

A reevaluation of the enigmatic Permian synapsid *Watongia* and of its stratigraphic significance

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Abstract: The enigmatic synapsid *Watongia*, initially described on the basis of fragmentary remains from the Chickasha Formation of Oklahoma as an early therapsid (a gorgonopsian), is redescribed and is shown to represent the largest known varanopid synapsid. Its assignment to the Varanodontinae (Varanopidae: Synapsida) is supported by several diagnostic features, including a strongly recurved marginal dentition with both posterior and anterior, unserrated, cutting edges, quadratojugal with two discrete superficial rami, a large lateral tuberosity on the postorbital, short, deep excavations on the neural arches, and a broad, short radiale. The presence in *Watongia* of a posterolateral process of the frontal precludes therapsid or sphenacodontid affinities. The previously described preparietal that provided the strongest evidence of therapsid affinities for *Watongia* is shown to be based on misinterpreted skull fragments that were incorrectly assembled. The presence of a varanopid in the Chickasha Formation is consistent with a Guadalupian age (Middle Permian), and in the absence of large sphenacodontids and therapsids, *Watongia* was probably the top predator of its terrestrial vertebrate community.

Résumé : Le synapside énigmatique *Watongia*, fondé sur un fossile fragmentaire de la Formation Chickasha de l'Oklahoma avait été initialement classé parmi les thérapside (parmi les gorgonopsiens). Notre étude démontre que *Watongia* représente le plus grand varanopidé connu. Son appartenance au taxon Varanodontinae (Varanopidae: Synapsida) est soutenue par plusieurs caractères diagnostiques, incluant la forme des dents, qui sont incurvées vers l'arrière, un quadratojugal avec deux processus superficiels, une grande protubérance latérale sur le postorbitaire, des excavations courtes et profondes sur les arcs neuraux, et un os radial nettement plus large que long. Des états primitifs de *Watongia* qui indiquent que ce taxon n'est ni un thérapside, ni un sphenacodontidé incluent un procès postérolatéral du frontal. Le préparietal précédemment décrit, qui fournissait la preuve la plus convaincante que *Watongia* était un thérapside, était fondé sur une interprétation de fragments crâniens qui avaient été inoprement assemblés. La présence d'un grand varanopidé dans la Formation Chickasha est compatible avec l'âge Guadalupien (Permien Moyen) de cette formation, et *Watongia* était probablement un des plus grands prédateurs terrestres de sa communauté.

Introduction

The pioneering work of Olson (1962, 1968) in the Chickasha Formation (Permian) of Oklahoma has resulted in the discovery of an unusual assemblage of continental vertebrates in sediments that have been suggested to be of Guadalupian age (Fay 1964). According to the most recent chronostratigraphic subdivisions of the Permian, the Guadalupian corresponds to the Middle Permian (Jin et al. 1997). This age assignment for the Chickasha Formation has been recently the subject of dispute, with Reisz and Laurin (2001) presenting continental vertebrate evidence for a Guadalupian age (Middle Permian) of the Chickasha Formation, and Lucas (2002) arguing that a late Leonardian age (Early Permian) was more likely. This disagreement is based mainly on the apparent

conflicting evidence provided by terrestrial vertebrate and marine invertebrate fossils. Whereas the recent evidence provided by the terrestrial vertebrates (Reisz and Laurin 2001) is particularly striking and strong, with the same taxon (*Macroleter*) being present in Oklahoma and Northern Russia, the contrary evidence provided by the marine invertebrates is more open to dispute (see Discussion in Reisz and Laurin 2002).

This continental vertebrate assemblage of the Chickasha Formation is characterized by the presence of caseids, varanopids (see Reisz and Dilkes (2003) for an explanation for the use of this taxonomic designation), captorhinids, and the parareptile *Macroleter*. Similar faunal assemblages are found in Russia in the late Kazanian Mezen basin and Pinega (Reisz and Laurin 2001). In contrast to the abundance of

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Fig. 1. Skeletal elements of *Watongia meieri* UCMP 143278: (A) Left scapula and cleithrum in medial view; (B) left interclavicle in ventral and dorsal views; (C) left ulna in ventral and dorsal views; (D) humerus in distal ventral and proximal ventral views; (E) skull fragment from the left side of the supraorbital region in ventral and dorsal views; and (F) skull fragment from the right side of the supraorbital region in ventral and dorsal views. cl, cleithrum; del, deltoideus process; ec, ectepicondyle; en, entepicondyle; f, frontal; im, impression of bone, indicating extent of ulna; p, parietal; pep, pectoralis process; pf, postfrontal; sc, scapula; sp, supinator process.

continental vertebrate fossils in Mezen and Pinega, few, incomplete specimens represent the Chickasha fauna. Thus, the affinities of many of these specimens were difficult to evaluate. Recent studies of parareptiles (Ivakhnenko 1987; Ivakhnenko et al. 1997), including new materials from the Mezen complex (Reisz and Berman 2001), have enabled us to determine that the only known presumed *Seymouria* specimen of the Chickasha Formation is in fact *Macroleter*, formerly thought to have been endemic to, and a common member of, the Mezen fauna (Reisz and Laurin 2001). This new interpretation is more consistent with the idea that the Chickasha Formation is of Guadalupian age, because *Seymouria* is otherwise only known in the Wolfcampian and Leonardian.

The last vertebrate of the Chickasha assemblage to be described was *Watongia*, an enigmatic form that Olson (1974) placed within the Family Gorgonopsidae, a group of therapsids that is normally restricted to Upper Permian sediments of Russia (Ivakhnenko et al. 1997) and South Africa (Smith and Keyser 1995). Our reexamination of these remains reveals that *Watongia* is in fact a varanopid synapsid, and this strengthens our conclusion that the Chickasha fauna is part of the caseid–varanopid complex. This discovery also results in increasing significantly our understanding of varanopid evolution.

