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OSTEODERMS OF JUVENILES OF *STAGONOLEPIS* (ARCHOSAURIA: AETOSAURIA) FROM THE LOWER CHINLE GROUP, EAST-CENTRAL ARIZONA

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Abstract—We describe for the first time small (<25 mm) dorsal paramedian, lateral, and appendicular/ventral scutes (osteoderms) of aetosaurs from the Blue Hills in Apache County, east-central Arizona. These diminutive scutes, collected by C.L. Camp in the 1920s, preserve diagnostic features of the common Adamanian aetosaur *Stagonolepis*. *Stagonolepis wellesi* was already known from the Blue Hills, so identification of juvenile scutes of *Stagonolepis* simply confirms the existing biostratigraphic and paleogeographic distribution of the genus. Still, application of the same taxonomic principles used to identify larger, presumably adult, aetosaur scutes suggests that juvenile aetosaurs should provide the same level of biostratigraphic resolution obtained from adults.

Keywords: Arizona, aetosaur, juvenile, *Stagonolepis*, Chinle, Blue Mesa Member

INTRODUCTION

Aetosaurs are an extinct clade of heavily armored, primarily herbivorous, archosaurs known from Upper Triassic strata on all continents except Antarctica and Australia (Heckert and Lucas, 2000). The osteoderms (scutes) of aetosaurs are among the most common tetrapod fossils recovered from the Upper Triassic Chinle Group, and are typically identifiable to genus (Long and Ballew, 1985; Long and Murry, 1995; Heckert and Lucas, 2000). This in turn has facilitated development of a robust tetrapod-based biostratigraphy of the Chinle Group and other Upper Triassic strata worldwide (e.g., Lucas and Hunt, 1993; Lucas and Heckert, 1996; Lucas, 1997, 1998). In spite of this, aetosaurs are relatively poorly understood, as only *Aetosaurus ferratus* Fraas, 1877 is known from a relatively complete growth series (Fraas, 1877; Fraas, 1896) and *Stagonolepis robertsoni* Agassiz, 1844 remains the only taxon with a relatively modern, monographic treatment of its anatomy (Walker, 1961). This is in large part because, in spite of the abundance of aetosaur scutes in the fossil record, skulls and diagnostic appendicular and axial skeletal material remain comparatively rare. Consequently, much of what we know of aetosaurs is based on comparison of osteoderms between taxa.

Since Long and Ballew (1985), most workers have simply used isolated scutes to document the presence of known taxa and occasionally to identify new ones (e.g., Hunt and Lucas, 1990, 1991; Long and Murry, 1995; Heckert and Lucas, 1998, 1999; Small, 1998; Heckert et al., 1999; Zeigler et al., 2002). Here, we utilize the diagnostic properties of aetosaur scutes to identify juvenile specimens of the common aetosaur *Stagonolepis* from the Upper Triassic of eastern Arizona.

Institutional abbreviation: UCMP = University of California Museum of Paleontology, Berkeley.

STRATIGRAPHY AND AGE

All of the specimens we describe and illustrate here come from the Blue Hills, just north and east of St. Johns, Arizona, listed as UCMP locality 7308 (Fig. 1). These scutes were collected by Charles Camp of the UCMP in the 1920s from concentrations of small vertebrates he termed "meal pots" (Camp, 1930). It is clear that all of Camp's Blue Hills localities are in the uppermost Bluewater Creek Formation or lowermost Blue Mesa Member of the Petrified Forest Formation, principally the latter (Camp and Welles, 1956; Heckert and Lucas, 2002a). These localities yield a

