

Chapter 5

First European Record of a Varanodontine (Synapsida: Varanopidae): Member of a Unique Early Permian Upland Paleoecosystem, Tambach Basin, Central Germany

David S Berman, Amy C. Henrici, Stuart S. Sumida, Thomas Martens, and Valerie Pelletier

Abstract A new genus and species of varanodontine varanopid, *Tambacarnifex unguifalcatus*, is described on the basis of the greater portion of the postcranium and a closely associated partial left dentary from the Lower Permian (Wolfcampian) Tambach Formation, the lowermost unit of the Upper Rotliegend, of the Bromacker locality in the midregion of the Thuringian Forest near Gotha, central Germany. *Tambacarnifex unguifalcatus* can be distinguished from all other varanopids on the basis of unique features of its vertebrae and unguals. A cladistic analysis of Varanopidae resolves *T. unguifalcatus* as nested within the varanodontines as the sister taxon of *Varanops* in a terminal dichotomy, which in turn forms the sister clade of the terminal dichotomy *Varanodon*+*Watongia*. The position of *Aerosaurus* is unaltered from previous analyses as the basal taxon of Varanodontinae. *Elliotsmithia*, which has been assigned alternately to both the varanodontines and the mycterosaurines, is resolved as a member of the

latter. *Tambacarnifex unguifalcatus* is, therefore, the only varanodontine known from outside of North America. Within the Mycterosaurinae clade *Mycterosaurus* and *Mesenosaurus* resolve as a terminal dichotomy with *Elliotsmithia* and *Heleosaurus* related as successive sister taxa. As in previous analyses, *Archaeovenator* retains its position as the basal taxon of Varanopidae. *Tambacarnifex unguifalcatus* was an apex predator in a unique, heretofore undocumented Early Permian paleoecosystem in which the vertebrates were highly terrestrial inhabitants of an upland terrestrial setting, and constituted an early stage in the evolution of the modern terrestrial vertebrate trophic system, with herbivores greatly outnumbering apex predators in diversity, abundance, and biomass.

Keywords Bromacker locality • Tambach Formation • Paleoenvironment • Paleobiology • Trophic system • Eupelycosauria

This chapter includes one or more new nomenclatural-taxonomic actions, registered in Zoobank, and for such purposes the official publication date is Sep 2013.

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Introduction

The varanodontine varanopid described herein is a member of an extensive terrestrial vertebrate assemblage collected from the Lower Permian Tambach Formation of the Bromacker locality, an area of small, abandoned sandstone quarries scattered over an area of less than 0.5 km² in the midregion of the Thuringian Forest, Thuringia, central Germany. The Tambach Formation, which forms the lowermost formational unit of the Upper Rotliegend Group or Series in this area, comprises a 200 to 400-m-thick unit of conglomerates, sandstones, and mudstones. It has been interpreted generally as divided into three informal units: a lower and upper conglomerate separated by a middle interval of sandstone and minor mudstones referred to as the Tambach Sandstone,

which has long been known for its exceptionally well-preserved vertebrate trackways (Voigt et al. 2007). Outcrops of the Tambach Formation are restricted to an area of about 50 km² and were deposited in a small, internally drained paleograben, termed the Tambach Basin, whose original aerial extent was approximately 200–300 km².