Institutional abbreviations

BP, Bernard Price Institute for Paleontology, University of the Witwatersrand, Johannesburg, South Africa; UCLA VP: University of California at Los Angeles, Vertebrate Paleontology collection, USA; UCMP: University of California Museum of Paleontology, Berkeley, USA.

Systematic paleontology

Synapsida Osborn, 1903

Eupelycosauria Kemp, 1982

Varanopidae Romer and Price, 1940

Varanodontinae Reisz and Berman, 2001

Watongia meieri Olson, 1974

HOLOTYPE: UCMP 143278, formerly UCLA VP 3132, skull fragments, incomplete forelimbs, and shoulder girdle, and a few vertebrae, gastralia, and ribs (Figs. 1–5).

REVISED DIAGNOSIS: Very large varanopid characterized by the presence of a distinct canine that is at least twice the size of other maxillary teeth, and a large postfrontal; other potential autapomorphies include the presence of a strongly curved radius, very large pisiform, greatly reduced head of clavicle, narrow scapula.

Shares with *Varanodon* and *Aerosaurus* the presence of a massive, sculptured postorbital tubercle.

HORIZON AND LOCALITY: Chickasha Formation, level of middle part of Flowerpot Formation, El Reno Group, Guadalupian,

Middle Permian. From locality BC7 (Olson 1965), NW1/4, NE1/4, Section 33, Township 18N., Range 11E., Blaine County, Oklahoma.

Description and comparison

The holotype and only known specimen of *Watongia* (UCMP 143278) is represented by the disarticulated, somewhat scattered, fragmentary remains of a single skeleton in red, sandy shale. Only the anterior part of the skeleton was preserved; the skull had weathered out, and most of it had disintegrated and washed away. The skull fragments include two recognizable pieces of the skull table in the region of the frontal–parietal suture with part of the orbital margin (Figs. 1E, 1F), a fragment of the postorbital bone, the posterior fragment of the quadratojugal, and fragments of the maxilla with broken pieces of teeth attached to them (Figs. 2A–2C). Parts of the postcranial skeleton are also preserved, including several anterior vertebrae (Fig. 3), rib fragments, as well as parts of the left scapula and cleithrum (Fig. 1A), part of the interclavicle (Fig. 1B), and left clavicle (Fig. 4A). In addition to some gastralia, parts of the right and left forelimbs are also preserved (Figs. 1C–1D, 4B, 5).

Olson described a poorly preserved fragment of the skull table that he interpreted as showing a preparietal bone. This skull fragment provided the strongest evidence for the therapsid affinities of *Watongia*, even though other aspects of this fragment were inconsistent with this assignment. For example, the shape of the suggested anterolaterally oriented parietal–frontal suture, and the large size of the suggested preparietal were not seen in any known gorgonopsian or therapsid. We have carefully examined this piece of the skull table and found that it was composed of three pieces that were glued together with heavy, thick glyptal. When we dissolved the glue with acetone, two of the contact surfaces that were obscured by glue were revealed to lack any contiguity, indicating that two of the three pieces that formed the so-called preparietal did not belong together. More importantly, the disarticulated pieces gave us a very different picture of the skull roof of *Watongia*. The larger of the two pieces (Fig. 1F) includes mainly the orbital portion of the right frontal, part of the right postfrontal, and a small medial fragment that can be readily interpreted as an anteromedial process of the right parietal, rather than the preparietal as interpreted by Olson. Unlike in sphenacodontids, the dorsal surface of the frontal does not have a transverse suture with the parietal. Instead, as in varanopids and most non-sphenacodontid Permian–Carboniferous synapsids, the frontal extends an acuminate posterolateral process between the parietal and postfrontal (Fig. 6). Posterolaterally, a fragment of the right postfrontal and its orbital margin are preserved. The relative size and shape of this portion of the postfrontal is somewhat different from some varanopids, incising more deeply the frontal, and consequently being broader in the orbital region than in forms