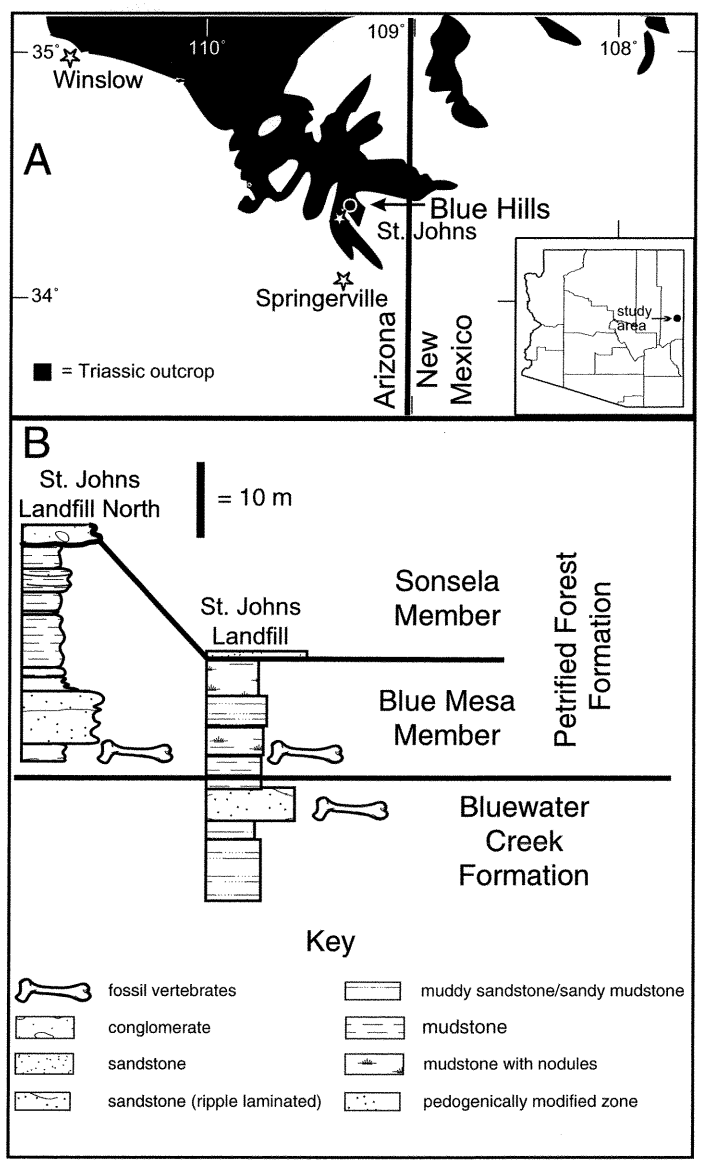

FIGURE 1. Index map and generalized stratigraphic section showing the geographic and stratigraphic position of the aetosaur scutes described in this paper.

