, interclavicle; ic, intercentrum; il, ilium; it, intertemporal; j, jugal; l, lacrimal; m, maxilla; m.f., Meckelian fenestra; n, nasal; na, neural arch; op, opisthotic; p, parietal; pal, palatine; pa.f., para-articular foramen; pf, postfrontal; pm, premaxilla; po, postorbital; pp, postparietal; pra, prearticular; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sm, septomaxilla; sp, splenial; spp, postsplenial; sq, squamosal; st, supratemporal; t, tabular; v, vomer.

SYSTEMATIC PALEONTOLOGY

Class Amphibia
Order Temnospondyli
Superfamily Edopoidea
Family Cochleosauridae Broili *in* Zittel, 1923

Revised Diagnosis.—Primitive temnospondyl amphibians characterized by elongate antorbital region that consists mainly of elongate nasals, premaxillae, and vomers and that accommodates anterior palatal fossae and elongate, anteriorly widened choanae; no lateral lines; four-bone circumorbital series consisting of jugal, postorbital, postfrontal, and prefrontal; septomaxilla sculptured and included in skull roof; prefrontal triangular and elongate; intertemporal present; modest tabular horns; no squamosal contribution to supratympanic shelf; modest supratympanic flange; jugal-pterygoid contact excludes ectopterygoid and maxilla from subtemporal fossa; pterygoids contact cultriform process but do not meet anteriorly; premaxilla bears palatal buttress anteromedially inside marginal tooth row; pterygoid flange downturned ventrally and embays anteromedial part of subtemporal fossa; single elongate Meckelian fenestra; intercentra thin walled; interclavicle rhomboidal, reduced slightly, not elongated; iliac blade compressed laterally with little anteroposterior expansion and rudimentary posterodorsal process.

Chenoprosopus Mehl, 1913

Type Species.—*Chenoprosopus milleri* Mehl, 1913.
Revised Diagnosis.—Cochleosaurid temnospondyl distinguished from *Cochleosaurus* by more narrow and acuminate snout; pineal foramen closed in large or

adult individuals; no postparietal lappets; little to no septomaxilla-lacrimal contact; shorter jugal-lacrimal contact; maxillary teeth set closely, elongate, and slightly recurved; anteromedial margin of choana rounded; basal articulation sutured in large individuals; denticulated ridge directed posterlaterally from vomerine tusk site; and splenial contributes to mandibular symphysis.

Chenoprosopus lewisi, new species

Holotype.—USNM 437646, a nearly complete skull and associated postcranial elements. Collected in 1989 by Kenneth W. Craddock.
Type Locality, Stratigraphic Interval, and Age.—E. Robbins Survey, abstract 389, approximately 2 km west of Shannon, Clay County, Texas; UTM 14SNN66740346, Antelope 7.5′ topographic quadrangle. Approximately 2.5 m below the base of informal sandstone member 13, Markley Formation, Bowie Group, of Hentz and Brown (1987); Pueblo Formation, Wichita Group, of Romer (1974). Virgilian-Wolfcampian boundary interval, Permo-Carboniferous.
Diagnosis.—Chenoprosopine cochleosaurid differentiated from *Chenoprosopus milleri* by appreciable contacts between maxilla and nasal and between postorbital and supratemporal, and by reduced vomerine tusks located at anteromedial margin of choana.

Etymology.—In honor of Arnold D. Lewis. Since his first trip to north-central Texas with the late Alfred S. Romer in 1954, Arnie's extraordinary collecting talents and preparation skills have enhanced greatly our knowledge of late Paleozoic vertebrates.

DESCRIPTION

Skull

The skull shows little post-mortem disturbance and is nearly complete (Fig. 1, 2). In dorsal view, its outline is distinctly triangular, and the jaw articulation lies posterior to the level of the occiput. The otic notch is deep, open fully posteriorly, and bordered by the tabular, supratemporal, and squamosal. In the snout region, a median depression is flanked by longitudinal ridges that extend from the anteromedial margin of the orbits to the anterolateral portion of each nasal. The orbits are fairly large, circular, positioned midway along the skull length, and widely spaced. The slightly elongate external nares are situated close to the skull margin, where they open dorsolaterally. A small pineal foramen is present. In lateral view, a low profile is imparted by a gently rounded junction between the skull table and cheek region.

Despite the comparatively small size of the skull, the degree of ossification and the development of dermal sculpture indicate that the specimen may be regarded as adult. A sculpture of subcircular pits, considered as a mature condition in eryopoids (Boy, 1988, 1989, 1990) and other temnospondyls, predominates on the skull table and orbital margins. Areas of ridge-and-groove ornament indicative of intensive growth zones (Bystrow, 1935) are developed chiefly on the snout and cheeks. As in *Chenoprosopus milleri, Cochleosaurus,* and *Macrerpeton* [*Mytaras*], dermal sculpture is subdued within the antorbital depression. No lateral lines are developed.