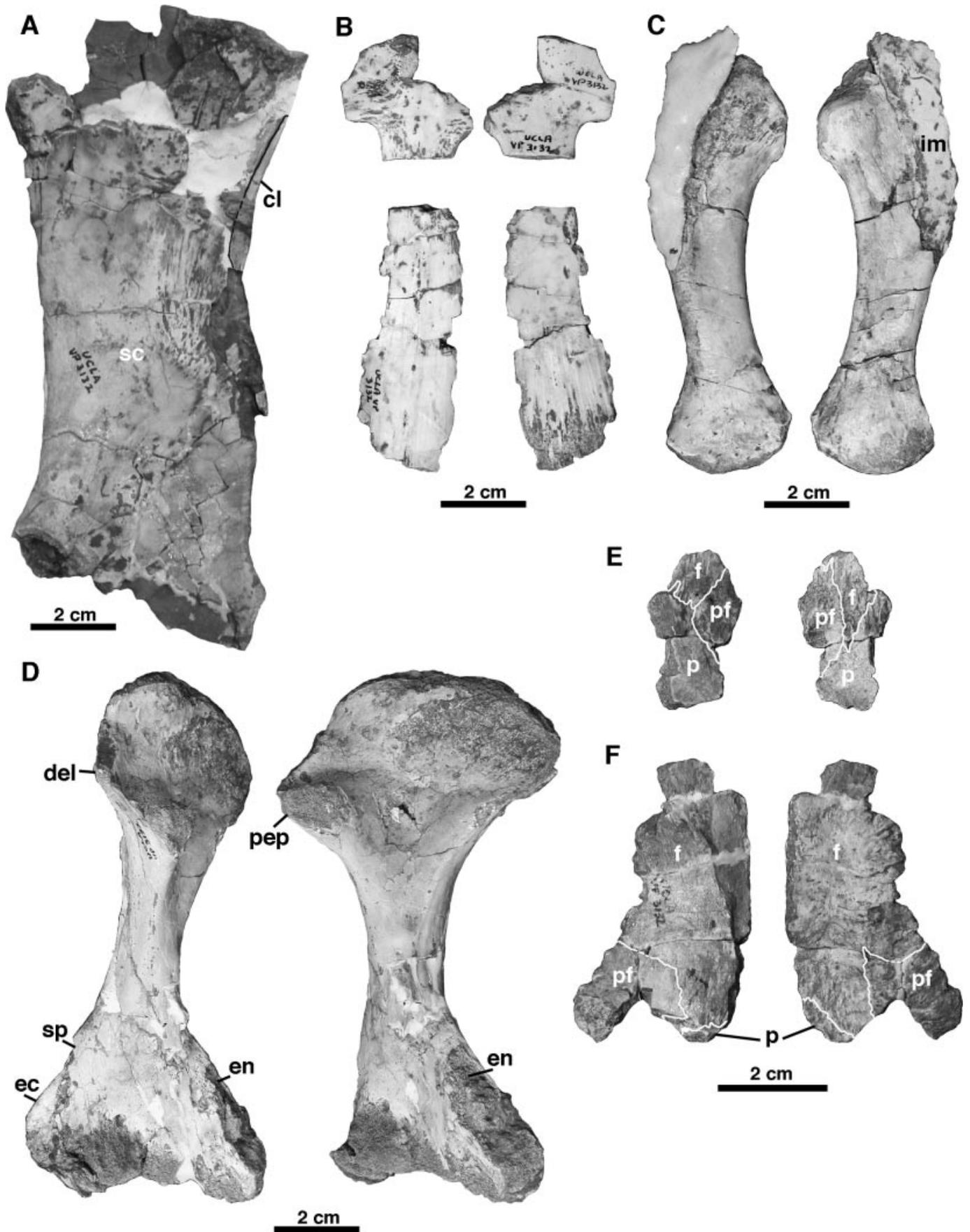


Fig. 2. Skeletal elements of *Watongia meieri* UCMP 143278: (A) Marginal tooth in medial, anterior, and occlusal views; (B) right quadratojugal in lateral and medial views; and (C) lateral tuberosity of the right postorbital in dorsal and lateral views.

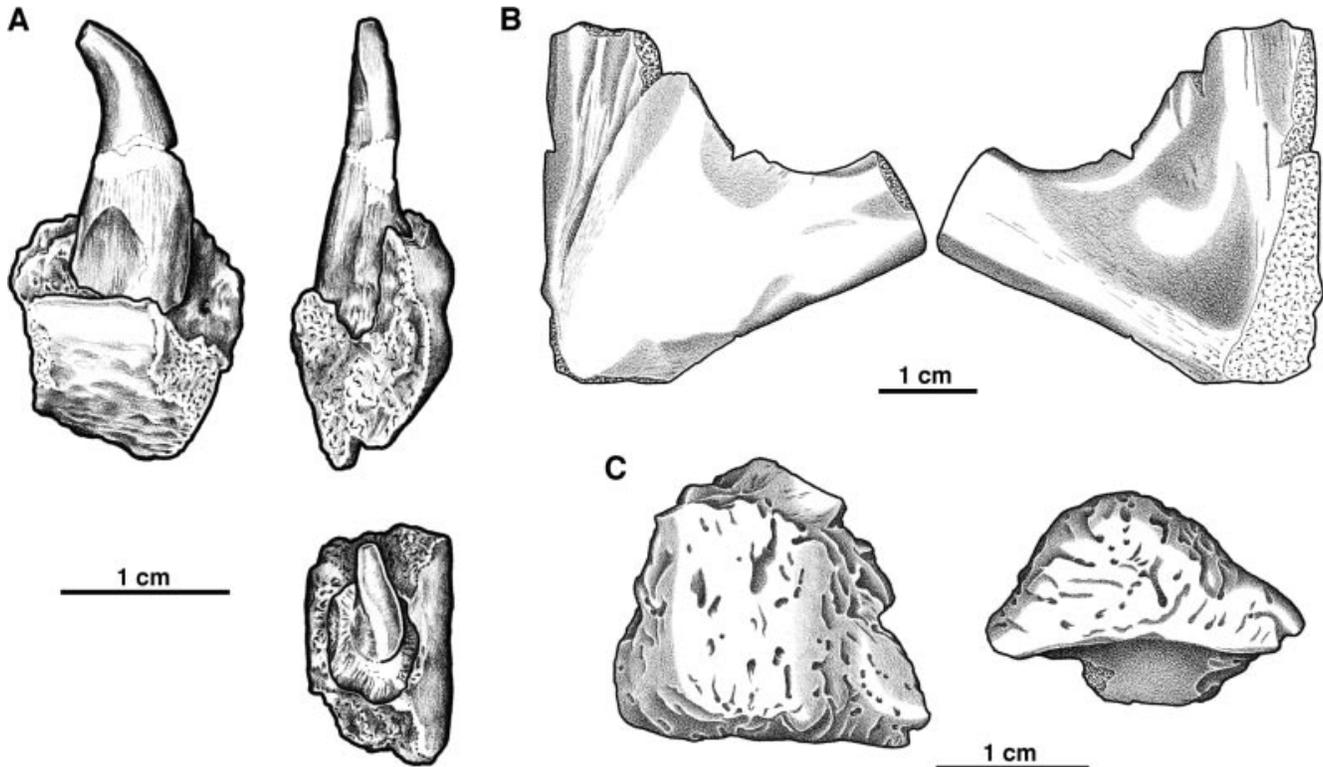
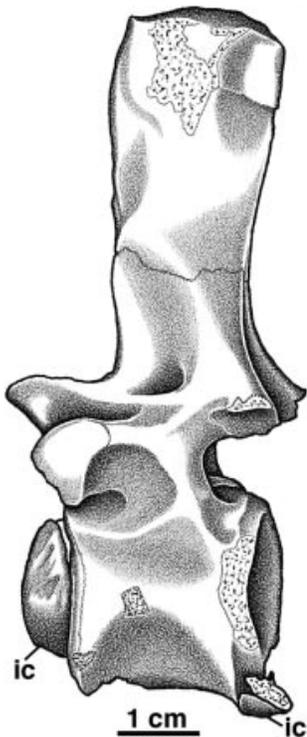


Fig. 3. Anterior dorsal vertebra of *Watongia meieri* UCMP 143278, in lateral view. ic, intercentrum.