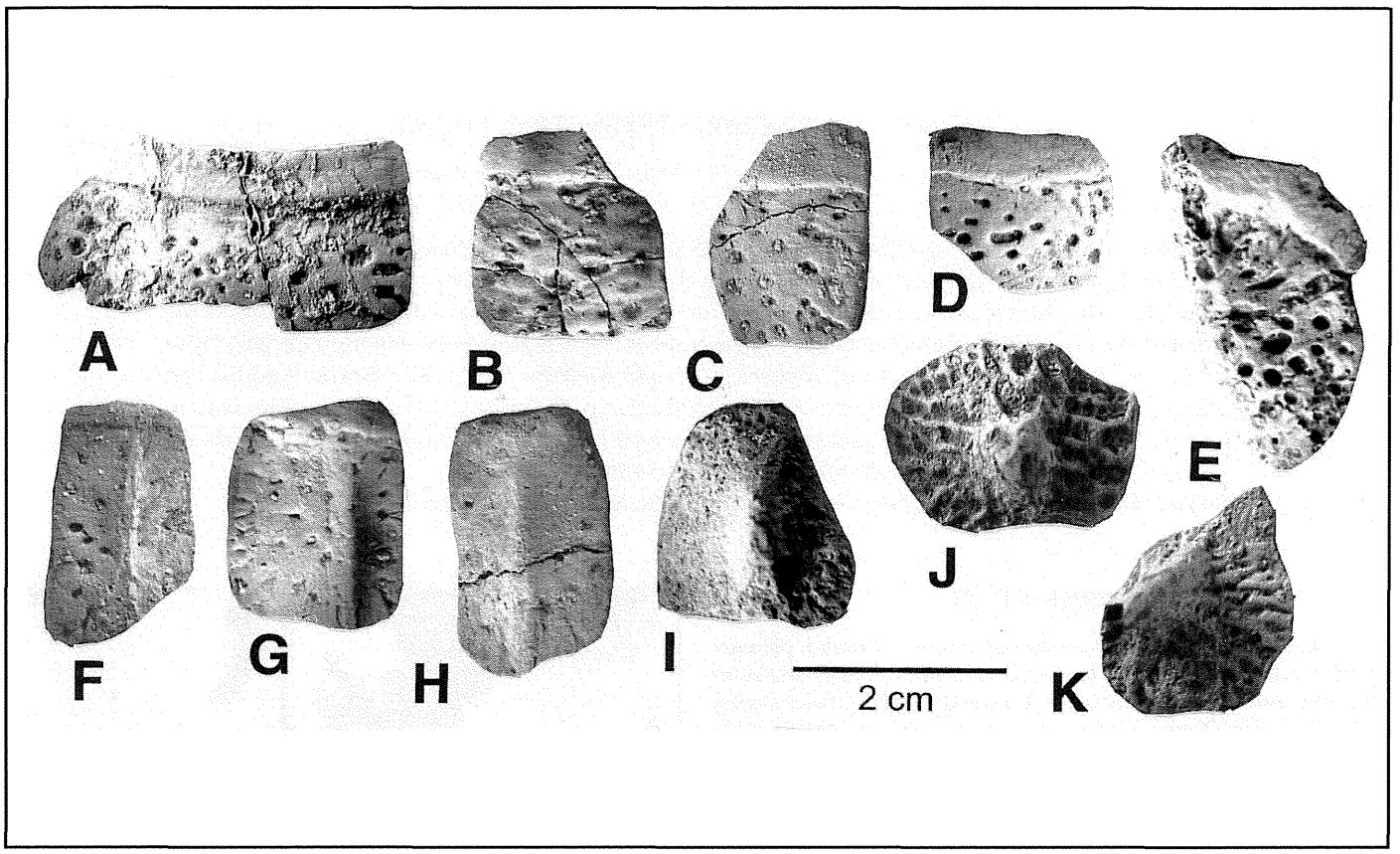

FIGURE 2. Scutes of juvenile *Stagonolepis* sp. (A-H) and *Desmatosuchus* (I-K) in exterior (dorsal or lateral) view. All are from UCMP locality 7307 in the Blue Hills northeast of St. Johns, Arizona.**A**, UCMP 175055, incomplete paramedian scute; **B**, UCMP 175056, incomplete paramedian scute; **C**, UCMP 175054, incomplete paramedian scute; **D**, UCMP 175051, incomplete paramedian scute; **E**, UCMP 175065, incomplete paramedian scute; **F**, UCMP 175087, incomplete lateral scute; **G**, UCMP 175088, incomplete lateral scute; **H**, UCMP 175064, incomplete lateral scute; **I**, UCMP 175134, incomplete lateral scute of *Desmatosuchus* sp.; **J**, UCMP 175106, incomplete paramedian scute of *Desmatosuchus* sp.; UCMP 175110, incomplete lateral scute of *Desmatosuchus* sp. All are approximately x 1.5.

tetrapod fauna that includes the phytosaur *Rutiodon*, the aetosaur *Stagonolepis*, and diverse other tetrapod taxa. This assemblage, while slightly lower stratigraphically, is essentially identical to the type Adamanian assemblage from the Blue Mesa Member at Petrified Forest National Park (Lucas and Hunt, 1993; Long and Murry, 1995; Heckert and Lucas, 1997, 2002a; Lucas et al., 1997). Consequently, the Blue Hills vertebrate fauna can confidently be assigned an Adamanian (latest Carnian) age.