Although the tip of the snout is missing, the intact and attached mandibular symphysis indicates that only a minor portion of each premaxilla has been lost. A small triangular piece of bone preserved on the left side of the longitudinal
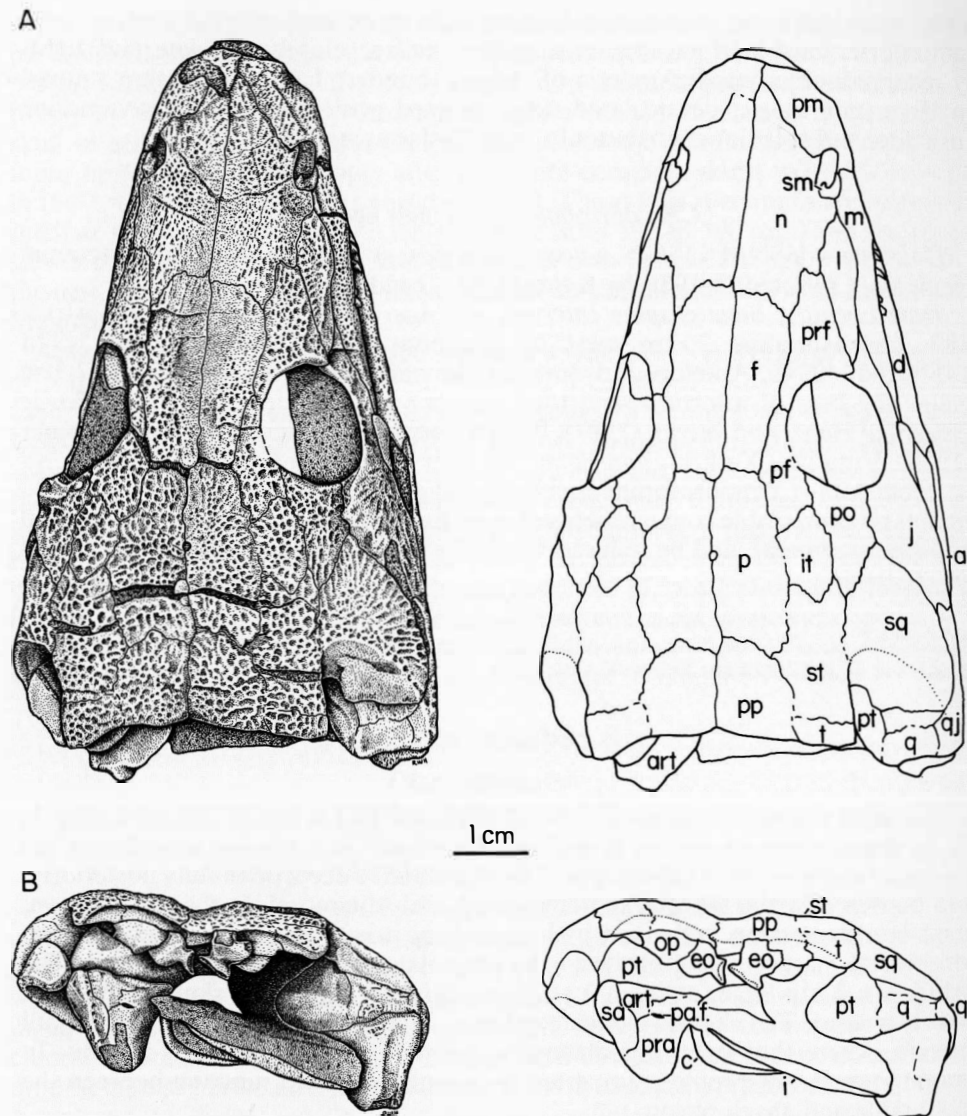
Fig. 1.—*Chenoprosopus lewisi,* holotype, USNM 437646. A, dorsal view. B, occipital view.

midline appears to be part of the left premaxilla rather than a discrete internasal ossification; by either interpretation, the median configuration of the premaxillae and nasals is asymmetrical. The premaxilla-nasal suture extends posterolaterally from the dorsal midline to the external naris, where the premaxilla forms the anterior margin of the narial opening.

The bases of six successive labyrinthine teeth are preserved on the left pre-maxilla. They are of uniform size, with a basal diameter approximately one-third
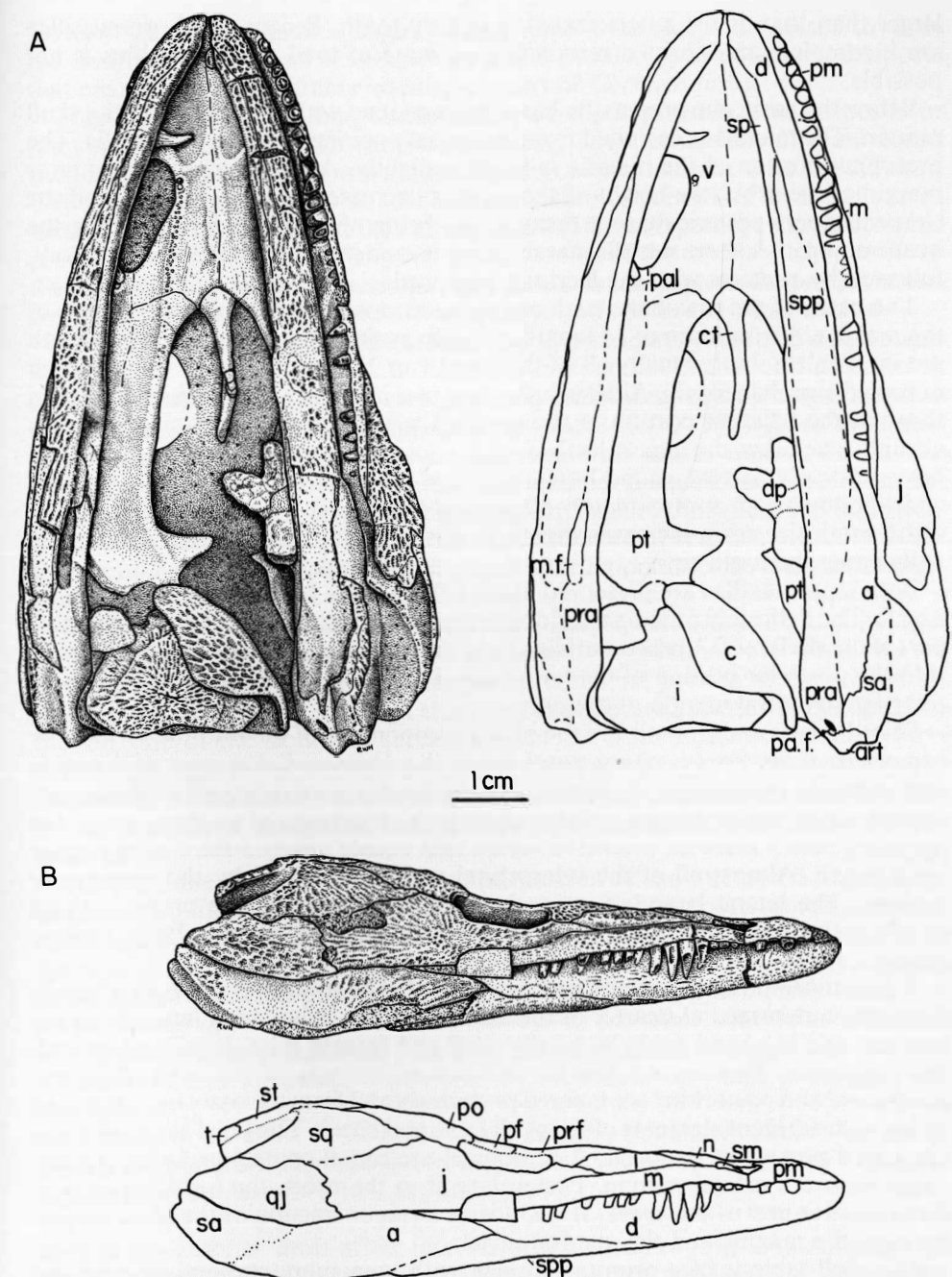
Fig. 2.—*Chenoprosopus lewisi,* holotype, USNM 437646. A, ventral view. B, right lateral view; angular-surangular suture is based on left mandibular ramus.

larger than that of the anteriormost maxillary tooth. Because both premaxillae are incomplete anteriorly, a reasonable estimate of total tooth positions is not possible.

