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A PROCOLOPHONID (PARAREPTILIA) FROM THE OWL ROCK MEMBER, CHINLE FORMATION OF UTAH, USA

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ABSTRACT

An isolated skull of a procolophonid is described from the Owl Rock Member of the Chinle Formation in the Abajo Mountains of southeast Utah. Although poorly preserved, this specimen exhibits features that demonstrate a phylogenetic relationship with leptopleuronine procolophonids. These include the dentition, the greatly expanded orbitotemporal opening, the prominent quadratojugal spikes, and the shape of the jugal.

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INTRODUCTION

The Procolophonidae are a group of small parareptiles (*sensu* Laurin and Reisz 1995) with a widespread distribution in the Triassic whose remains have been found on every continent. Erected by Owen (1876), *Procolophon*, from the Lower Triassic of South Africa (Watson 1914; Broili and Schröder 1936) and Antarctica (Colbert and Kitching 1975), is the best-known taxon and its skull has been described in detail (Kemp 1974; Carroll and Lindsay 1985). The first member of the clade to be named was *Leptopleuron* from the Upper Triassic Lossiemouth Sandstone (Owen 1851) but at the time its affinities were poorly understood. Preserved as natural molds in the Lossiemouth Sandstone, the material has proved difficult to work with and as a consequence details of the skeletal structure have remained somewhat obscure. Recently, Spencer, working with latex

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casts taken from the original molds, has begun to elucidate some of the details of the skull, in particular the braincase (Spencer 2000). Whereas a number of different taxa have been described from the Triassic of Russia, most of them have been based solely on jaw elements, with only the skull of *Tichvinskia* (Ivakhnenko 1973) being described in any detail.

Hypsognathus from the Newark Supergroup of eastern North America was first described by Gilmore (1928). This characteristic procolophonid, closely related to *Leptopleuron*, is now known from several localities and has been described in some detail (Colbert 1946; Sues et al. 2000). In recent years, additional procolophonid taxa have been described from the Newark Supergroup (Baird 1986; Sues and Olsen 1993; Sues and Baird 1998), including the leptopleuronine *Scoloparia*, that is represented by two partial skulls and other isolated elements. Isolated jaw material has also been recognized within the Triassic fissure assemblages of southwest Britain (Fraser 1986; Walkden and Fraser 1993), and although more complete specimens are known, this taxon has yet to be fully described (Walkden and Fraser 1993). Together this material appears to comprise at least three separate taxa.

Here we describe a single small procolophonid skull from the Owl Rock Member of the Chinle Formation of Utah. This specimen represents the first described associated cranial material of a procolophonid from the Chinle Formation. Sues et al. (2000) mention the occurrence of several partial skulls of procolophonids together with postcranial remains from the Owl Rock Member of Arizona that are very similar to *Hypsognathus*. However, these are distinct from the new specimen from Utah (H.-D. Sues, personal commun., 2003). *Libognathus sheddi* (Small 1997) is a procolophonid taxon from the Upper Triassic Dockum Group of Texas. Unfortunately, because it is based exclusively on lower jaw material, *Libognathus* cannot be compared to the present specimen. Originally described as a species of *Trilophosaurus* by Murry (1987), *Chinleogomphius jacobsi* was moved to the Procolophonidae by Sues and Olsen (1993) based on similarities in the dentition. This taxon is known from the *Placerias* Quarry in Arizona, in the lower part of the Chinle Formation. The maxillary teeth are known, but differ greatly from the Utah specimen described here. Heckert (2004) described isolated fragmentary procolophonid material from Arizona and New Mexico that is not comparable with the present specimen.

This specimen was prepared by the late Will Downs and is deposited in the collections of the Museum of Northern Arizona, Flagstaff, Arizona (MNA).