DESCRIPTION

We identified 52 scutes or scute fragments of *Stagonolepis* in the UCMP collection, and we illustrate eight of those scutes here (Fig. 2A-H), together with three juvenile scutes of the contemporaneous aetosaur *Desmatosuchus* from the same locality for comparison (Fig. 2I-K). In all cases, the juvenile *Desmatosuchus* scutes (=*Acaenasuchus* of Long and Murry, [1995]) have coarser, more irregular pitting and bosses that do not contact the posterior margin of the scute. These characteristics effectively separate *Desmatosuchus* scutes from *Stagonolepis* (see also Heckert and Lucas, 2002b).

We identify four basic kinds of juvenile *Stagonolepis* scutes in this sample: (1) dorsal paramedian scute and scute fragments of small individuals (Fig. 2A-D); (2) fragmentary scutes of slightly larger individuals (Fig. 2E); (3) lateral scutes and scute fragments of smaller individuals (Fig. 2-H); and (4) ventral scutes and scute fragments (not illustrated). The distribution of these scutes is given in Table 1.

Paramedian scutes

Scutes we identify as dorsal paramedian scutes of *Stagonolepis*: (1) possess an anterior bar; (2) are significantly wider than long (W:L > 2:1, but less than 4:1); (3) possess a keel or knob on the dorsal surface that contacts the posterior margin of the scute; (4) have an ornamentation consisting of a radial (sunburst) pattern of pits and grooves emanating from the keel/knob; (5) lack transverse ventral keels. Taken together, these characteristics match well the diagnoses of *Stagonolepis* (=*Calyptosuchus*) provided by Long and Ballew (1985), Long and Murry (1995) and Heckert and Lucas (2000, 2002c). To amplify these points, we briefly describe several of the illustrated specimens.

Small dorsal paramedian scutes

The best preserved scute, UCMP 175055 (Fig. 2A), is a right dorsal paramedian scute. It is slightly more than twice as wide (37 mm) as it is long (18 mm), gently arched or flexed, with a low keel medial (left) of the center of the scute. The posterior margin is damaged, but the preserved scute exhibits a very faint radial "sunburst" pattern of slightly elongated pits and ridges.

We interpret UCMP 175056 (Fig. 2B) as an incomplete left dorsal paramedian scute. The keel or boss is not preserved, but the ornamentation is clearly emanating from a point medial to the break, indicating that the scute was originally at least twice as wide as it is long (~ 20 mm). This scute is flatter (less flexed) than UCMP 175055.

Another scute, UCMP 175054 (Fig. 2C), is a dorsal parame-

TABLE 1. Distribution of juvenile *Stagonolepis* scutes from the Blue Hills (UCMP locality V7305) by size and anatomical position.

Small paramedians (Group1)	Larger paramedians (Group 2)	Small laterals (Group 3)	Smallventral/appendicular scutes (Group 4)
175051-175058	175059	175061-175062	175089
175060	175065	175064	175095
175063	175075?	175070	
175066-175067		175078-175079	
175072		175081-175083	
175074		175087-175088	
175076-175077		175092-175094	
175080		175096-175097	
175085-175086			
175098-175099			

dian scute that is too incomplete to assign to a side with certainty, although it appears to be a left. It is 16 mm long and more flexed or transversely arched than the other illustrated paramedian scutes. The ornamentation consists of pits that are more or less randomly arranged, although the ones nearest the edge of the scute are elongated into a more elongate set of furrows radiating from the center of the scute.

Similarly, UCMP 175051 (Fig. 2D) is probably an incomplete left dorsal paramedian scute. This scute is only slightly wider than long as preserved, but clearly was much wider originally. Although at first glance the pitting appears to be random, closer examination reveals that the pits are clearly arranged in a radial pattern, with a particularly striking alignment of five nearly equally sized pits emanating from the postero-central to antero-lateral margins.