Vertebrate remains were first discovered in the ‘Tambach Sandstone’ at the Bromacker locality in 1974 (Martens 1980, 1982), and a program of intensive, systematic excavation was initiated in 1993 (by the authors DSB, ACH, SSS, and TM) and has continued to the present. To date, three closely associated quarries have been excavated, collectively regarded as the Bromacker locality, which are located near the center of the Tambach Basin and cover a total area of about 700 m². In terms of abundance of specimens, diversity of taxa, and quality of preservation the Bromacker locality has become the most productive locality for Lower Permian terrestrial vertebrates in Europe. To date, 12 taxa of tetrapods have been identified from the Bromacker locality. Anamniotes (“amphibians”) include: the ostodolepidid microsauro *Tambaroter carrolli* Henrici, Martens, Berman, and Sumida, 2011; the amphibamid *Georgenthalia clavinasica* Anderson, Henrici, Sumida, Martens, and Berman, 2008; the trematopids *Tambachia trogallas* Sumida, Berman, and Martens, 1998 and *Rotaryus gothae* Berman, Henrici, Martens, Sumida, and Anderson, 2011; the seymouriamorph *Seymouria sanjuanensis* Vaughn 1966, (Berman and Martens 1993; Berman et al. 2000a; Klembara et al. 2005, 2006, 2007); and the diadectomorphs *Diadectes absitus* Berman, Sumida, and Martens, 1998, and *Orobates pabsti* Berman, Henrici, Kissel, Sumida, and Martens, 2004. The amniotes include: the eureptile (rather than the defunct taxa ‘Captorhinidae’ and ‘Protorothyrididae’) *Thuringothyris mahlendorffae* Boy and Martens, 1991 (Müller et al. 2006); the bolosaurid parareptile *Eudibamus cursoris* Berman, Reisz, Scott, Henrici, Sumida, and Martens, 2000; the sphenacodontid synapsid *Dimetrodon teutonis* Berman, Reisz, Martens, and Henrici, 2001 (Berman et al. 2004b); a new, undescribed caseid synapsid (Berman et al. 2009; Reisz et al. 2010); and a new varanopid synapsid first reported in 2009 (Berman et al. 2009) and described herein as *Tambacarnifex unguifalcatus*. Of these, all but one was recovered from the Tambach Sandstone of the Bromacker locality proper. The skull of *Tambaroter carrolli* (Henrici et al. 2011) and a closely associated articulated skeleton of the diadectomorph *Diadectes absitus*, an ubiquitous member of the Bromacker locality assemblage, were recovered from the upper conglomerate member in the village of Tambach-Dietharz. All of the vertebrates from the Tambach Formation are otherwise unreported from Europe, yet share a strong commonality with those of the mixed terrestrial-aquatic assemblages from the well-documented, lowland terrestrial environments

almost exclusively found in the Lower Permian sediments of the United States (Berman and Martens 1993; Berman et al. 1997, 1998, 2000a, 2001, 2009; Eberth et al. 2000). As such, the Bromacker vertebrates have provided the first irrefutable, biological evidence of a predrift continent of Euramerica and the first substantial use of terrestrial vertebrates to correlate a Lower Permian horizon in Europe, the Tambach Formation, with the standard terrestrial Lower Permian section of north-central Texas, indicating an earliest Permian Wolfcampian age (Sumida et al. 1996; Berman and Martens 1993; Berman et al. 1997, 1998, 2001).

The Bromacker locality and its vertebrate assemblage comprise a unique paleoecosystem, with highly terrestrial vertebrates inhabiting an upland terrestrial setting, that is otherwise undocumented in the Early Permian. As such, it constitutes an initial stage in the evolution of the modern terrestrial vertebrate trophic system or food chain, in which the herbivores greatly outnumber the apex predators in diversity, abundance, and biomass.

Systematic Paleontology

Synapsida Osborn, 1903

Eupelycosauria Kemp, 1982

Varanopidae Romer, 1936

Varanodontinae Reisz and Berman, 2001

Tambacarnifex gen. nov.

Type species: *Tambacarnifex unguifalcatus* sp. nov.

Diagnosis: Varanodontine varanopid eupelycosaur characterized by the following autapomorphies of the neural spines (observed in the partially preserved articulated series of posterior dorsals of serial position 13–23) and in the unguals of the manus and pes: neural spines inclined anteriorly, gradually increasing in serial height from either end of column to serial position 18, and alternating in width; unguals of digits I, III, and IV of the manus and IV of the pes (the only ones preserved) strongly recurved and greatly elongated, with that of manus digit I being subequal to the combined lengths of its penultimate phalanx and metacarpal; unguals of manus digits III and IV and pes digit V exceed the combined lengths of their penultimate and antepenultimate phalanges by 59, 50, and 29 %, respectively; extremely slender (distal to basal) retractor tubercle with a depth only slightly exceeding the width, and with the medial and lateral surfaces converging dorsally to a narrow, rounded ridge.

Etymology: *Tamba*, referring to the Tambach Basin, which the holotypic individual inhabited, and from the Latin *carnifex*, meaning executioner, referring to its role as an apex predator.

Tambacarnifex unguifalcatus sp. nov.

Holotype: MNG (collections of the Museum der Natur Gotha, Germany) 10596, greater part of postcranial skeleton preserved both in bone and as impressions on counterpart blocks.

Paratype: MNG 15037, partial left dentary exposed in lateral view.

Horizon and Locality: Tambach Formation of the Bromacker locality, an area of small abandoned and intermittently active sandstone quarries scattered over an area of less than 0.5 km² in the midregion of the Thuringian Forest approximately 1.5 km north of the village of Tambach-Dietharz and 20 km south of the town of Gotha, central Germany. Two superimposed stratigraphic successions at the Bromacker locality, characterized by their facies associations, are referred to as the Lower and Upper beds (Eberth et al. 2000). Both the holotype and paratype were recovered from the lower of two massive, red-brown, very fine-grained sandstone and siltstone sheetflood deposits separated by a 50 cm stratigraphic interval within the massive siltstones to very-fine-grained-sandstones of the 50–100 m thick Tambach Sandstone. This level is near the base of the Upper Beds, as defined by Eberth et al. (2000). On the basis of its vertebrate assemblage the Tambach Sandstone of the Bromacker locality is considered Early Permian (Wolfcampian) (Sumida et al. 1996).