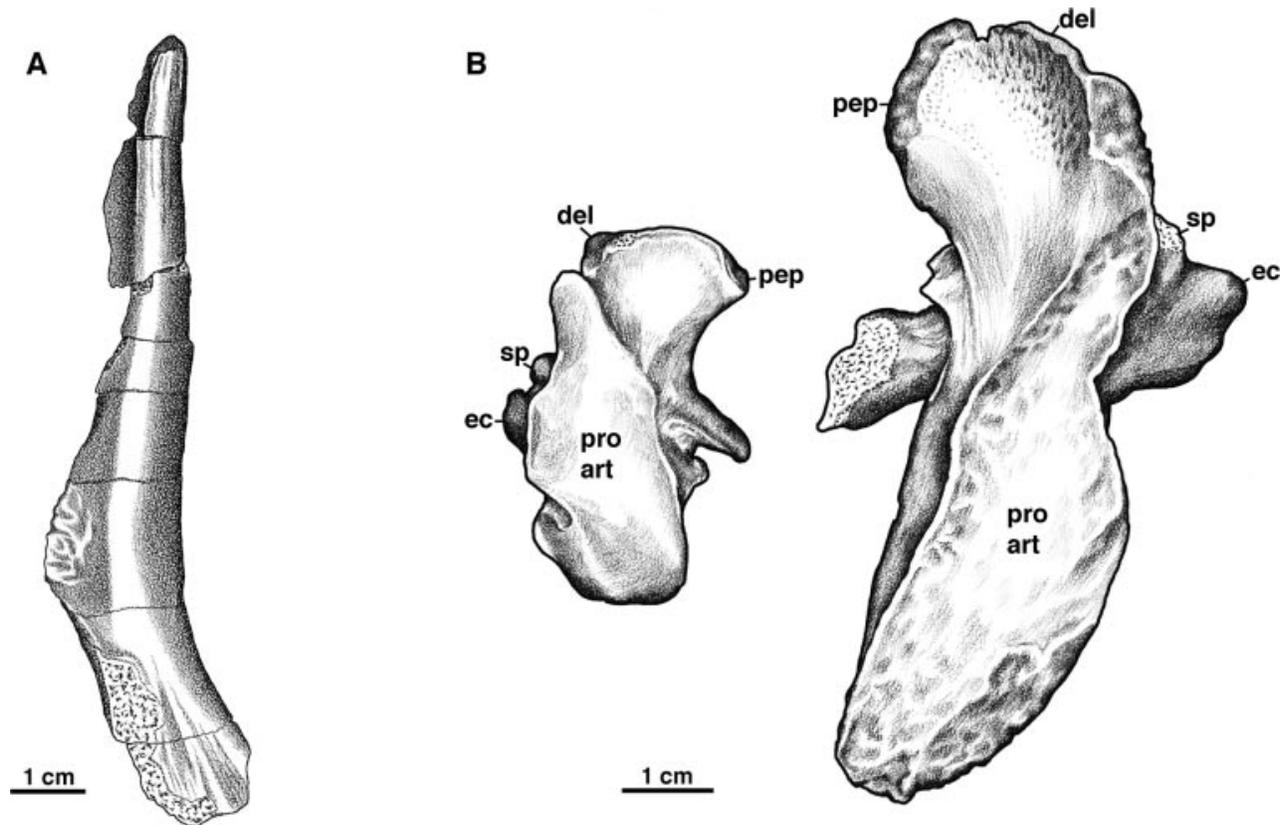


like *Aerosaurus* (Langston and Reisz 1981) or *Varanodon* (R. Reisz, personal observation). In this respect, *Watongia* resembles more closely the condition seen in *Varanops*.

The second, smaller fragment of the skull roof (Fig. 1E), which was incorrectly attached to the larger piece, can be recognized to belong to the left side of the skull table in the same general area as the larger piece and represents the same skull elements, the posterior V-shaped posterolateral process of the frontal, a fragment of the left parietal medial to the frontal, and a fragment of the postfrontal lateral to the frontal. Both of these fragments are entirely consistent with the pattern of the skull roof of varanopid synapsids (Reisz and Berman 2001), as seen in Fig. 6, and entirely different from those of sphenacodontians and therapsids.

Olson (1974) was quite correct in recognizing the presence of a caniniform tooth among the broken teeth that have been recovered, but the known fragments of the maxilla do not offer us any useful information about the length of the tooth row. Among the numerous fragments of this animal that were collected by Olson, there were three fragmentary tooth crowns. After extensive study of the maxillary fragments, a good contact was discovered between one of these teeth and one of the tooth bases (Fig. 2A). This allowed us to describe for the first time the nature of the dentition in *Watongia*. The maxillary tooth has a broad base and a strongly recurved crown, similar in outline to the teeth of *Aerosaurus* and *Varanodon*. As in these taxa, well-developed anterior and posterior cutting edges are present along most of the height of the crown, and the preservation is of sufficiently high quality to determine that both cutting edges lacked serrations, in contrast to the condition seen in more basal varanopids.

Fig. 4. Left clavicle of *Watongia meieri* UCMP 143278 in medial view (A), and left and right humeri of *Varanops* and *Watongia* in proximal articular view. pro art, proximal articular surface; del, deltoideus process; ec, entepicondyle; pep, pectoralis process; sp, supinator process.



Among the disarticulated pieces of skull that were not described by Olson (1974), we were able to recognize two skull fragments, parts of the right quadratojugal and postorbital that exhibit diagnostic features of varanopid synspsids. We recognized these elements because our understanding of varanopid cranial anatomy has increased significantly in the last three decades, with the redescription of several taxa (Langston and Reisz 1981; Berman and Reisz 1982; Reisz et al. 1998; Reisz and Berman 2001).