Larger scute fragments

The larger scutes from UCMP 7308 tend to be poorly preserved. The best preserved of these, UCMP 175065 (Fig. 2E), is probably a lateral scute of a larger individual. There is a well-developed anterior bar and a clearly radial pattern of pits radiating from a well-developed median keel. This scute is 27 mm long and concave internally. UCMP 175065 and UCMP 175075 appear broadly similar and probably pertain to a similar-sized (if not the same) individual, but are not as well preserved as the smaller paramedian scutes illustrated here.

Small lateral scutes

Each of the lateral scutes we describe here are longer than wide and essentially flat except for a median ridge that rises from near the center of the scute and terminates at the center of its posterior margin. Otherwise, they are similar to paramedian scutes in possessing anterior bars and a radial ornament of pits and grooves. Some may be caudal dorsal paramedian scutes, but such scutes tend to have much more pronounced bosses, regardless of taxon, than is evident in this sample (Case, 1922, 1932; Long and Ballew, 1985; Long and Murry, 1995).

A typical lateral scute, UCMP 175087 (Fig. 2F), is 23 mm long and 15 mm wide, with a prominent keel running most of the length of the scute. The scute is not sharply flexed or angulated, but is slightly concave medially.

A similar scute, UCMP 175088 (Fig. 2G), is more equant (23 mm long, 18 mm wide) with a well-developed keel. The keel is very slightly offset from the center of the scute.

The largest of the presumed laterals, UCMP 175064 (Fig. 2H), is very similar to UCMP 175087 except that it is slightly longer (26 mm long, 19 mm wide)

Ventral/appendicular(?) scutes

The ventral portion of the aetosaur carapace is typically composed of 6-8 columns of scutes that are narrower than the dorsal paramedian scutes (Walker, 1961; Long and Ballew, 1985; Long and Murry, 1995). These scutes are seldom found articulated and are not often described (Case, 1932; Walker, 1961; Heckert and Lucas, 1999). Generally, these scutes are equant or nearly so (but can be longer than wide), and usually lack bosses or keels, but are similar to dorsal paramedian scutes in possessing an anterior bar or lamina and a similar pattern of pitting (Heckert and Lucas, 2000)

Similarly, appendicular scutes are known from *Stagonolepis* (Case, 1932; Walker, 1961), *Typothorax* (Hunt et al., 1993) and *Coahomasuchus* (Heckert and Lucas, 1999) but are seldom described in detail (Heckert and Lucas, 2000). Known appendicular scutes of aetosaurs are typically round and ornamented with pits in either a random or radial pattern (Heckert and Lucas, 2000). To date no one has attempted to identify aetosaurs to the genus-level using appendicular scutes.

One of the specimens we examined, UCMP 175089, is either a ventral or appendicular scute. It possesses both a median ridge and a radial pattern of faint pitting similar to the lateral scutes illustrated here, but lacks an obvious anterior bar and is more ovoid than most ventral scutes. The long axis is 21 mm long and the short axis is 14 mm wide. This scute most closely resembles appendicular scutes of *Stagonolepis*, but probably pertains to a larger (subadult?) individual. A similar scute, UCMP 175095, is slightly smaller (19 mm long, 13 mm wide) but otherwise similar. These are also similar to, but much larger than, the gular (throat) ventral scutes of *Coahomasuchus* (Heckert and Lucas, 1999). Such scutes have not been reported for *Stagonolepis*, but this may be an artifact of preservation. We consider UCMP 175089 and UCMP 175095 appendicular or ventral scutes of *Stagonolepis*.

MICROSCOPIC EXAMINATION

We examined one of the scutes we describe here, UCMP 175055, under the scanning electron microscope (SEM) (Fig. 3) to test our hypothesis that these were indeed juvenile scutes and not adult scutes of a small aetosaur superficially similar to *Stagonolepis*. We used the SEM to examine the scute in cross-section and look for evidence of remodelled bone, such as would be expected in an adult animal. What we found (Fig. 3B-C) was relatively undisturbed, laminar bone such as would be expected in a juvenile archosaur that had not experienced significant bone remodelling (e.g., Ricqlés, 1976; Horner et al., 2001). Consequently, we are confident that the scutes illustrated here are those of juvenile aetosaurs.