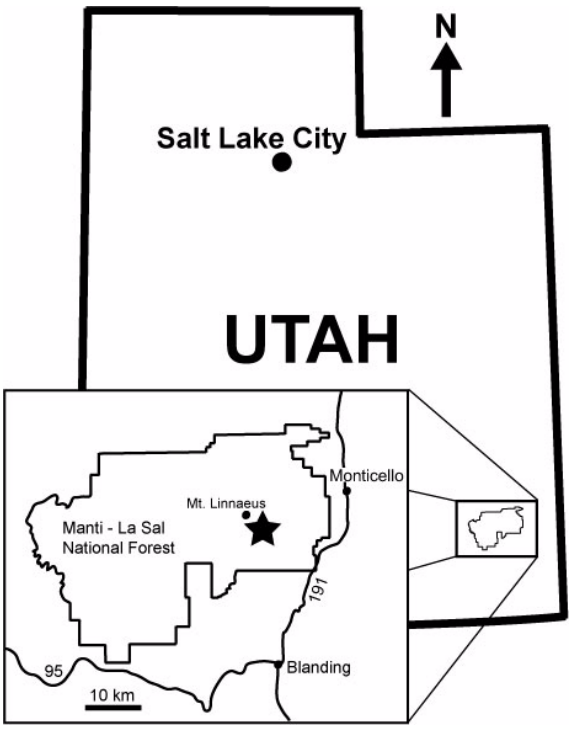

Figure 1. Locality map. Star indicates the location of the procolophonid specimen within Manti-La Sal National Forest, Utah.

GEOLOGIC SETTING

The specimen was found southeast of Mt. Linnaeus in the Abajo Mountains of southeastern Utah, in an area called the Red Bluffs, part of the Manti-La Sal National Forest (Figure 1). The Abajo Mountains were formed when an igneous intrusive body uplifted and exposed the Mesozoic continental strata (Witkind 1964). In the immediate vicinity of where the procolophonid specimen was recovered, the exposed strata in ascending order are the Owl Rock Member of the Upper Triassic Chinle Formation, Church Rock Member of the Chinle Formation, and Upper Triassic/Lower Jurassic Wingate Sandstone (Figure 2) (Stewart et al. 1972). Although the skull was recovered in a block as float, its location and matrix make it fairly likely that it originated from the Owl Rock Member. Extensive prospecting of the area has revealed that bone is fairly common within the Owl Rock Member but is absent from the Church Rock Member and Wingate Sandstone. Most bone within the Owl Rock Member at the locality occurs within channel conglomerates that are dominated by intraformational clasts (Figure 2). However, the matrix surrounding the procolophonid indicates it is

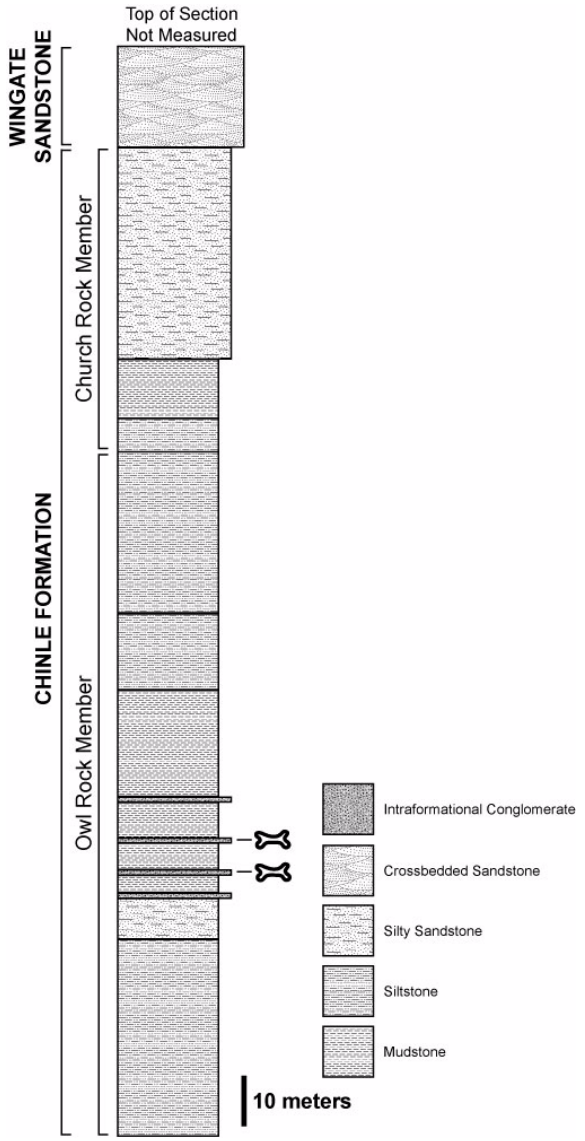

Figure 2. Stratigraphic section at the locality where the procolophonid specimen was recovered. Bone symbols indicate stratigraphic levels containing vertebrate fossils (although not necessarily the procolophonid specimen).

derived from a fine-grained dark red mudstone or siltstone that is one of the most common fluvial sediments within the Owl Rock Member.