Below the naris, the premaxilla has a short contact with the maxilla at the skull margin. The maxilla is excluded from the narial opening by the septomaxilla. The preorbital portion of the maxilla is swollen slightly. At the level of the anterior margin of the orbit, the height of the maxilla decreases abruptly by half, and the element tapers posteriorly to a termination below the jugal before reaching the quadratojugal. A short maxilla-nasal suture is evident on both sides of the skull, followed by contacts with the lacrimal and jugal.

The bases of the maxillary teeth are apposed closely to the external margin of the maxilla. A minimum of 34 maxillary tooth positions is estimated. Many teeth are incomplete, but virtually all of the first 11 or 12 alveoli appear to have been occupied simultaneously. Although the first two maxillary teeth are smaller than those of the adjacent portion of the premaxillary dentition, tooth size increases abruptly such that the largest teeth occupy sites three through seven. These teeth have relatively narrow, round bases, recurved distal halves, and sharply pointed ends. Following an approximately 50 percent decrease in height at about position eight, tooth size again increases slightly at position nine before diminishing gradually along the tooth row.

Both septomaxillae are preserved essentially in place between the maxillae and nasals. The delicately pitted posterior section of this small element is a very minor part of the skull roof. A process arising from the medial side extends anterolaterally into the posterior portion of the narial opening, and a larger lateral flange forms the posteroventral margin of the naris.

Paired nasals and frontals are the major components of the midline series. The expansive, transversely convex nasal forms the dorsomedial margin of the naris and contacts the maxilla, lacrimal, and prefrontal posterolaterally. The nasal-frontal suture trends anteromedially towards the longitudinal midline, where the opposing nasals share an extensive suture that equals nearly a third of the entire skull length. Almost all of the interorbital region is formed by the rectangular frontals. The lateral boundary of each is joined equally by the prefrontal and postfrontal. Posteriorly, the frontals overlap the parietals along a fairly straight suture.

A circumorbital series of four bones is present. The triangular prefrontal, which forms the anteromedial quarter of the orbital margin, is bounded laterally by the lacrimal and jugal and medially by the nasal and frontal; it has brief contact with the postfrontal between the frontal and the medial rim of the orbit. Both the postfrontal and postorbital are tapered posteriorly and form a grossly interdigitated union with adjacent elements of the skull table and cheek. The jugal alone encloses the lateral portion of the orbit. A brief jugal-prefrontal contact excludes the lacrimal from the orbital margin. Posterolateral to the orbit, the jugal expands to form a major part of the cheek; it also forms a minor fraction of the skull margin between the maxilla and the quadratojugal.

The skull table is of a primitive design with long supratemporal-postparietal contacts and large intertemporals. Most of the sutures are sinuous and a few are difficult to trace. The pineal foramen is small and flush with the skull surface. From its anterior junction with the frontal, the parietal is contacted laterally by the postfrontal, intertemporal, and supratemporal, and posteriorly by the post-

parietal. The postparietal is slightly longer than wide and is depressed towards the midline. There is no development of the pedal-shaped postparietal lappets that characterize comparably sized specimens of Cochleosaurus.

Together with the adjoining tabulars, the paired postparietals form the posterior margin of the skull table. In occipital view (Fig. 1B), a posteriorly directed dorsal shelf is developed on the postparietals and diminishes laterally onto the tabulars. Below and perpendicular to this shelf, the postparietal consists of an unsculptured vertical flange that contacted the exoccipital medially and perhaps the paroccipital process laterally. A similar flange on the underside of the tabular clearly received the paroccipital process. Though the right tabular is incomplete, the posterolateral corner of the left tabular is bluntly acuminate and moderately downturned.

All of the lateral margin of the tabular and approximately half of the supratemporal border the otic notch. A dorsal shelf comparable to that of the occiput is formed by these elements and overhangs an unsculptured vertical flange of modest size; in descriptions of the dissorophoid otic notch (Bolt, 1974), these two structures have been termed the supratympanic shelf and supratympanic flange. The courses of supratemporal-tabular and supratemporal-squamosal sutures on the flange cannot be determined with certainty. In front of the notch, the supratemporal joins the squamosal. Medial to a brief supratemporal-postorbital contact, the suture between the supratemporal and intertemporal forms a posteriorly directed V.

The posterior cheek region consists of the jugal, squamosal, and quadratojugal. As the largest of these elements, the squamosal adjoins the postorbital and supratemporal medially and comprises the anterolateral portion of the otic notch, which is not sculptured; although this thin, unsculptured portion is disrupted on the left side of the skull and incomplete on the right side, it appears to have overlapped both the pterygoid and quadrate within the otic notch. Laterally, the squamosal is bounded by the jugal and quadratojugal. In lateral view (Fig. 2B), the convex lateral margin of the quadratojugal extends slightly below the jaw articulation.

The quadrate forms the posteroventral portion of the otic notch and suspensorium. A rudimentary dorsal process is preserved on the posteromedial portion of the right quadrate; a similar boss is present in a more-damaged condition on the right quadrate of UCMP 33439. Although this projection may be homologous to the dorsal quadrate process of dissorophoids (Bolt and Lombard, 1985), imperfect preservation precludes anything beyond topologic comparisons. Medial to this process, the quadrate is joined by the pterygoid.

Description of the palate is hindered by the mandible, which is attached and obscures most of the marginal elements. I have employed a variety of preparation techniques in an effort to delimit palatal sutures, but most contacts cannot be traced. In general structure, however, the palate is very similar to that of Chenoprosopus milleri as described by Langston (1953).

The most striking palatal feature is an elongate choana that nearly reaches the level of the anterior limit of the interpterygoid vacuities (Fig. 2A). Although the lateral margin of the choana is not exposed, the opening lacks the anterior expansion and triangular shape that characterizes Cochleosaurus. Anterior palatal fossae occur on the vomers as modest concavities separated by a thin longitudinal septum; the fossae may be formed in part by the premaxillae, but no vomer-premaxilla suture can be determined. The length of each interpterygoid vacuity

is approximately three times greater than its width, or equal to about a third of the skull length. From their anterior closure against the cultriform process, the vacuities widen and become broadly rounded near the level of the basal process.