DISCUSSION

The diminutive scutes we describe here possess multiple diagnostic characteristics of the aetosaur *Stagonolepis*. These include anterior bars, moderately wide paramedian scutes , paramedian and lateral scutes with a dorsal knob contacting the posterior margin of the scute, radial (albeit weak) ornamentation of pits on the dorsal surface, and a lack of ventral keels. This combination of characters is known only in the aetosaur *Stagonolepis* (Heckert and Lucas, 2000). Because the scutes we identify here lack any remodeling of the bone, we believe that they represent juvenile individuals, and thus we can rule out the possibility that these scutes represent an adult of a new, small-bodied taxon closely allied to *Stagonolepis*.

Importantly, these scutes are distinct from the juvenile *Desmatosuchus* scutes from the same locality (Fig. 3I-K; Heckert and Lucas, 2002b). Juvenile *Desmatosuchus* (=*Acaenasuchus*) scutes differ from juvenile *Stagonolepis* scutes in the characteristics that differentiate adults of the two taxa. Thus, juvenile *Desmatosuchus*

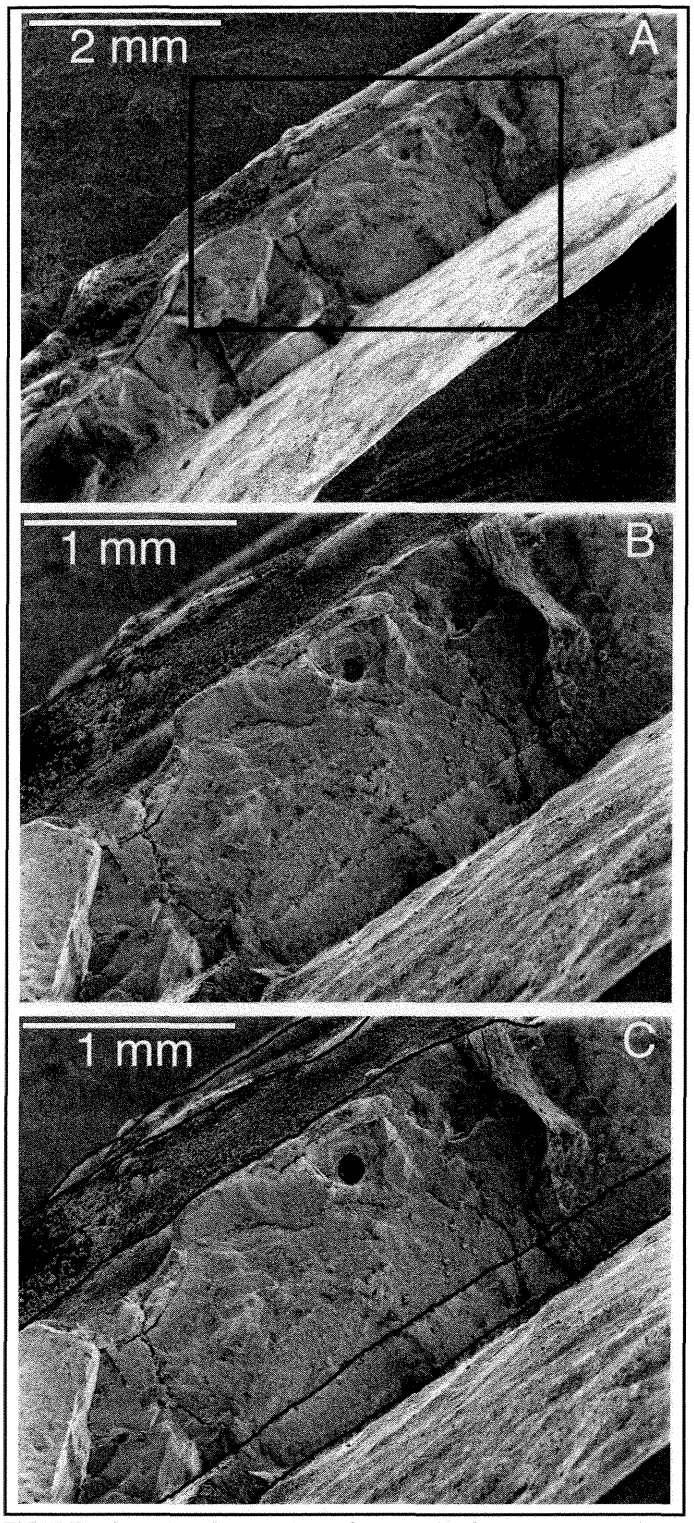

FIGURE 3. Scanning electron microphotographs showing a cross-section of a broken scute, UCMP 175055. **A**, Overview of cross-section; **B**, Close-up of area in box in A; **C**, Close-up with lines drawn showing laminar "layers" of bone that lack evidence of reworking.

scutes lack anterior bars, have a coarser and more random pattern of pitting, with less regular pits, and more pronounced knobs or even spikes on the lateral scutes. The differences between these scutes and the juveniles of *Stagonolepis* we identify here are thus at least as pronounced as the differences between adults of the two taxa (Heckert and Lucas, 2000).

We note here that we only assign the scutes we describe here to *Stagonolepis* sp. Presently, there are two recognized species of *Stagonolepis*, *S. robertsoni* Agassiz, 1844 and *S. wellesi* (Long and Ballew, 1985). Generally speaking, *S. wellesi* is much larger than *S. robertsoni* and typically has a more pronounced ornamentation, particularly in terms of the robustness of the knobs on the dorsal paramedian and lateral scutes (Long and