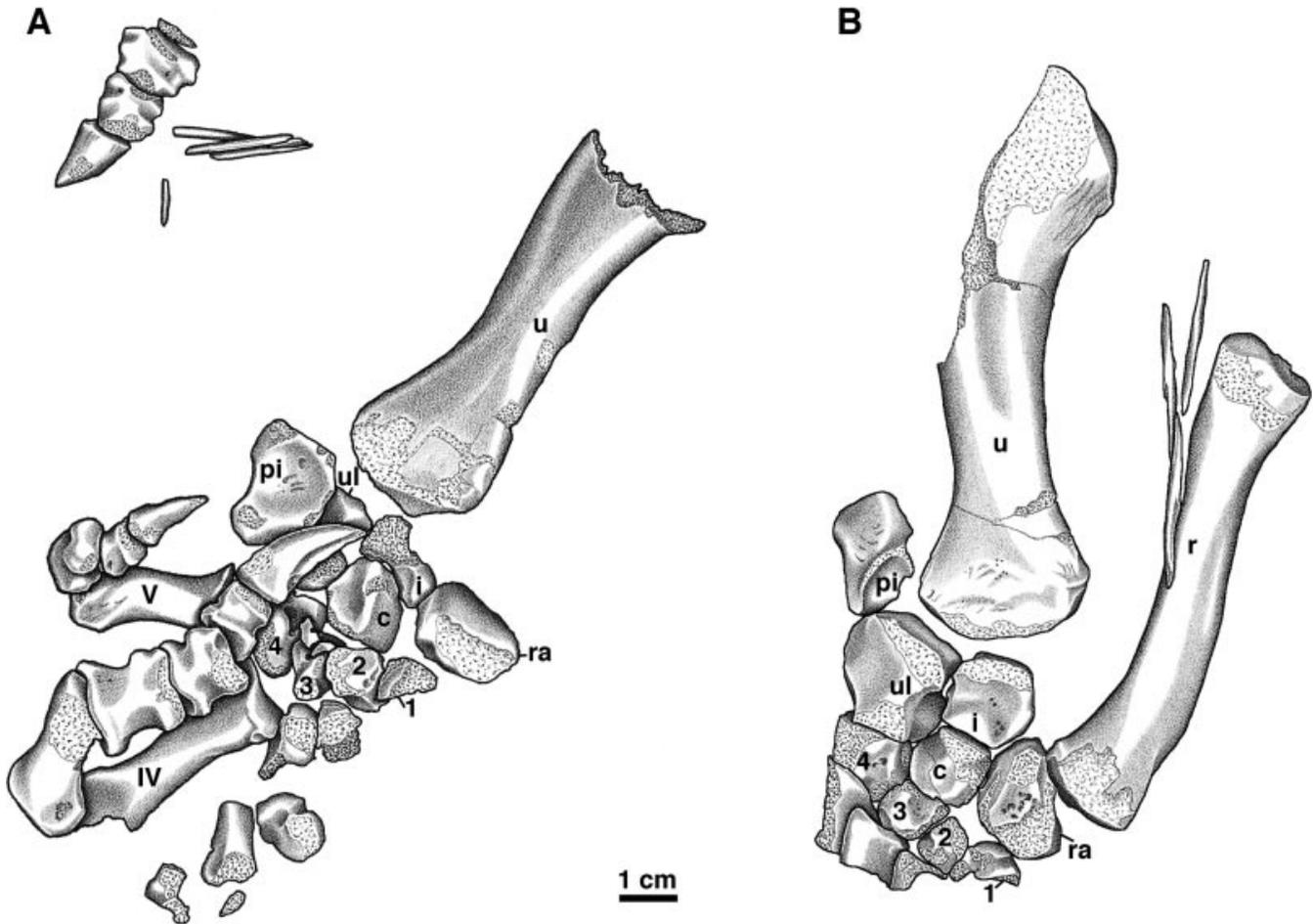
We identified the large fragment of the left quadratojugal (Fig. 2B) on the basis of comparisons with that of *Varanodon*. The fragment consists of the posteroventral portion of the bone, which forms distinct borders of the temporal fenestra and of the ventral and posterior edges of the skull. In lateral view the bone bears a series of striations that mark the sutural contact with the squamosal, where this bone overlies the quadratojugal. The anteroventral process of this bone represents the subtemporal bar, and it forms both the ventral edge of the skull and the posteroventral corner of the temporal fenestra. In all these features, this element is similar to that seen in *Varanodon* (Fig. 6) and *Aerosaurus* (Langston and Reisz 1981, fig. 4), although the angle formed between the subtemporal and posttemporal rami is less acute in *Watongia* than in the other two varanodontines. The morphology of this element is unique to varanodontine synspsids, and its presence in *Watongia* provides strong evidence that it belongs to this taxon.

Similarly, it was possible to recognize another autapomorphic

feature of varanopid synspsids, the lateral process or tuberosity of the postorbital bone (Fig. 2C). This distinct process of the postorbital bone is present in all Permian mycterosaurine and varanodontine varanopids where this area is preserved. It is readily recognizable in *Mesenosaurus* (Reisz and Berman 2001), *Elliotsmithia* (Reisz et al. 1998), *Varanodon*, and *Aerosaurus* (R. Reisz, personal observation). The lateral process is developed to its greatest extent in the late varanopids *Varanodon* and *Elliotsmithia*, where it forms a distinct, ornamented tuberosity. This is also the case for *Watongia*. Unfortunately, this region of the skull is more difficult to interpret in other varanopids. For example, the lateral surface of the postorbital bone is damaged on both sides of *Mycterosaurus* FMNH-UC 692 (Berman and Reisz 1982, fig. 2), so that a modest lateral process of the postorbital is only partially preserved on the left side. The left postorbital of another specimen of *Mycterosaurus*, FMNH-UC 169 (Berman and Reisz 1982, fig. 6A) is also partially preserved and shows a lateral process at the posterodorsal corner of the orbit. The primitive condition (absence of lateral process of postorbital) is represented by a Carboniferous basal varanopid (Reisz and Dilkes, 2003) from Kansas.