A small, poorly preserved vomerine tusk and replacement pit occupy a small platform near the anteromedial margin of the choana. In contrast to *C. milleri*, in which the vomerine tusks are larger and placed in a more lateral position, the condition of *C. lewisi* resembles that of *Cochleosaurus*. A large, detached tooth at the anterior end of the right choana is interpreted as a displaced dentary tooth. At the posterolateral margin of the choana, a second palatal tusk is present on the palatine and is accompanied by a replacement pit; the basal diameter of this tusk is slightly greater than that of the largest maxillary tooth. A probable ectopterygoid tusk cannot be observed because of the obstructing mandible. As in *C. milleri*, a denticulated ridge extends posterolaterally from the anteromedial margin of the choana to the anterior third of the interpterygoid vacuity, and much of the pterygoid is covered by smaller denticles.

The medial edge of the palatal ramus of the pterygoid is thickened along the margin of the interpterygoid vacuity. This feature merges anteriorly with the denticle-bearing ridge of the vomer described above. The relationships between the pterygoids, vomers, and cultriform process appear to be the same as *C. milleri*: a very brief pterygoid-cultriform contact closes the anterior portion of each interpterygoid vacuity, and the pterygoids do not meet anteriorly along the midline. Like most other cochleosaurids, however, the anteromedial termination of the pterygoids is very difficult to interpret. The basal process of the pterygoid is triangular, as in *Cochleosaurus florensis* (Godfrey and Holmes, in press), and apparently not sutured to the parasphenoid, which is not preserved in USNM 437646. At the level of the basal articulation, a posterolaterally directed, slightly downturned flange arises from the palatal ramus to embay the anteromedial portion of the subtemporal fossa. On the medial surface of the vertically oriented quadrate ramus of the right pterygoid, a modest horizontal shelf may represent the posterior portion of the excavatio tympanica. A shorter, deeper recess is present along the same plane just anterior to the posteromedial end of the pterygoid.

The parasphenoid is represented only by the anterior half of the cultriform process. The sphenethmoid, the main parasphenoidal body, and the basisphenoid are absent.

The articular surface of the quadrate is not exposed. Judging from the left articular and right quadrate, which can be seen in dorsal and posterior views respectively, the transverse axis of articulation has a modest anteromedial orientation, and the medial condyle is slightly lower than the smaller lateral condyle. The quadratojugal appears to have contributed to the lateral condylar facet.

A small portion of the epipterygoid may be preserved on the right side of the skull. Here, within the otic notch, the thin posteroventral part of the squamosal appears to have been lost along a transverse break. If identified correctly, the epipterygoid was extensively ossified.

As shown by Fig. 1B, the occipital portion of the braincase is disrupted and incomplete. Because the posterior part of the skull roof is collapsed and the exoccipitals are displaced, the exact nature of the posttemporal fossae cannot be determined. On the basis of the left side of the occiput, however, the fossa appears to have been small and enclosed entirely by the exoccipital, paroccipital process, and postparietal. The exoccipital is attached to the postparietal by a stout ascending process. Below a constriction that flanked the foramen magnum, each

exoccipital expands to contribute a crescent-shaped condyle that would have formed about a third of the occipital condyle. The basioccipital is not present. The left paroccipital process, which appears to be in place, has a broad contact with the occipital flange of the tabular and postparietal.

Lower Jaw

The lower jaw of USNM 437646 differs little from those of *Chenoprosopus milleri, Cochleosaurus,* or *Macrerpeton* [*Mytaras*]. Several areas cannot be described, however, because both rami are inextricably closed in a near lifelike position. Both dentary tooth rows, the coronoids, and the adductor fossae are obscured. The posteromedial portion of the right ramus is covered by the partial pectoral girdle, and weathering of the deepest part of each ramus has left only impressions of internal bone surfaces (Fig. 2).

Dermal sculpture similar to that of the skull is developed on the lateral and ventral portions of the jaw. Whereas most of the dentary and postsplenial bear a pitted pattern, the angular and surangular are dominated by ridge-and-groove ornament. No lateral line sulci are present; those described with reservation by Langston (1953) in *C. milleri* are only dermal sculpture.

From the dorsoventrally low symphyseal region, the depth of the lower jaw increases to a maximum at the level of the anterior part of the adductor fossa. Although the dorsal surface of the mandible cannot be observed, the jaw articulation appears to be elevated slightly above the tooth row. A broad groove is developed on the posteroventral face of the articular region. On the medial surface below the anterior portion of the adductor fossa, a single elongate Meckelian fenestra is enclosed by the prearticular and postsplenial; the articular may form the posterior margin of this opening as in *Cochleosaurus florensis* (Godfrey and Holmes, in press) and *Chenoprosopus milleri,* but contacts cannot be determined with certainty in this region. An oval para-articular foramen is present adjacent to the articular-prearticular contact on the posteromedial surface of the prearticular.

Even though both postsplenials are incomplete, they clearly are elongate elements that form nearly two-thirds of the ventral portion of each ramus. Examination of UCMP 33439 shows that the postsplenial ("angular" of Langston, 1953) of *C. milleri* also is a major element, extending for approximately half the length of the mandible. In both species, the postsplenial ends posteriorly at the level of the posterior end of the Meckelian fenestra. In contrast to the relatively simple sutures between the dentary, splenial, postsplenial, angular, and prearticular, the angular-surangular suture is strongly interdigitated on the lateral surface of the mandible. The surangular joins the prearticular along the upturned posteroventral portion of the lower jaw and terminates against the articular before reaching the medial surface.

Displacement of the suspensorium region on the left side of the skull reveals much of the glenoid fossa of the left articular. The fossa is oriented anteromedially and is divided into lateral and medial facets by a subtle ridge; the medial facet is depressed relative to lateral facet. A small retroarticular process merges ventrally with the ridge that forms the inner margin of the articular groove noted above.