Note: Lucas (2006) subdivided the North American Wolfcampian and Leonardian into a series of five faunachrons, which in ascending order are the Coyotean, Seymouran, Mitchellcreekian, Redtankian, and Littlecrotonian. He placed the vertebrate assemblage from the Bromacker locality of the Tambach Formation in the Seymouran faunachron, which spans the Wolfcampian-Leonardian boundary. The Seymouran was defined by the first occurrence of *Seymouria*, which is currently best known by *S. sanjuanensis* Vaughn, 1966, and *S. baylorensis* Broili, 1904, and is restricted to the Seymouran and Redtankian. Since *S. sanjuanensis* has a widespread occurrence that includes Utah, New Mexico, and Germany (Bromacker locality), Lucas (2006) suggested that it is probably the best index taxon for the Seymouran faunachron. Even though the Seymouran faunachron spans the Wolfcampian-Leonardian boundary, North American occurrences of *S. sanjuanensis* are restricted to the Wolfcampian (Berman et al. 1987; Sumida et al. 2004), indicating that the Bromacker locality is best regarded as Wolfcampian on this basis.

Diagnosis: As for genus.

Etymology: From the Latin *unguis*, nail, claw, or talon, and *falcatus*, sickle-shaped, referring to the long, strongly recurved unguals of the holotype.

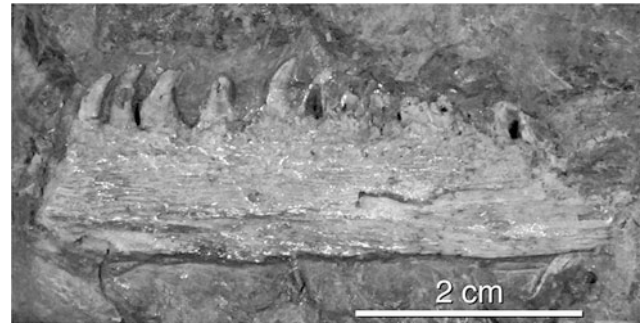


Fig. 5.1 *Tambacarnifex unguifalcatus*, paratype, MNG 15037. Partial left dentary in lateral view

Description and Comparisons

General

Assignment of the isolated, partial paratypic dentary MNG 15037 (Fig. 5.1) to *Tambacarnifex unguifalcatus* is based on its dentition being characteristic of the varanodontines and quite distinct from those of the other members of the Bromacker assemblage, and its size being appropriate to belong to the holotype. The holotypic postcranial skeleton MNG 10596 is preserved on two large counterpart blocks (Figs. 5.2, 5.3), and at the time of excavation many elements were partially or entirely lost, but in most instances are represented as impressions. However, because the impressions often provide useful information, they have been whitened for better visibility, and in the description that follows those elements represented as impressions are indicated as such. Because there is no consistency among authors, nor do they typically provide an explanation of how the various limb elements are oriented relative to one another or to the axial column when describing them in various views, it seems best to clarify the scheme used here to prevent confusion. It essentially follows that of Romer and Price (1940, p. 137): the propodials are viewed as extending directly laterally from the girdles and the epipodials, manus, and pes as extending directly anteriorly with the entire limb in the same horizontal plane. Therefore, the four major descriptive aspects of the propodials are dorsal, ventral, anterior, and posterior and for the epipodials dorsal, ventral, medial, and lateral, whereas in the descriptions of the manus and pes the standard dorsal and ventral orientations are used.

Based on the cladistic analysis of Maddin et al. (2006), with alterations suggested by Campione and Reisz (2010), several diagnostic features clearly support the assignment of