Olson compared the skull elements that he used for the original description of *Watongia* with those of *Dimetrodon* and came to the conclusion that the skull was probably 24–26 cm in length. However, we disagree with this interpretation because the proper comparison is with a varanopid like *Varanodon*, rather than the much more massively built *Dime-*

Fig. 5. Articulated portions of the right (A) and left (B) forelimbs of *Watongia meieri* UCMP 143278. c, centrale; i, intermedium; pi, pisiform; r, radius; ra, radiale; u, ulna; ul, ulnare; 1–4, distal carpals; IV–V, metacarpals.



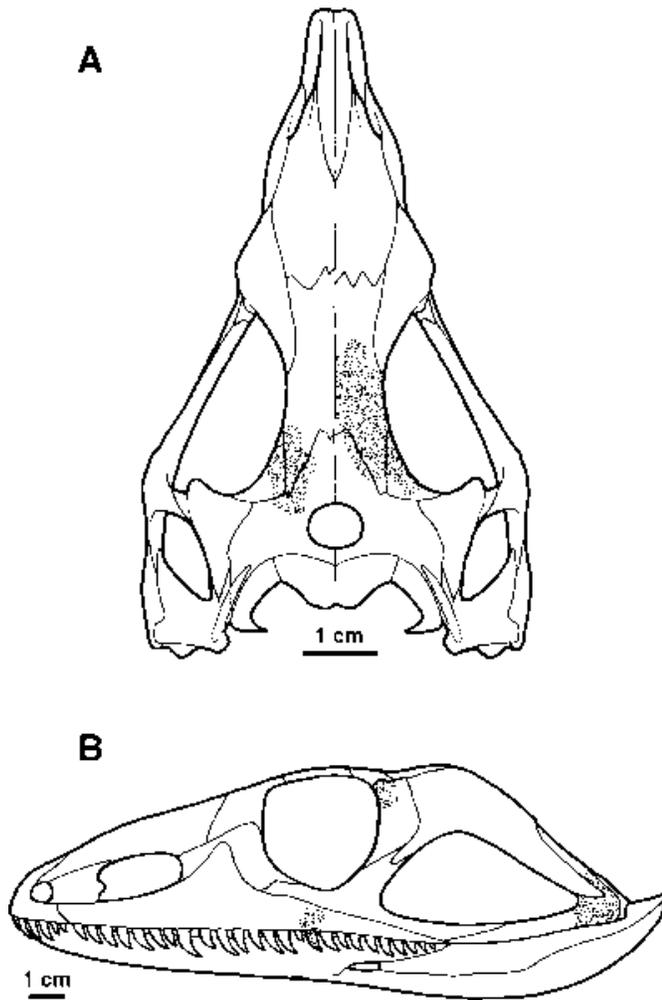
trodon. None of the skull table elements are sufficiently complete to give us the opportunity to establish with any confidence the length of the skull. The only available measurement is the width of the frontal at the level of the orbital contact between the frontal and postfrontal bones. If our identifications of the quadratojugal and postorbital tubercle are correct, then comparisons with the appropriate parts of the *Varanodon* skull indicate that *Watongia* is significantly larger. A more reliable estimate of body size in *Watongia* is based on the well-preserved vertebrae (See Table 1 for comparative data), indicating an estimated length of about 2 m.

The axial skeleton is represented by several vertebrae, including a complete anterior dorsal vertebra (Fig. 3). In contrast to therapsids (Orlov 1958), this dorsal vertebra has a well-preserved intercentrum and an anteroposteriorly broad neural spine that is subrectangular in lateral view and almost as long as the centrum. The general proportions of the neural spine are similar to those of *Varanops* and *Varanodon*, and at its base is a deep lateral excavation. This relatively short, deep neural excavation of the vertebra differs from those of sphenacodontids, which tend to be anteroposteriorly elongate. As in the other large varanopids, the body of the centrum is pinched strongly ventrally to form a narrow ridge, but not the sharp keel that is present in sphenacodontids. The known

vertebrae of *Watongia* are indistinguishable from those of *Varanops* and *Varanodon*, except for their much larger size (Table 1).

The preserved shoulder girdle elements include a nearly complete left clavicle and left cleithrum, a partial interclavicle, and left scapula. The clavicle (Fig. 4A) is much more slender than that of sphenacodontids or edaphosaurids, which have exceedingly broad heads. In varanopids the head tends to be quite slender, but still remains distinct from the shaft. The clavicular head of *Watongia* is closest in proportions to that of *Varanodon* and slightly more slender than in either *Varanops* or *Aerosaurus*. The cleithrum (Fig. 1A) appears to be complete and is exceedingly slender, much more slender than in *Varanodon* and may represent an autapomorphy of *Watongia*. The interclavicle is too fragmentary to provide much useful information but has no therapsid-like lateral expansion of the shaft and is generally similar to those of Permo-Carboniferous synapsids (Fig. 1B). Unfortunately, the interclavicle is poorly known in other varanopids, preventing comparisons within this clade. The scapula also lacks any diagnostic features that would help in assigning *Watongia* to a particular clade of synapsids, although it could be used to suggest that it is not a therapsid because it is more primitive in having a comparatively wide blade (Fig. 1A). The striations on the medial surface of the blade, close to the location of the

Fig. 6. Skull reconstructions of *Mesenosaurus* in dorsal view and *Varanodon* in lateral view, showing in dark patches the location of the known skull fragments of *Watongia* UCMP 143278, from Figs. 1E–1F, and 2B–2C, respectively.



clavicular tip, are more striking than in other synsapsids, but may only be considered as a potential diagnostic feature of *Watongia*.