Postcranial Skeleton

A significant portion of the pectoral girdle is preserved in association with the skull. Additional postcranial elements have been removed from or left on the
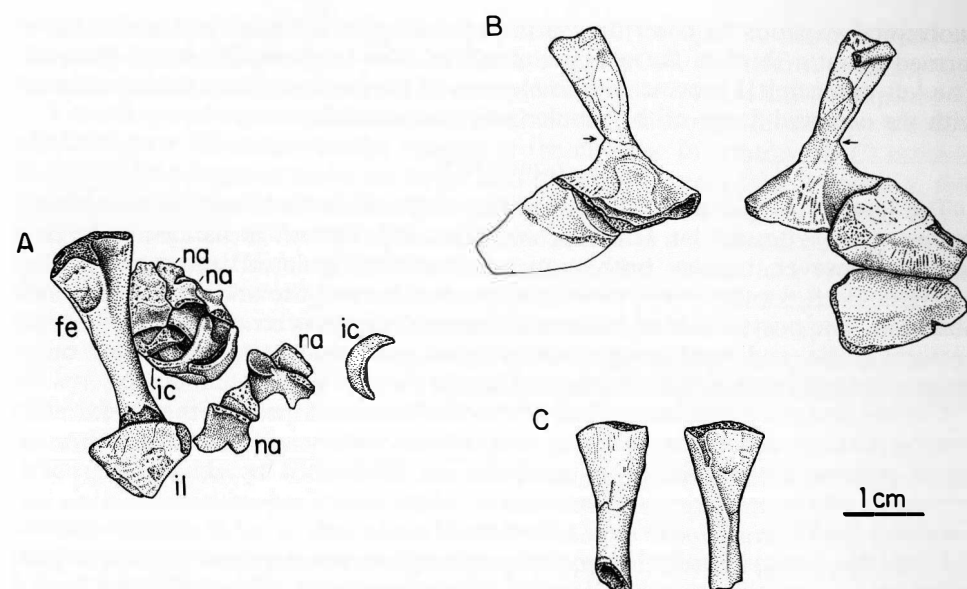
Fig. 3.—*Chenoprosopus lewisi*, holotype, USNM 437646. A, partial left femur in posterodorsal view, partial left ilium in medial view, and vertebral remains as preserved in coprolitic association. B, left, right ilium and ischium in lateral view (unshaded area covered by matrix); right, right ilium and ischium, and left ischium in medial view (arrow indicates position of break on ilium). C, proximal half of right femur in dorsal and ventral views.

surface of an approximately 60 mm-long spiral coprolite that was found next to the skull. To my knowledge, these are the only postcranial remains that can be attributed to *Chenoprosopus* with certainty. A Texas specimen mentioned by Romer (1947) in conjunction with *C. milleri* was found to pertain to another genus upon full preparation (W. Langston, personal communication). Although the material described below is limited, it resembles the few postcranial elements of *Cochleosaurus* that have been illustrated or described (Steen, 1938; Klembara, 1985).

Several vertebral elements are exposed partially in a mostly jumbled and damaged state on or adjacent to the coprolite (Fig. 3A). Four neural arches are present, two of which are in articulation. The absence of well-defined transverse processes suggests that these represent caudal vertebrae, but no hemal spines accompany the intercentra. Without additional data on cochleosaurid vertebrae, I cannot assign these remains to a specific part of the column. As preserved, the neural spines are short and unornamented. The anterior and posterior zygapophyses are nearly on the same horizontal plane, and they appear to be inclined only little. Below the anterior zygapophysis, the pedicle projects ventrolaterally and, where preserved in three neural arches, terminates in an anteroposteriorly broad, unfinished, ventrolaterally facing surface. The central elements are crescent-shaped and are presumed to be intercentra. They are not thickened internally and consist mainly of finished bone externally. Such thin-walled construction is found also in the vertebrae of *Dendrerpeton* (Carroll, 1967). No rib facets are present.

The anterior half of the interclavicle is exposed in ventral view and is partially

underlapped by the left clavicle (Fig. 1, 2A). An unsculptured bone preserved adjacent to the right side of the interclavicle cannot be identified. Ridge-and-groove ornamentation is the predominant sculpture on the external surface of both the interclavicle and clavicle. The width of the interclavicle is greatest at the level of its ossification center; half this width equals the anterior length of the element, as well as the greatest width of the clavicle. This suggests a rhombic interclavicle, as found in *Macrerpeton* [*Mytaras*] and *Cochleosaurus* (Steen, 1931, 1938). Most of the clavicular facet is intact on the right side, which indicates a relatively modest overlap between the interclavicle and clavicles. The clavicle is of typical design, consisting of a vertical cleithral process that arises from the posterolateral corner of the horizontally flat ventral plate.

With the exception of the pubis, the pelvic girdle is well represented. The lower half of the left ilium overlies the proximal portion of the left femur but cannot be removed without damaging both elements (Fig. 3A). As depicted in Fig. 3B, the detached right iliac blade has been restored to the main body of the right ilium. The acetabular area is defined sharply and is associated with a dorsal buttress typical of primitive tetrapods. Anterior to the acetabulum, the ilium turns laterally to form a flat anterior face that expands ventrally. Above the supra-acetabular buttress, the ilium continues as a simple blade that is oriented dorsoposteriorly in lateral perspective and recurved medially if viewed anteriorly or posteriorly. There is a very slight anteroposterior expansion beyond the "neck," but nothing comparable to that of roughly contemporaneous temnospondyls (*Eryops, Parioxys, Edops,* or various dissorophids). In medial view, a posteroventral concavity is defined by a curved ridge that extends from the midpoint of the ventral margin to the posterior edge of the iliac blade. Anterior to this ridge, the ilium is striated and thickened. The end of the iliac blade may be incomplete as preserved, and the area of a possible ilio-sacral attachment is covered by a bone fragment; though the latter may be a rib, it is too small for a sacral rib.

A simple iliac blade with little anteroposterior expansion has been interpreted as a juvenile condition in primitive temnospondyls on the basis of the diminutive *Eugyrinus* and several ilia attributed to *Dendrerpeton* (Milner, 1980*b*). Although this may be true, the ilium described here for *Chenoprosopus* compares favorably with significantly larger ilia from Florence that Klembara (1985) attributed to *Cochleosaurus,* as well as the largest known ilia of *Amphibamus lyelli,* an Upper Carboniferous dissorophoid from Linton, Ohio (Hook and Baird, 1984). A partial ilium assigned to *Edops* (Romer and Witter, 1942) differs in that it shows considerable expansion above the acetabulum.

The ischia are preserved in a flattened manner such that they contact each other along their ventral margins. Both are exposed fully in medial view, but only the anterior portion of the external surfaces has been prepared. The bone is thin except where it swells to enclose the posteroventral portion of the acetabulum, which is bordered by a pronounced ridge. Posterior to the acetabular area, the external surface of the ischium is concave and faces ventrolaterally. A roughened symphyseal contact between the ischia is not apparent; rather, the posteroventral portion of the internal face is striated vertically to suggest a ligamentous attachment.