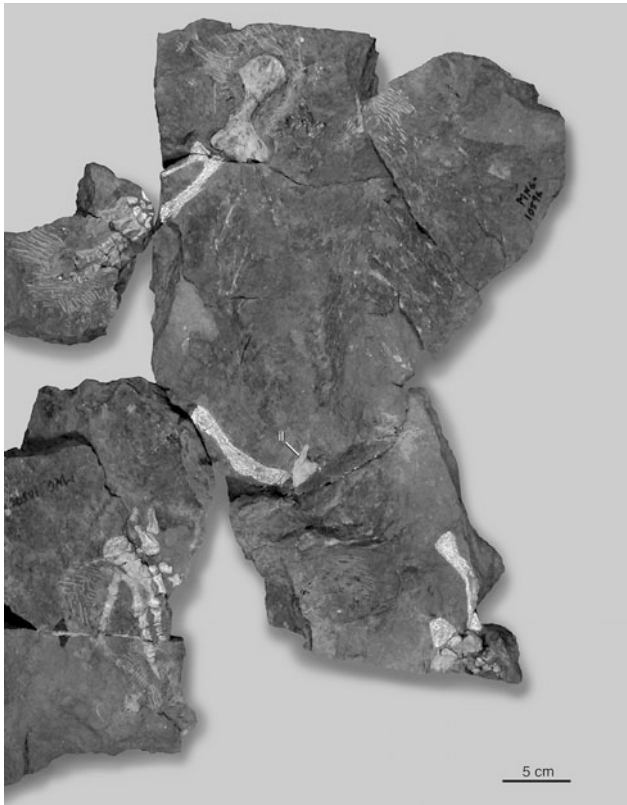


Fig. 5.2 *Tambacarnifex unguifalcatus*, holotype, MNG 10596. Partial postcranial skeleton exposed mainly in dorsal aspect on opposite side of counterpart block in Fig. 5.3



Fig. 5.3 *Tambacarnifex unguifalcatus*, holotype, MNG 10596. Partial postcranial skeleton exposed mainly in ventral aspect on opposite side of counterpart block in Fig. 5.2. *dv* dorsal vertebra, *il* ilium, *pu* pubis

Tambacarnifex unguifalcatus to Varanodontinae: marginal teeth strongly recurved and mediolaterally flattened; deep, elongate excavations at base of the neural spine; and heads of the humerus greatly expanded and connected by a short, narrow, rounded shaft. Comparisons of *T. unguifalcatus* with other varanodontines are limited to a single species from each of five genera and rely on a short list of pertinent descriptions. These include: Dilkes and Reisz (1996) and Reisz et al. (1998) for *Elliotsmithia longiceps* Broom, 1937; Langston and Reisz (1981; although also see Pelletier 2013) for *Aerosaurus wellesi* Langston and Reisz, 1981; Maddin et al. (2006) and Campione and Reisz (2010) for *Varanops brevirostris* (Williston, 1911) (reassigned from *Varanosaurus* by Williston 1914); Olson (1965) for *Varanodon agilis* Olson, 1965; and Olson (1974) and Reisz and Laurin (2004) for *Watongia meieri* Olson, 1974. Repetitive citation of these references, therefore, has been substantially eliminated below as unnecessary.

Isolated Dentary

The isolated dentigerous jaw element (MNG 10595, paratype) found closely associated with the holotype is tentatively identified as a left dentary in lateral view (Fig. 5.1). Narrow, sutural scars along the ventral margin may indicate the contacts of splenial and angular. Furthermore, there are no signs of a canine swelling or a dorsal process to suggest that the jaw element is a maxilla. Twelve teeth of varying completeness are preserved. As in varanodontines, they are recurved, although possibly less so than in some varanopids, mediolaterally flattened, sharply pointed, and non-serrated. The series is incomplete anteriorly and posteriorly, and the teeth increase in height and width anteriorly except for the anteriormost two being narrower. Surface sculpturing consists of densely packed, short, minute longitudinal ridges.