Both forelimbs are partially preserved, providing information on the anatomy of the humerus, radius, ulna, and manus. Contrary to Olson's interpretation of these elements, all the available evidence is consistent with varanopid affinities for *Watongia*. Olson argued that the forelimbs showed a combination of sphenacodontid and therapsid features, with the humerus, radius, and ulna resembling more those of therapsids, and manus being more similar to those of sphenacodontids. We disagree with this interpretation. For example, the humerus (Figs. 1D, 4B) was more severely damaged than Olson realized; thus, several basal synapsid features were obscured. For instance, the entepicondyle is large, and the supinator process is widely divergent from the shaft, but there is no ectepicondylar foramen. As in varanopids, the humerus is lightly built, with a relatively long, slender, rounded shaft and broadly expanded proximal and distal ends. Although damaged at both ends to some extent, it is possible to determine that both humeri were flattened, reducing their original torque to slightly above 60°. In

addition, the proximal head has similar proportions to that of varanopids, with much of the head lying in a single plane, and its articular surface running along much of the head. As in *Varanops* and *Aerosaurus* (Fig. 4B), there is a well-developed deltopectoral crest that is set well off from the proximal head, with an accessory ridge that runs ventrally from the ventral surface of the proximal head to the crest. Between the accessory ridge and the deltopectoral crest a moderately concave surface is present. This is similar to the condition seen in other varanopids and in strong contrast to the condition seen in sphenacodontians and therapsids, where the accessory ridge is absent or poorly developed. At the distal end of the humerus, a significant portion of the entepicondyle is missing, as indicated by the thickness of the broken surface, and only the medial edge of the entepicondylar foramen is preserved. Olson was quite correct in indicating that there was no ectepicondylar foramen, but nevertheless failed to recognize the large base of the damaged supinator process. In all of these features, the humerus of *Watongia* is similar to those in *Varanops*, *Aerosaurus*, and *Mycterosaurus*, in which the humerus is well preserved. There are no specifically therapsid features in the humerus of *Watongia*.

Both the radius and ulna of *Watongia* (Figs. 1C and 5) resemble closely those of the varanodontines *Varanodon* and *Varanops*. These elements are not well preserved in *Aerosaurus*. The radius of *Watongia* is very short, compared with its humerus (Table 1). As in the other varanodontines just mentioned, the radius has a strong curvature along its shaft, and the ulna has an unusually modest, thin olecranon. The latter feature is in strong contrast to the primitive amniote condition of a tall, massive olecranon seen in other basal synsapsids.

The preserved left and right manus of *Watongia* (Fig. 5) show the primitive synapsid condition of a large pisiform, a wide, robust intermedium, and relatively broad, spatulate terminal phalanges. As in other varanodontines, the pisiform is unusually large relative to other parts of the manus, the radiale is unusually short and broad, and the 4th metacarpal is disproportionately long and broad, nearly twice the length of the 5th metacarpal. Comparisons with the manus of *Aerosaurus* may be misleading because the only known remains of this part of the skeleton belongs to the holotype, which is an immature individual. Therefore, the proportions of the manus and the shape of the phalanges are misleading, giving the impression of a slender, elongate manus. The typical varanodontine proportions of the limb are more properly represented by the adult pes of this specimen (UCMP 40097), which shows a relatively short, broad tarsus and broad, spatulate terminal phalanges. This is also the condition seen in the manus of *Varanodon*. In particular, the terminal (ungual) phalanges of these forms differ significantly from those of sphenacodontids and early therapsids in being broad and spatulate, the primitive condition for synsapsids, rather than transversely slender and elongate.

Phylogenetic analysis

We coded *Watongia* in the data matrix of Reisz and Dilkes (2003) and added a few characters (Table 2) that would allow us to determine the relationships of this taxon within the Varanopidae. Reptilia was used as the outgroup. The state for each character was reconstructed for Reptilia, by

Table 1. Size of varanopids.

Taxon	Maximal centrum length (mm)	Estimated total body length, including tail (m)	Radius length (mm)	Humerus length (mm)
<i>Varanops brevirostris</i>	13	1.10	62	73
<i>Aerosaurus greenleeorum</i>	12	1.02	—	—
<i>Varanodon agilis</i>	17	1.2–1.4	57	124
<i>Watongia meieri</i>	26	2.0	86	130
<i>Dimetrodon milleri</i>	27	1.95	—	150
<i>Dimetrodon booneorum</i>	25	2.18	119	144
<i>Titanophoneus potens</i>	39.9	3.39	181.0	244

Table 2. Characters added to the matrix of Reisz and Dilkes (2003) and character coding for *Watongia*.

(54) Supraglenoid foramen: present (0); absent (1)								
(55) Clavicular head: large (0); small (1)								
(56) Radiale maximum width/length ratio: 1 or less (0); > 1 (1)								
(57) 5th/4th metacarpal length ratio: 0.65 or more (0); < 0.65 (1)								
(58) Phalangeal length/width ratio: 2 or more (0); < 2 (1)								
Character number	5	10	15	20	25	30	35	40
State in <i>Watongia</i>	??11?	??21?	1?1??	??1??	?????	?????	1??21	??22?
Character number	45	50	55					
State in <i>Watongia</i>	??21?	?1???	??211	111				

Note: For the definition of the character states, see Reisz and Dilkes (2003).

checking basal parareptiles and eureptiles for character congruence. Analysis of the matrix in PAUP* 4.0b10 (Swofford 1998) using the Branch and Bound algorithm yielded five equally parsimonious trees, with a single polytomy close to the base of Varanopidae (Fig. 7A). The 50% majority-rule consensus tree is fully resolved (Fig. 7B). Removal of the problematic varanopid from South Africa BP/1/5678 (Modesto et al. 2001) yielded a single most parsimonious tree of the same topology as the 50% majority-rule consensus tree (Fig. 7B). One thousand bootstrap replicates (using the Branch and Bound algorithm) were performed to assess the robustness of the tree, and a decay analysis was performed for the same purpose.

The results show that some clades are very robust, with bootstrap frequencies above 90% and decay indices of at least 3. In particular, the position of *Watongia* appears to be very robust because its sister-group relationship with *Varanodon* and the clade that includes these two taxa, *Aerosaurus* and *Varanops*, are among the most robust of the phylogeny. Thus, despite the fragmentary nature of the specimen, the position of *Watongia* among varanopids appears to be unproblematic. By contrast, the positions of the mycterosaurines and of *Elliotsmithia* appear much less secure.