Most of the left femur is preserved on the coprolite, but the proximal end is detached and its position is occupied by the incomplete left ilium (Fig. 3A). The proximal half of the right femur was prepared free of matrix (Fig. 3C). Based

primarily on the nearly complete left femur, a length of 29 mm is estimated. Both ends are unfinished, and the lateral face of the posterior distal condyle is collapsed inward. Because the outermost part of the posterior condyle has been lost to weathering, the anterior condyle appears to extend more distally. In dorsal view, the anterior or medial surface of the femur is markedly concave, and both ends expand to almost three times the width of the shaft. The anterior and posterior distal condyles are divided by a well-defined intercondylar fossa. Viewed end-on, the proximal end resembles an asymmetric D. This unfinished area merges anteroventrally with the unossified tip of the internal trochanter. Although the area of the fourth trochanter is damaged and cannot be assessed, the adductor crest clearly is a continuation of the ridge that accommodates the internal trochanter. The crest is a sharp, anteroposteriorly trending ventral ridge that is developed most strongly on the proximal to middle portion of the shaft. On the posteriorly exposed part of the left femur, the crest appears to diminish distally and merge with the medial boundary of the popliteal space. The incomplete nature of the distal end of the femur precludes any recognition of discrete aritcular surfaces.

Dermal Ossifications

A. D. Lewis, who skillfully prepared the skull, reports that much of the intermandibular area was occupied by scales. Several of these remain attached to the left mandibular ramus and the cultriform process (Fig. 2A). Though they are preserved infrequently and not likely to survive mechanical preparation, similar ossifications are found in other Permo-Carboniferous amphibians. Many oatshaped scales contained in the coprolitic mass were not salvaged because of their intimate association with more significant postcranial elements.

Discussion

Characteristics and Species of Chenoprosopus

The great size difference between the unique specimen of *Chenoprosopus lewisi* and all specimens of *C. milleri* makes generic definition somewhat difficult and specific differentiation suspect. To a lesser extent, similar problems exist among *Cochleosaurus bohemicus* (represented by a large sample from Nýřany, Czechoslovakia, that encompasses considerable size variation: Steen, 1938; Milner, 1980a), *Cochleosaurus florensis* (known from three skulls of small to intermediate size from Florence, Nova Scotia: Rieppel, 1980; Godfrey and Holmes, in press), and an unnamed species of *Cochleosaurus* from Linton, Ohio (known from two incomplete skulls of intermediate size: "*Leptophractus*" of various authors, "*Gaudrya*" of Hook and Baird, 1986). Pending the completion of a redescription of *C. bohemicus* by S. E. K. Sequeira, I have relied on growth trends in European eryopoids (Meyer, 1858; Boy, 1988, 1989, 1990) to judge what variations may be size-related in cochleosaurids.

Chenoprosopus is distinguished by a suite of characters that are presented above in the diagnoses of the genus and the family to which it belongs, the Cochleosauridae. Among these features are several shared derived characters that serve to differentiate the genus from *Cochleosaurus* and other primitive temnospondyls: (1) snout more narrow and acuminate than in comparably sized specimens of *Cochleosaurus, Macrerpeton,* and *Parioxys*; (2) little to no septomaxilla-lacrimal contact (discussed below); (3) length of jugal-lacrimal contact equal to or, with

size increase, shorter than jugal-prefrontal contact; and (4) anterior portion of elongate choana expanded slightly laterally, rather than straight-sided as in *Parioxys,* and rounded anteromedially, rather than angular as in *Cochleosaurus.*

A feature of *Chenoprosopus milleri* interpreted first by Williston (1918) as a premaxillary palatal tusk pair on the basis of FMNH UC 155 requires comment. The "tusks" are included in an early reconstruction of the palate (Romer, 1947), and their positions along the midline are approximated by dashed circles in the reconstruction provided by Langston (1953). This area is not exposed on *C. lewisi.* I have examined FMNH UC 155, which offers the largest known palate of the genus, and concur with Langston (1953:374) that these imperfectly preserved features are not tusks. Their anteromedial position coincides with a buttress found in the long-snouted loxommatid *Megalocephalus pachycephalus*; in that example, Beaumont (1977) suggested that the buttress served to reinforce the snout against sagittal shearing.

Most differences between *Chenoprosopus lewisi* and *C. milleri* relate to the size disparity between these taxa. The much smaller size of *C. lewisi* probably accounts for the presence of a pineal foramen (see discussion in following section), a proportionally longer postsplenial, and comparatively shorter snout and vomers. In *C. lewisi,* however, a short but indisputable nasal-maxilla contact separates the septomaxilla and lacrimal. Although an identical configuration was reconstructed for *C. milleri* by Langston (1953), his illustration of the principal specimen (UCMP 33439, his fig. 5) shows that the nasal-maxilla contact is absent or reduced to a point contact; examination of this and two other skulls of *C. milleri* confirms the condition depicted in his specimen drawing. I know of no primitive temnospondyls in which a nasal-maxilla contact is obliterated with growth. To the contrary, a nasal-maxilla contact is attained or elaborated with increased size in the eryopoids *Sclerocephalus* (Boy, 1988) and *Archegosaurus* (Meyer, 1858). Moreover, a nasal-maxilla contact is maintained in all specimens of both species of the long-snouted loxommatid *Megalocephalus* (Beaumont, 1977). I conclude that the greater nasal-maxilla contact of *C. lewisi* is a derived character for the species.

A primitive aspect of *C. lewisi* is an appreciable postorbital-supratemporal contact similar to that found in nearly all temnospondyls that possess an intertemporal. This contact is greatly reduced on the dorsal surface of the best preserved skull of *C. milleri* (UCMP 33439), which allows the squamosal to reach the posterolateral corner of the intertemporal. The left side of the smallest specimen of *C. milleri* (UCMP 34174) shows the primitive postorbital-supratemporal contact; this skull, however, was ground and etched to reveal sutures and does not necessarily reflect the condition of the dorsal surface. As illustrated by Steen (1938), the relationships between the postorbital and supratemporal, and therefore the squamosal and intertemporal, are variable in the much-flattened skulls of *Cochleosaurus bohemicus,* but it is not evident how or if this variation is related to size. Thus, I suggest that the intertemporal-squamosal contact of *Chenoprosopus milleri* be considered provisionally as a derived feature for the species.