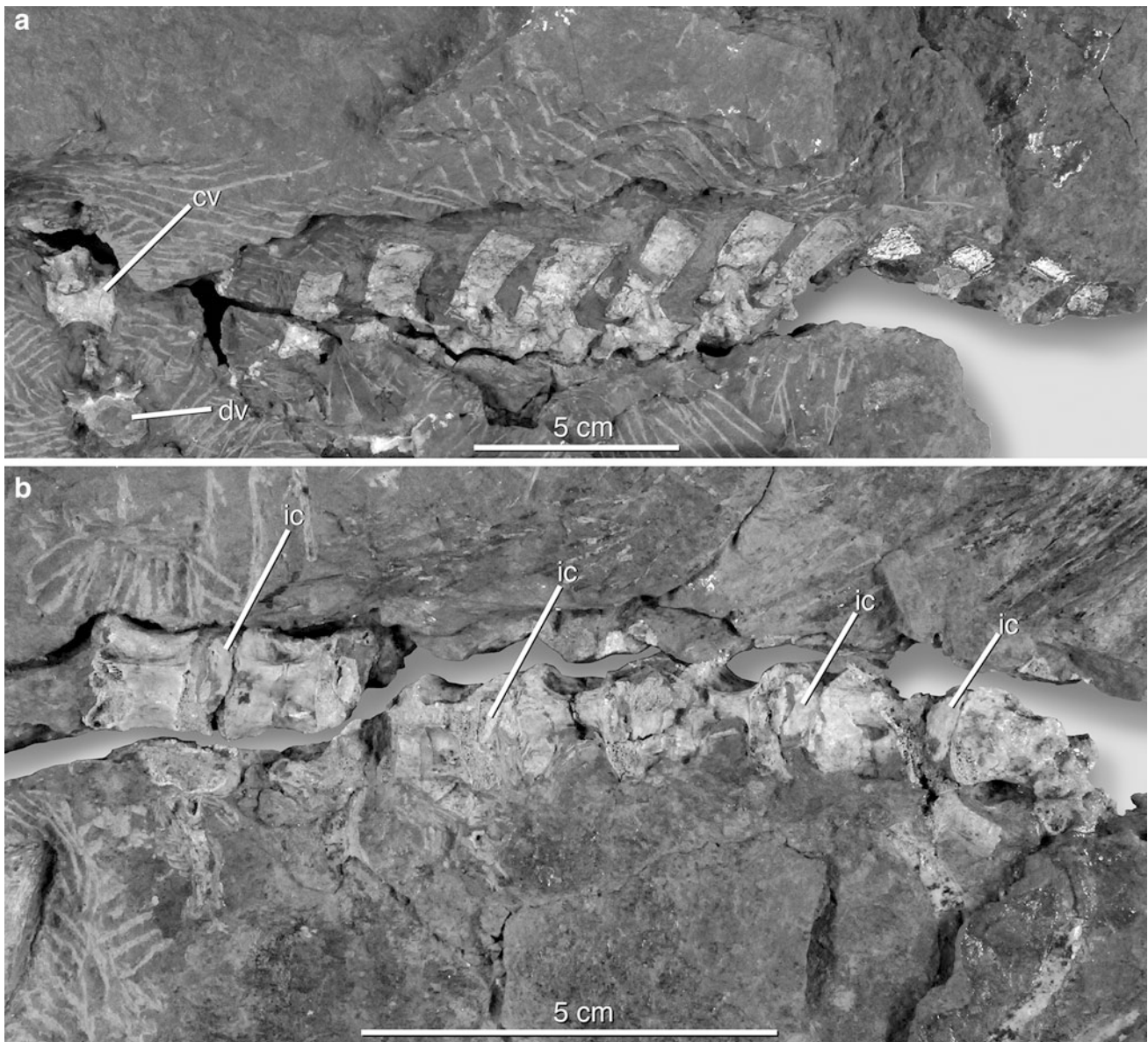


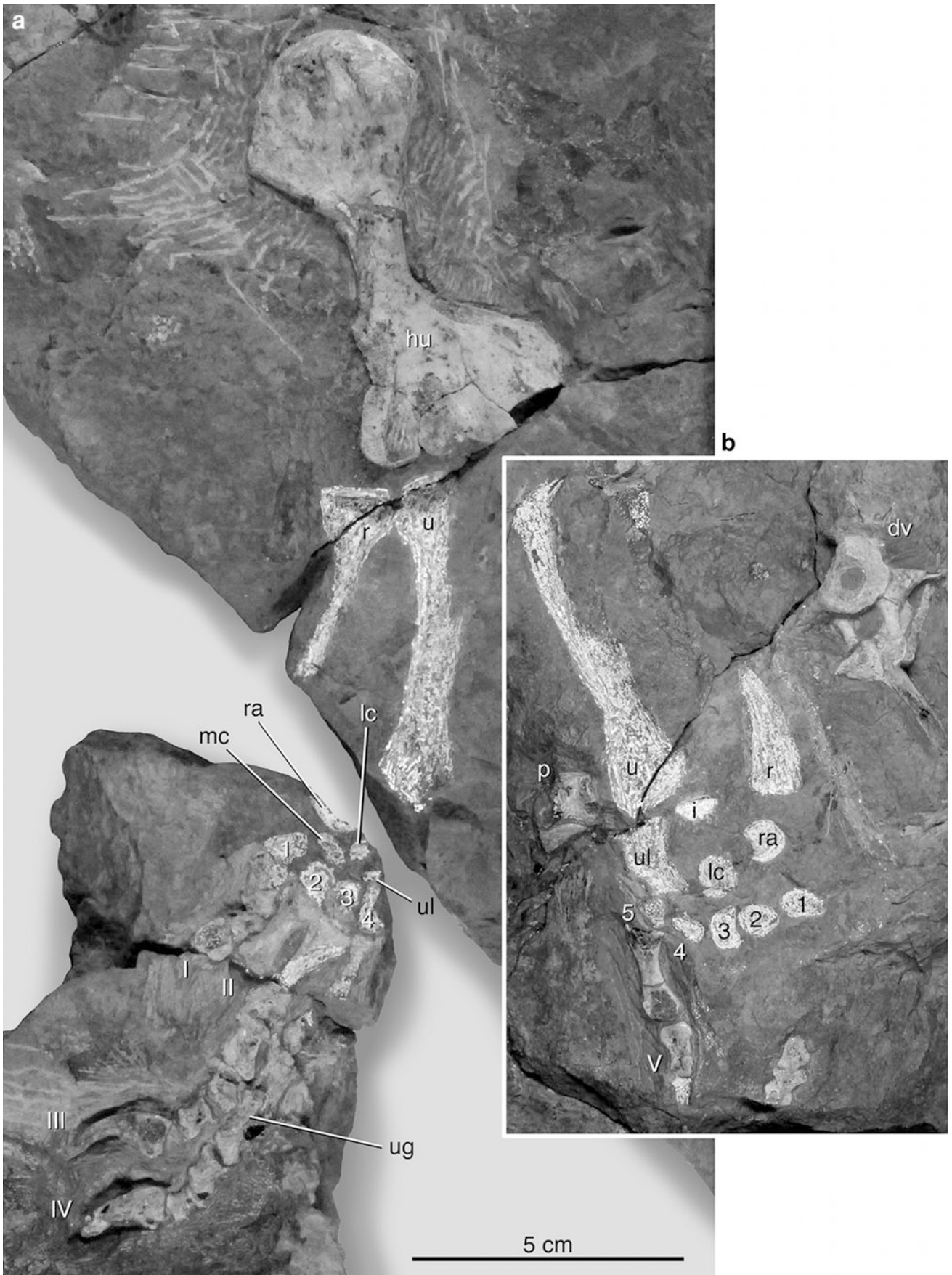
Fig. 5.4 *Tambacarnifex unguifalcatus*, holotype, MNG 10596. Partially preserved series of 11 articulated posterior dorsal vertebrae believed to represent serial positions 11–23 (anterior to *right*). **a** Lateral view of series as exposed on opposite side of counterpart block

in Fig. 5.3, and **b** ventral view of centra 6–11 as exposed on counterpart block in Fig. 5.3. *cv* cervical vertebra, *dv* dorsal vertebra, *ic* intercentrum

Axial Skeleton

The axial skeleton is represented by a partially preserved series of 11 articulated presacral vertebrae (Figs. 5.3, 5.4) and several scattered, isolated vertebrae. The first four anterior vertebrae of the articulated series are represented only by the distal ends of the neural spines and the fifth only by the neural arch and spine. The last six are mostly complete, primarily missing fragments along a break in the block that extends through the ventral margins of the centra. The series is believed to approximate serial

positions 13–23 and, therefore, would include only dorsal vertebrae. This estimate is based on two features: (1) the gap between the posterior end of the series and the approximate position of the missing sacrum, which could have accommodated four vertebrae (the position of the sacrum is based on the assumption that the partially preserved left pelvis and proximal end of the left femur are preserved in their correct relationship to the axial column; Fig. 5.3); and (2) according to Langston and Reisz (1981) the dorsal vertebrae in *Aerosaurus wellesi* reach their greatest height at serial position 18, which in the holotype