Discussion

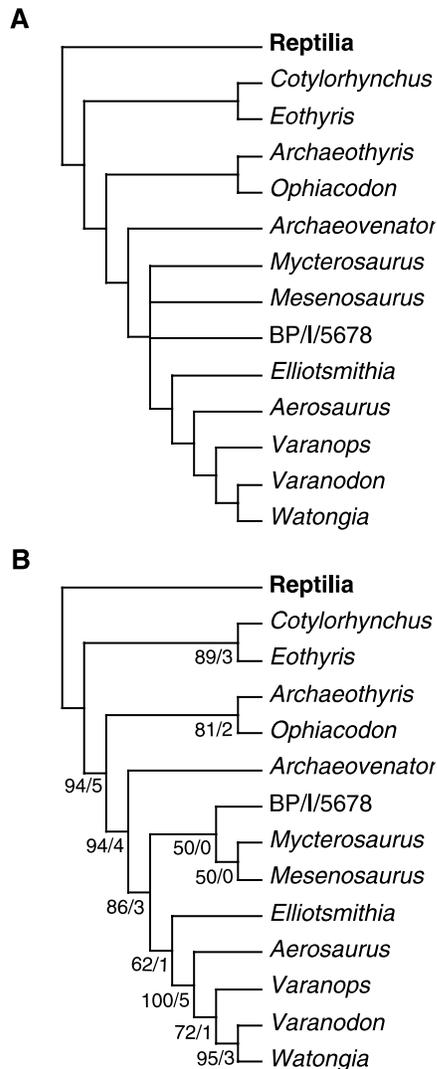
The available osteological evidence, although scant and fragmentary, provides sufficient data to indicate that *Watongia* is a varanopid, a member of Varanodontinae (Reisz and Berman 2001). *Watongia* is by far the largest known varanopid, much larger than even the largest previously known form, *Varanodon* (Table 1). Further evidence that *Watongia* is not a therapsid is provided by its primitive bone histology (Ricqlès 1976,

p. 129), which is entirely “pelycosaurian” in nature and unlike that of any known therapsid.

It is somewhat puzzling that Olson ignored the clearly varanopid features of this animal, especially in view of his earlier description of *Varanodon*. However, several factors seem to have conspired to mislead him: (1) The skeletal remains of *Varanodon* are not very well preserved and were distorted by dorsoventral flattening; (2) the existence of such a large varanopid, as indicated by the skeletal remains of *Watongia*, was totally unexpected; and (3) Olson was intensely searching for therapsid remains in the Guadalupian of Oklahoma to match his supposed therapsids from Texas. It is noteworthy that, as is the case for *Watongia*, reexamination of all his proposed therapsids from North America has resulted in the recognition that they represent the extremely fragmentary, distorted remains of caseids and sphenacodontids (Sidor and Hopson 1995).

Contrary to most Permo-Carboniferous groups of synapsids, varanopids continued to diversify during the Middle Permian. Of the known clades of predominantly Early Permian synapsids, only caseids and varanopids extend into the Middle Permian, together with the therapsids. Thus, the presence of this large varanopid in the Chickasha Formation is entirely consistent with an early Guadalupian age for these sediments (see Reisz and Laurin 2002 for a more detailed discussion). Chickasha varanopids and caseids are characterized by large size, as exemplified by *Varanodon* and *Watongia*, and *Cotylorhynchus bransonii*, and *Angelosaurus romeri*, respectively. Varanopids continue to diversify and disperse into the Middle Permian, but are characteristically small predators, similar to or even smaller than the Early Permian *Mycterosaurus*. In the absence of large sphenacodontids or therapsids, *Watongia* is the only known candidate for top predator of the Middle Permian of

Fig. 7. Phylogeny. (A) Strict consensus of the five most parsimonious trees. Each tree requires 97 steps, has a consistency index of 0.6907, a CI excluding uninformative characters of 0.6842, a retention index of 0.8101, and a rescaled consistency index of 0.5596. (B) 50% majority-rule consensus tree of the five most parsimonious trees. The numbers next to the nodes represent the bootstrap frequency and the decay index, respectively. Varanopidae Romer and Price 1940 (converted clade name) is defined as all taxa that are more closely related to *Varanops brevirostris* than to *Ophiacodon mirus*, *Edaphosaurus cruciger*, and *Sphenacodon ferox*.



North America, before the advent of the large biarmosuchian and dinocephalian therapsids of the later part of the Middle Permian and of the Late Permian. Similarly, the caseid fossil record extends to the top of the Middle Permian in Russia, but is represented by a medium-sized form from the Kazanian and early Tatarian of northern Russia (Ivakhnenko et al. 1997).

Conclusion

The Chickasha vertebrates, although rare and relatively poorly preserved, provide a unique window into the evolutionary history of terrestrial vertebrates during the earliest

part of the Middle Permian. This assemblage differs from those of the Early Permian in lacking the “most advanced” Permo-Carboniferous synapsids, the large herbivorous edaphosaurids and the large predatory sphenacodontids. Instead, we see the presence of very large basal synapsids and eureptiles, the caseids and captorhinids, respectively, and the top predators appear to be members of the basal synapsid clade of varanopids. The available evidence suggests that this unusual faunal assemblage bridges the typical, well known faunas of the Early and Late Permian. This Middle Permian fauna is not dominated by recent groups, but instead, is predominantly composed of basal synapsid and eureptile clades that extend to the base of the Permian. Therapsids must have existed at that time because their stem must have diverged from sphenacodontines by the beginning of the Permian (Asselian), at the latest, and they appear in the fossil record in the Artinskian (Laurin and Reisz 1996), but seemingly remaining as a relatively rare member in preserved Laurasian communities that persisted until the Late Permian (Tatarian).

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