The Upper Triassic Chinle Formation is exposed throughout southern Utah, southeastern Colorado, northeastern New Mexico, and northern Arizona (Stewart et al. 1972), and represents dominantly fluvial floodplain sediments. In southeastern Utah, the Shinarump Conglomerate, Monitor Butte Member, Moss Back Member, an undifferentiated Petrified Forest Member, Owl Rock Member, and Church Rock Member represent the Chinle Formation in ascending sequence. In the Abajo Mountains, Stewart et al. (1972: p. 288) interpreted the lowest exposed unit as the Moss Back Member, and did not identify the Petrified Forest Member. At the locality itself, the unit in contact with the igneous intrusion is the Owl Rock Member. In this area, the Owl Rock Member is dominated by slope to ledge-forming orange, red, and purple mudstone-siltstones. Thin layers of fine sandstones are also present. Interspersed between these layers are ledge-forming units of intraformational conglomerates and pedogenic limestone that is generally purple in color (Figure 2).

Recently, debate has centered on the interpretation of the depositional setting of the Owl Rock Member. A number of workers suggested that the unit was dominated by lacustrine and marginal lacustrine environments with the limestones representing lake deposits (e.g. Blakey and Gubitosa 1983; Dubiel 1989, 1993). This interpretation was challenged by Lucas and Anderson (1993) who interpreted all the limestones as exclusively pedogenic in nature and, thus, having no bearing upon their depositional setting. With this in mind, Tanner (2000) undertook a detailed sedimentologic study of the Owl Rock Member. He found that while the limestones did display a pedogenic component, they were not exclusively so, and probably represented small ephemeral lakes and ponds within a predominantly fluvial system. This interpretation also confirms that the Owl Rock Member conforms to the general Late Triassic-Early Jurassic trend of increasing aridity (Tanner 2000). Thus, the Owl Rock Member most likely represents a fluvial floodplain with sinuous streams and small ephemeral lakes and ponds that was drier than the underlying Petrified Forest Member.

DESCRIPTION

The specimen, MNA V9953, comprises the major portion of the skull minus the mandible and preserves most of the marginal tooth rows (Figure 3). However, the surface bone is largely eroded away or poorly preserved and as a consequence no sutures can be detected. The skull roof was partially weathered prior to collection of the specimen. Although the bone is worn and poorly preserved, the general shape of the skull and the dentition can be discerned, providing the opportunity to make direct comparisons with known Late Triassic procolophonids.

As preserved it is a very low flat skull (Figure 3.3). This might be partially a result of distortion, although other Late Triassic procolophonids, such as *Hypsognathus* are also known to have dorsoventrally compressed skulls.

In dorsal view the skull is approximately triangular in shape (Figure 3.1). The prominent oval orbitotemporal openings are directed dorsally. These openings are greatly extended posteriorly, markedly reducing the distance between the posterior margin of this opening and the posterior margin of the skull roof. Indeed, it would appear that this distance is approximately equal to the narrowest point across the frontals. Although the posterior corner of the skull is missing on the right side, it is possible to partially reconstruct it as the mirror image of the left side (Figure 3.1). On this basis it is clear that the skull was broader than it was long. The frontals are constricted slightly toward the anterior margin of the orbits. A perfectly circular slightly raised area of matrix occurs along the midline of the skull roof between the anterior parietals. This area most likely represents the pineal foramen. The posterior margin of the skull has been eroded, and the braincase is missing.

On the left side the quadratojugal bears at least three prominent spines (Figure 3.1, 3.3), although additional spines may have broken off. The jugal extends down below the level of the maxillary tooth row and its ventral margin appears to slope posteroventrally (Figure 3.2, 3.3).

The snout is damaged, and it is difficult to distinguish between the premaxillary and maxillary dentition. The tooth row is inset from the lateral margin of the skull. Post-mortem distortion has pushed the tooth row of the left side anteriorly, making it appear that the right side has more teeth. There appear to be two premaxillary teeth (Figure 3.2), which although damaged, are clearly labio-lingually expanded with a simple ridged occlusal surface. Four maxillary teeth are preserved on either side (Figure 3.2). Although the more derived procolophonids tend to exhibit reduction in marginal tooth numbers, tooth count is not necessarily significant for phylogenetic analysis. Differences in tooth count are known to represent ontogenetic variation in other procolophonids (Gow 1977; Sues and Baird 1998).