◀ **Fig. 5.5** Left forelimb and manus of *Tambacarnifex unguifalcatus*, holotype, MNG 10596. **a, b** As exposed on counterpart blocks in Figs. 5.2 and 5.3, respectively. *I–V* digits, *I–5* distal carpals, *dv* dorsal vertebra, *hu* humerus, *i* intermedium, *lc* lateral centrale, *mc* medial centrale, *p* pisiform, *r* radius, *ra* radiale, *u* ulna, *ug* ungual, *ul* ulnare

of *Tambacarnifex* would be the sixth vertebra of the series. The presacral count, therefore, is estimated at 27, which is the typical number of presacrals in basal synapsids and recorded in *Varanops breviostris* (Romer and Price 1940) and *Aerosaurus wellsi* (Langston and Reisz 1981; Pelletier 2013). Only the centra of the fifth through eleventh vertebrae of the series are preserved, and, although they are slightly incomplete and distorted, rough measurements of their greatest centrum length and height yield a rather consistent 1.4 and 1.6 cm, respectively. As in other varanodontines, the neural spines are anteroposteriorly broad in lateral view, moderately tall, and subrectangular with a slight expansion distally and a flat dorsal margin. Furthermore, as in *Varanops* and *Aerosaurus*, there are deep, narrow, elongate, lateral excavations at the base of the neural spines (Fig. 5.4a) that are slightly inclined posteroventrally from the vertical. In *Varanodon* and *Watongia* the excavations differ in being much shallower and far less elongated.