The size and position of the vomerine tusks in *C. lewisi* resemble more closely those of *Cochleosaurus* than of *Chenoprosopus milleri.* In the latter taxon, the tusk is robust and situated anterior to the apex of the choana. In *C. lewisi,* the tusk is smaller than most of the maxillary teeth, the accompanying replacement pit also is reduced, and both are positioned near the anteromedial margin of the choana. Notably, the palatine tusk and pit are of the expected, larger size.

Table 1.—*Derived characters of (1) cochleosaurids and (2) edopoids reported recently in the literature (Godfrey and Holmes, in press; Sequeira and Milner, in press). See text for discussion.*

1. Cochleosaurid characters
    1.1. Closure of parietal foramen in adults.
    1.2. No lateral line sulci.
    1.3. System of prominent, rounded ridges on skull roof that separate depressed areas of muted sculpture.
    1.4. Squamosal lacks posterodorsal process; lateral edge of supratemporal exposed broadly along anterodorsal margin of otic notch.
    1.5. Lateral ala of pterygoid contacts jugal, excludes ectopterygoid and maxilla from subtemporal fossa.
    1.6. Extreme elongation of premaxillae and vomers produces elongate preorbital region and posterior position of both external and internal nares.
    1.7. Large premaxillae with posterolaterally directed premaxilla-nasal sutures.
    1.8. Elongate, triangular choanae wider anteriorly than posteriorly.

2. Edopoid characters
    2.1. Enlarged premaxillaries with a long common median suture; small naris set well back along snout.
    2.2. Jugal-prefrontal contact excludes lacrimal from orbit margin.

Relationships of Chenoprosopus

Since the time Langston (1953) considered the relationships of *Chenoprosopus,* our knowledge of potentially related forms from coal-bearing Upper Carboniferous rocks has improved thanks largely to the advent of acid-etching and latex-microcasting preparation (Baird, 1955). Although these findings have yet to be presented in a detailed manner, several taxa described in earlier works are recognized now as incomplete remains of better represented species. Such junior synonyms include *Gaudrya latistoma* Fritsch [=*Cochleosaurus bohemicus* Fritsch: Sequeira and Milner, in press] and *Leptophractus dentatus* Moodie and *Mytaras macrognathus* Steen [=*Macrerpeton huxleyi* (Cope): Hook and Baird, 1986], among others. Over the same time period, discovery of new material in the Upper Carboniferous of Nova Scotia has provided a new species of *Cochleosaurus* (Rieppel, 1980; Godfrey and Holmes, in press) and has clarified some aspects of the primitive temnospondyl *Dendrerpeton* (Godfrey et al., 1987, and ongoing work). Additional specimens of *Dendrerpeton* have been described from Jarrow, Ireland, by Milner (1980b), who also noted a *Cochleosaurus*-like form in the same assemblage.

These advances and the discovery of the small *Chenoprosopus* specimen described here underscore Langston's close association of the "long-faced" forms *Chenoprosopus* and *Cochleosaurus.* But whereas Langston suggested the recognition of two separate families, the Chenoprosopidae and Cochleosauridae, additional data on both genera have revealed no major differences, and most subsequent workers have grouped these taxa together within the senior family, the Cochleosauridae. A second genus attributed to the Chenoprosopidae by Langston is *Macrerpeton* [*Mytaras*], a very odd temnospondyl known from less than five Linton specimens and two fragmentary examples from a recently discovered deposit at Five Points, Ohio (Hook and Baird, 1986, in press). Similarities with *Chenoprosopus* include an expansive snout and vomers; elongate choanae; and long, slender, slightly recurved maxillary teeth. Because a redescription of this poorly known material is underway, further commentary is premature.

The "long-faced" ramus of Langston's bipartite edopoid phylogeny apposed several "short-faced" genera, of which only *Edops* has survived as a valid taxon. Unlike the cochleosaurids and *Dendrerpeton,* no additional data of significance have come forth recently on *Edops,* and it continues to be known mainly from an extremely large, incomplete skull from the Lower Permian of Texas (Romer and Witter, 1942). Unfortunately, this troublesome form is the basis for the superfamily Edopoidea, which consists at present of the Edopidae and Cochleosauridae.

Recent studies by Godfrey and Holmes (in press), Milner and Sequeira (in press), and Sequeira and Milner (in press) have included cladistic analyses of the Cochleosauridae and the Edopoidea. Although these efforts have corrected errors of previous contributions, I believe that critical questions of character polarity and significance remain. Table 1 presents the characters put forth by these authors for cochleosaurids and edopoids; in some cases, I have modified slightly the original statements in order to simplify expression.

Character 1.1, closure of the parietal foramen in adults, is problematic because a well-ossified specimen of the Linton cochleosaurid (AMNH 6954) with an estimated minimum skull length of 130 mm has a pineal foramen. The opening also is present in *Chenoprosopus lewisi,* which falls within the size range of the skulls of *Cochleosaurus florensis* (skull lengths from 84 to 123 mm), all of which have no foramen. The smallest skull of *Chenoprosopus milleri* (length of 189 mm) lacks the opening. Pending a more complete documentation of the parietal foramen in the single-population growth series of *Cochleosaurus bohemicus,* I regard this character as provisional at the family level.

The lack of lateral line sulci (Godfrey and Holmes, in press), character 1.2, is of practical use in identifying fragmentary cochleosaurid remains but can be assigned little phylogenetic significance. Likewise, the system of ridges and depressions on the skull roof and associated variations in dermal sculpture (character 1.3) occurs in a great number of other forms, including panderichthyid fishes (Schultze and Arsenault, 1985), loxommatid amphibians (Beaumont, 1977), and many dissorophoid and eryopoid-grade (especially zatrachydid) temnospondyls, and appears to be of little value in a discussion of relationships.

Godfrey and Holmes (in press) cite the lack of a posterodorsal process on the squamosal and the resulting contribution of the supratemporal to the dorsal rim of the otic notch (character 1.4) as a derived character for cochleosaurids. As noted correctly by Sequeira and Milner (in press), however, the supratemporal is the dominant element on the dorsal rim of the otic notch in many temnospondyls, and the squamosal-supratemporal configuration is only of consequence if a close relationship between cochleosaurids and *Edops* is accepted.