The maxillary teeth are transversely broadened (Figure 3.2). Wear facets on each tooth have obscured some of the structural details. They appear to possess a labial and a lingual cusp connected by anterior and posterior transverse ridges that form the margin of a deep occlusal basin. The anterior margin of the basin is always lower than the posterior margin. The labial cusp always appears higher than the lingual cusp, although both of these features could be a result of tooth wear. The wear patterns are very similar to that seen in an un-named procolophonid from the fissure deposits at Cromhall Quarry, England (Fraser 1986). However, the maxillary teeth in the Cromhall form are not as transversely broadened. Moreover the occlusal basins are considerably deeper in the Abajo form and comparable to that of *Hypsognathus*. The Late Triassic Brazilian form *Soturnia* also possesses an occlusal depression, although this is manifested as a prominent anterior-posterior groove on the occlusal surface, not a basin per se (Cisneros and Schultz 2003). *Scoloparia* differs greatly in having maxillary teeth with several cuspules on a single transverse ridge with no trace of an occlusal basin (Sues and Baird 1998). In palatal view, a bone extending anterior from the midline probably represents the right vomer (Figure 3.2). It does not preserve any teeth, although this is equivocal, because it is so poorly preserved. Posterior to the tooth row but anterior of the quadrate are a thin bone on either side extending posteriorly and slightly towards the midline (Figure 3.2). They possibly represent the pterygoids, but are too poorly preserved to confirm this identification.

DISCUSSION

It is clear that this procolophonid is very similar to the derived procolophonids *Leptopleuron* from the Lossiemouth Sandstone Formation, *Scoloparia* from the Wolfville Formation, Newark Supergroup, and *Hypsognathus* from the Newark Supergroup. In addition certain characters are also shared with the unnamed Cromhall taxon (Fraser 1986, figure 6) and *Soturnia* from Brazil.

Modesto et al. (2002) generated a phylogenetic hypothesis of the Procolophonoidea based on an extensive character list derived mainly from Sues et al. (2000). Although many of these characters cannot be coded for the present specimen because it is incomplete and poorly preserved, enough of them are observable, especially in the dentition, to provide a good estimate of its phylogenetic position. Key characters that are not preserved, but would have been useful, include the contribution of the prefrontals to the skull roof and lateral walls of the snout, and characters associated with the palate and braincase.

The Abajo form possesses a low number of maxillary teeth that have bases that are labio-lingually expanded. Both of these characters are synapomorphies of the Procolophonidae (Modesto et al. 2002). Other characters observed in this specimen that are found in most procolophonids, but lacking in some basal forms, include maxillary teeth with labio-lingually expanded crowns and maxillary teeth that are inset from the lateral surface of the ‘cheek’ (Modesto et al. 2002). An additional character that is equivocal in the Abajo form