Murry, 1995; Heckert and Lucas, 2000). Adult specimens of *Stagonolepis wellesi* are known from the same localities in the Blue Hills as the specimens described here (Long and Murry, 1995; ABH pers. obs.). *Stagonolepis robertsoni* is rarely preserved in the Chinle Group, although some isolated specimens may pertain to this taxon (Heckert et al., 1999). Elsewhere, *S. robertsoni* is known from the type locality (Lossiemouth Sandstone) in Scotland (Agassiz, 1844; Huxley, 1859, 1875; Walker, 1961), from the Alemoa Member of the Santa Maria Formation in Brazil (Lucas and Heckert, 2001), the Ischigualasto Formation in Argentina (Heckert and Lucas, 2002c) and, possibly, the Blasensandstein of Germany (Heckert and Lucas, 2000). The only one of these localities that may yield specimens of *S. wellesi* is the Ischigualasto Formation (Heckert and Lucas, 2002c). In general, the Blue Hills scutes more closely resemble those of *S. robertsoni* than *S. wellesi*. Thus, there are two possibilities for the Blue Hills scutes: (1) they represent very young juvenile individuals of *S. wellesi*, and the ornamentation of these juveniles is closer to that of *S. robertsoni* than that of adult *S. wellesi*; or (2) they represent slightly older individuals of the smaller *S. robertsoni*. Given that *S. wellesi* is much more common in the Chinle than *S. robertsoni*, and is in fact already known from the Blue Hills from several specimens of adults, we suspect that the scutes described here are juveniles of *S. wellesi*. Additional specimens are clearly necessary to test this and the resulting hypotheses, one of which is that smaller aetosaur taxa may be the result of heterochronic processes operating during aetosaur evolution.

CONCLUSIONS

This study demonstrates that the same criteria used to distinguish aetosaur taxa hold true when applied to smaller (juvenile) scutes. Indeed, careful observation and measurement of small aetosaur scutes distinguish common taxa such as *Desmatosuchus* and *Stagonolepis*, even when they co-occur at the same locality. Consequently, small aetosaur scutes should provide the same biostratigraphic resolution obtained by using larger, presumably adult, scutes.