In cochleosaurids, a jugal-pterygoid suture precludes the maxilla and ectopterygoid from the subtemporal fossa and prevents a maxilla-quadratojugal contact (character 1.5). This suture is more extensive and complex than that found in some saurerpetontid trimerorhachoids (*Acroplous*: Foreman, 1990; possibly *Saurerpeton* and *Erpetosaurus*). Although the maxilla has a short contact with the quadratojugal in *Edops* (Romer and Witter, 1942), the participation of either the pterygoid or ectopterygoid in the anterolateral closure of the subtemporal fossa cannot be assessed from the available material.

Detailed aspects of the elongate cochleosaurid snout are addressed by characters 1.6, 1.7, and 1.8. Extreme elongation of the premaxillae and vomers (character 1.6 in part) occurs also in archegosaurids and some trematosauroids, but these

taxa generally lack the more posteriorly positioned narial openings of cochleosaurids. Character 1.7, large premaxillae with posterolaterally directed premaxilla-nasal sutures, was treated with reservation by both Godfrey and Holmes (in press) and Sequeira and Milner (in press) because a similar condition exists in *Edops*.

An attribute of cochleosaurids that Godfrey and Holmes (in press) mention but which does not appear in their character list is the pterygoid-cultriform configuration. Though difficult to determine in most specimens, the pterygoids appear to contact the cultriform process but fail to join each other anteriorly. A nearly identical arrangement was described by Moustafa (1955) in the supposed eryopoid *Parioxys* from the Lower Permian of north-central Texas (Carroll, 1964). A full reinvestigation of this genus, which also has elongate choanae, may have a significant impact on existing hypotheses of edopoid-eryopoid relationships.

The edopoid characters of Table 1 are those that are said to unite the cochleosaurids and edopids in a primitive clade (Sequeira and Milner, in press). Character 2.1, premaxillary elongation associated with small, inset external nares, encompasses much of characters 1.6 and 1.7. A prefrontal-jugal exclusion of the lacrimal from the orbit (character 2.2) is found also in eryopoids (Milner, 1978) and, therefore, is not a unique shared derived character of edopoids.

To summarize, I regard the following characters as cochleosaurid synapomorphies: (1) elaborate jugal-pterygoid suture excludes maxilla and ectopterygoid from subtemporal fossa, (2) vomers elongated anterior to choanae, and (3) choanae elongate and wide anteriorly. The union of *Edops* and cochleosaurids within the Edopoidea appears to be supported strongly by only one synapomorphy: small inset external naris bordered by elongate premaxilla.

Most discussions of *Chenoprosopus* have noted similarities with *Archegosaurus*, a long-snouted eryopoid from the Lower Permian of Europe (Mehl, 1913; Romer, 1947; Langston, 1953). A close relationship between these two genera has been expressed recently in cladistic terms by Boy (1990), who also emphasized the tenuous nature of a close association between *Edops* and *Chenoprosopus*. If the hypothesis put forth by Boy is correct, the cochleosaurids represent the base of a lineage that culminated eventually in stereospondyls, and neither the Edopoidea nor the Eryopoidea are monophyletic.

Of the synapomorphies just noted, *Archegosaurus* has only the second cochleosaurid character, vomers elongated anterior to the choanae. It does, however, have a nasal-maxilla contact that is similar to that of *Chenoprosopus lewisi* and elongate, triangular prefrontals comparable to those of cochleosaurids (apomorphic characters 25 and 26 of Boy, 1990). Additional features of undetermined polarity shared by *Archegosaurus* and cochleosaurids include antorbital length greater than midorbital width, elongate premaxilla, modest tabular horns, and a simple iliac blade with only a rudimentary posterior process.

Sequeira and Milner (in press) rejected Boy's hypothesis largely on the basis of characters used by Milner (1989) in a cladistic synopsis of European eryopoid-grade temnospondyls. Among the derived characters reported by Milner for "higher temnospondyls" (taxa other than the dendrerpetontids, edopoids, and trimerorhachoids; loxommatids and colosteoids are not considered as temnospondyls) that appear to refute most convincingly a close relationship between *Chenoprosopus* and *Archegosaurus* are: (1) premaxilla with narrow marginal ramus and distinct alary process bordering large external naris, and (2) reduced basioccipital and enlarged exoccipitals resulting in bilobed occipital condyle. The premaxillary character requires comment because at least two types of alary processes may be

recognized. In one variety, the process terminates on the medial margin of the external naris, and the nasal-premaxilla suture remains fairly straight; as seen in *Archegosaurus*, this configuration can be derived directly from a cochleosaurid with small external nares simply by enlarging the narial opening. A second and more common sort of alary process, typified by *Eryops*, is set off distinctly from the external naris and affects a posteriorly directed V in the nasal-premaxilla suture. Because this "free" alary process occurs also in *Capetus*, a problematic Upper Carboniferous temnospondyl that lacks the prefrontal-jugal contact of both edopoids and eryopoids (Sequeira and Milner, in press), it may represent a primitive condition.

The second character considered as derived by Milner (1989) and Sequeira and Milner (in press) for higher temnospondyls also invites debate. The transition from a single occipital condyle to a bilobed or double configuration is known to have been achieved independently in other lineages, such as the trimerorhachid-saurerpetontid-brachyopid clade (Coldiron, 1978). Consequently, it could be argued that the exoccipital-dominated arrangement of archegosaurids developed from a cochleosaurid stock quite separate from a zatrachydid-eryopid-dissorophoid group. Other characters reported by Milner (1989) or by Sequeira and Milner (in press) as derived for archegosaurids within a higher temnospondyl clade could be obtained independently by slight modification of a *Chenoprosopus*-like cochleosaurid, including an extremely high skull length–width ratio, no intertemporal, paired anterior palatal vacuities, loss of the pterygoid flange, vomer and palatine contributions to the interpterygoid vacuities, and accessory palatal dentition.

Inasmuch as *Chenoprosopus* and *Archegosaurus* are roughly contemporaneous Lower Permian taxa of very similar ecomorphotypic plans but without geographic overlap, it is tempting to seek a common ancestral form in the Upper Carboniferous. *Cochleosaurus* certainly is not a candidate despite its cosmopolitan record in the late Westphalian, and the poorly known *Macrerpeton* similarly is too specialized. As noted by Milner and Sequeira (in press), there are cochleosaurid fragments from the Westphalian B of Joggins (Carroll, 1967:text-fig. 7A as *Dendrerpeton*), and somewhat older and more complete material from Jarrow (Milner, 1980*b*). The origin of cochleosaurids and a resolution of their relationships must be sought in yet-to-be-collected pre-Westphalian deposits.

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