Although the articulated series of the 11 dorsal vertebrae in *Tambacarnifex* exhibit an overall morphology very similar to that of other varanodontines, the neural spines can be distinguished by three unique features: (1) a pronounced anterior inclination, which is made especially evident by the anteroventral sloping of the dorsal margins; (2) a serial increase in height from either end of the series to the sixth vertebra, which is directly measurable in the last six vertebrae from 2.8 to about 1.7 cm; and (3) an alternation in spine width in the last seven vertebrae. The vertebrae lack a suture between the centrum and neural arch, indicating a mature stage of development. The midventral keel of the series has, as expected, the form of a low, but distinct, rounded ridge. The dorsal series also exhibits well-preserved intercentra, but there is no evident beveling of the centra to accommodate them, which may be not be obvious due to distortion and imperfect preservation. Three additional, incomplete, partially exposed, isolated vertebrae are preserved on the counterpart blocks containing the holotype. A short distance from the posterior end of the articulated dorsal series in Fig. 5.4a is a centrum and partial neural arch of a cervical exposed in left lateral view (centrum length 1.8 cm) and an anterior dorsal vertebra missing most of its neural spine exposed in anterior view (centrum width and height 1.5 and 1.9 cm, respectively). In Figs. 5.3 and 5.4b an anterior dorsal is visible in posterior view (overall height 2.0 cm and centrum width and height 1.6 and 1.9 cm, respectively) lying beside the impression of the partial left forelimb.

Ribs from the anterior to the midregion of the dorsal series of vertebrae are represented as narrow, posterolaterally arching rods that reach a maximum length in the anterior part of the dorsal series, then become much reduced posteriorly. The rib heads are preserved only as impressions, but appear characteristic of varanodontines. The capitulum expands slightly proximally, whereas the tuberculum is greatly reduced to a short, rectangular, dorsally directed protuberance on the upper surface of the rib. There is no triangular web of bone connecting the capitulum and tuberculum and the ribs are, thus, double-headed and can be considered dichoccephalous.

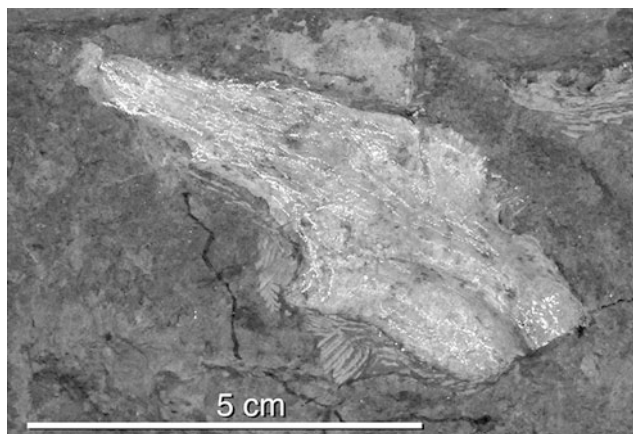
Appendicular Skeleton

The pectoral girdle is not represented and only the left forelimb and manus are partially preserved as bone and impression (Figs. 5.2, 5.3, 5.5) (lengths of propodials and epipodials are given in Table 5.1). The humerus is nearly complete and exposed in dorsal aspect, but obviously has been greatly flattened, so as to expose both heads in the same plane. The heads are moderately damaged, but show characters that are closely comparable to those of other varanodontines. They are greatly expanded and connected by a short, relatively narrow, rounded shaft. As in varanopids, the smooth, strongly convex articular margin of the proximal head is set off from a well-developed deltopectoral crest. Only the base of the supinator process remains, but appears to indicate that the process was directed strongly distomedially. Despite the loss of the lateral margin of the ectepicondyle, the distal head is noticeably more expanded than the proximal head, due mainly to the greatly flared entepicondyle. An elongate entepicondylar foramen is well exposed. The left radius and ulna are represented only as very incomplete dorsal and ventral impressions. All that the impressions safely reveal are modestly expanded ends.