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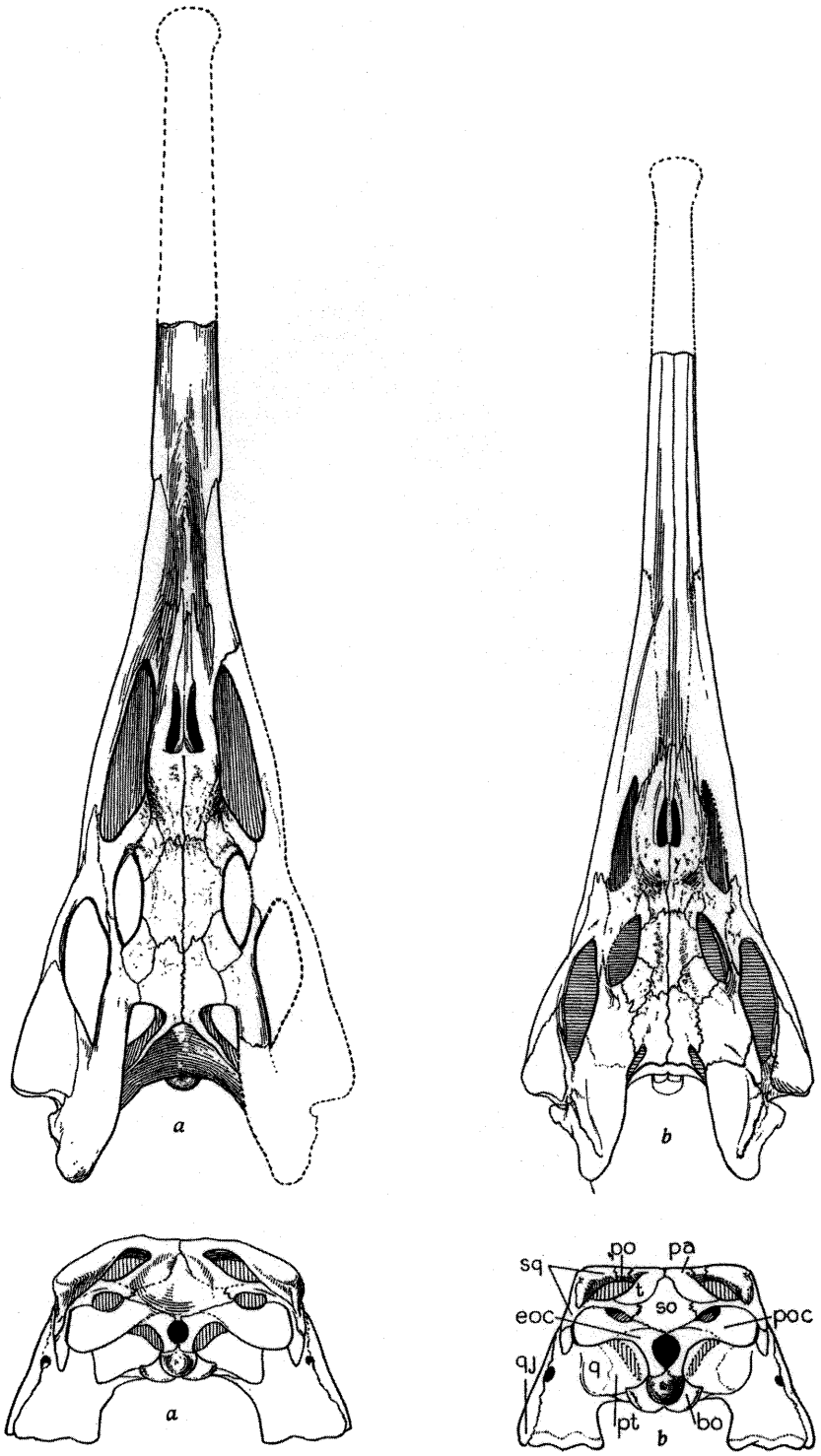

a, *Machaeroprosopus lithodendrorum*, 7034/26719 and *b*. *M. tenuis* (type), 7043/27018, x 1/6 (from Camp, 1930, fig. 2, p. 21).