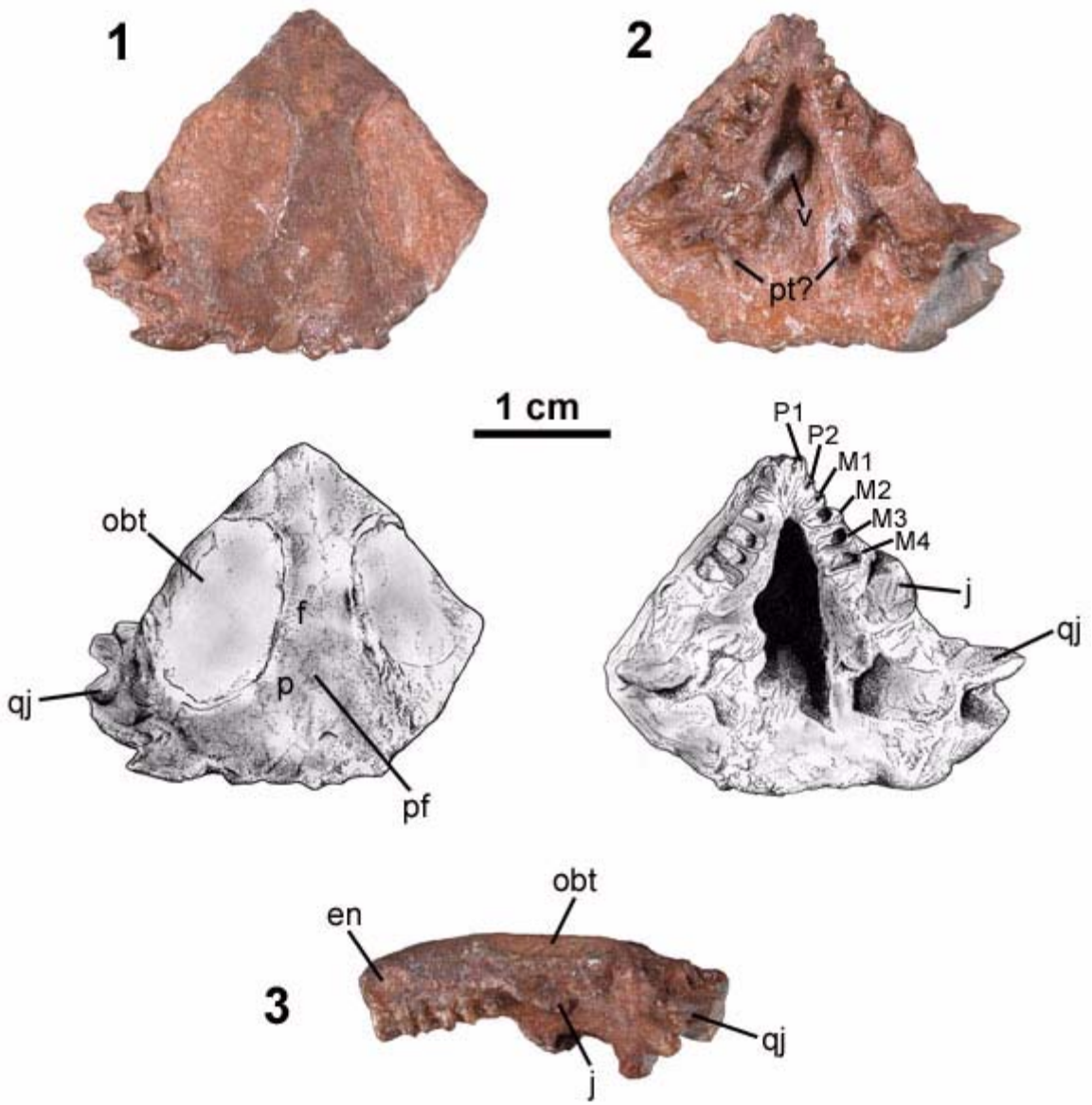

Figure 3. Photograph and illustration of procolophonid specimen MNA V9953 in 1) dorsal view; 2) ventral view; and 3) left lateral view. Abbreviations: en, external naris; f, frontal; j, jugal; M1, M2, M3, M4, maxillary teeth; obt, orbitotemporal opening; p, parietal; pf, pineal foramen; pt, pterygoid; P1, P2, premaxillary teeth; qj, quadratojugal; v, vomer.

is the lack of a postparietal, because the posterior margin of the skull roof is eroded. The Leptopleuroninae is a derived clade that is defined as all procolophonids more closely related to *Leptopleuron* than to *Procolophon*, and is identified by a host of characters (Modesto et al. 2002). Three of these characters can be observed in the Abajo form, making it identifiable as a leptopleuronine procolophonid. These are: two premaxillary teeth; orbit terminates well posterior to the pineal foramen; and two or more radiating quadratojugal spines (three in this specimen) (Modesto et al. 2002). One character in the analysis by Modesto et al. (2002) unites the present specimen with *Leptopleuron* and *Hypsognathus* to the exclusion of *Scoloparia*: the convex anteroventrally facing ventral margin of the jugal. *Soturnia* from Brazil also possesses this feature as well as another that defines this unnamed clade, the presence of one incisiform dentary tooth (Cisneros and Schultz 2003). If the palatine in the Abajo form does not have any teeth, and this is unconfirmed because the palate is poorly preserved and incomplete, then it would be united with *Hypsognathus* and *Soturnia* in a clade to the exclusion of all other procolophonids (Modesto et al. 2002; Cisneros and Schultz 2003). The presence of labial and lingual cusps separated by a transverse ridge in the maxil-

lary teeth is an additional character that may unite *Hypsognathus*, *Soturnia*, the Abajo form, and the Cromhall taxon. However, the maxillary teeth of *Leptopleuron* have never been described in detail, so the character state is unknown in that taxon. That such a deep occlusal basin is seen in the maxillary teeth of both the Abajo form and *Hypsognathus* may be evidence of a close relationship between the two. The new specimen is clearly allied with derived leptopleuronine procolophonids, but the lack of any autapomorphies or unique combination of character states precludes the erection of a new taxon.

Leptopleuronine procolophonids had a cosmopolitan distribution during the Late Triassic. Although the Abajo form seems to be allied with mostly Laurasian forms, this may be an artifact of our poor knowledge of Late Triassic Gondwanan procolophonids. The new specimen, *Leptopleuron*, *Hypsognathus*, *Soturnia*, and the Cromhall form are evidence for a global Norian radiation of leptopleuronines, suggesting that procolophonids diversified until their extinction at the end of the Triassic.

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