With the exception of the pisiform, all of the carpals are represented entirely or almost entirely as partial ventral (Figs. 5.2, 5.5) or dorsal (Fig. 5.3) impressions and, therefore, do not allow reliable description. Although only the impression of the distal margin of the radiale is preserved, it suggests that the element had a mediolateral width equal to or greater than its proximodistal length. The nearly complete pisiform is exposed in ventral view and presumably in its correct orientation near the junction of the ulna and the ulnare (Fig. 5.3). It is trapezoidal in outline, with the

Table 5.1 Length measurements (in mm) of limb bones of *Tambacarnifex unguifalcatus*

Left humerus	84
Left radius	57
Left ulna	63
Left femur	85
Left tibia	82
Right tibia	81
Right fibula	85

**Fig. 5.6** *Tambacarnifex unguifalcatus*, holotype, MNG 10596. Right ilium in lateral view as exposed in Fig. 5.3

proximal and distal margins being parallel to one another and the proximal margin being longer. The smoothly finished ventral surface is concave in transverse section with thickened medial and lateral margins. Metacarpals I–V are essentially complete, with I–IV exposed in dorsal view (Figs. 5.2, 5.5) and V in ventral view (Fig. 5.3). They exhibit the standard serial increase in length of I–IV, with the length of V being about 70 % of that of IV. The phalanges of the digits I, III, and IV are well preserved and exhibit the expected counts of 2, 4, and 5, respectively. In several features, however, the unguals are unique among varanodontines in being: (1) much more strongly recurved; (2) considerably longer, with the first unguual being subequal to the combined lengths of the preceding phalanx and metacarpal and the third and fourth unguuals being approximately 59 and 50 % longer than the combined lengths of their penultimate and antepenultimate phalanges, respectively (where the same measurements are available in the manus digits of *Aerosaurus*, *Varanops*, *Varanodon*, and *Watongia*, the unguuals are either far shorter or subequal); and (3) extremely slender dorsoventrally and mediolaterally distal to the flexor tubercle, with the third and fourth unguuals having depths of about 4 and 3 mm and widths of about 4 and 5 mm, respectively, and the medial and lateral surfaces converging dorsally to a narrow, rounded ridge. In

Aerosaurus, *Varanops*, *Varanodon*, and *Watongia* the unguuals are described as flattened dorsoventrally, with a width that is considerably greater than the depth. Maddin and Reisz (2007, p. 270) described the unguuals in *Varanops* as having “a strikingly flat, broad morphology in cross-section that is reminiscent of the condition in diadectids.” Yet, Campione and Reisz (2010) described the first unguual of the manus in a large specimen of *Varanops* as dorsoventrally thick, but that of the pes as dorsoventrally flattened.

All that remains of the pelvic girdles are the right ilium (Figs. 5.3, 5.6) and the basal portion of the left in lateral views (Fig. 5.2), and what appears to be the anteroventral portion of the left pubis (Figs. 5.3, 5.7a), which we tentatively regard to be exposed in lateral view with its convex ventral margin directed laterally from the vertebral column.

Only the left femur is represented, mainly as impressions of its anterior (Fig. 5.2) and posterior (Figs. 5.3, 5.7a) aspects except in the latter, where the distal end is preserved in anterior aspect, exposing the anterior head and the distal portion of the posterior head. The entire length and profile of the femur is represented by the impression of its anterior aspect, which clearly exhibits the typical varanopid features of being slender and having a slight sigmoid curvature, with the proximal head bent slightly upward and the distal head bent slightly downward.

The left tibia (Figs. 5.3, 5.7a) is complete, whereas the right (Figs. 5.3, 5.8a) is missing two short sections of the shaft, and both elements are exposed in medial aspect (the right also as impression in Figs. 5.3, 5.8b). As is typical in varanopids, the tibia is gracile and strongly bowed dorsally. The cnemial crest of the right tibia dominates the medial aspect of the proximal head, giving it a broadly triangular outline. The crest diminishes quickly distally, occupying the proximal third of the bone. Just medial and parallel to the distal end of the crest is a well-developed, highly rugose ridge that extends nearly to the distal end of the bone (Fig. 5.7a). The cnemial crest is separated from the lateral margin of the proximal head by a channel, termed the cnemial trough by Pawley and Warren (2006). Mediolateral crushing, however, has greatly narrowed the channel to a narrow slit.

Both fibulae are preserved (Figs. 5.3, 5.8), but only the left fibula is complete and exposed in medial aspect, whereas the right is exposed in ventral aspect and represented in part as bone and impression. The left tibia obscures all but the distal half of the left fibula, which appears as an anteroventrally narrow strut that is bowed slightly dorsally. Preservation of the right fibula includes the proximal head (partially hidden by the tibia) and the greater medial portion of the distal head, which is joined proximally by a short, narrow strip of the shaft. Preservation as impression is limited to the medial portion of the distal



Fig. 5.7 *Tambacarnifex unguifalcatus*, holotype, MNG 10596. **a** Partial left hindlimb and pes, and **b** partial left pes as exposed in Figs. 5.3 and 5.2, respectively. *as* astragalus, *ca* calcaneum, *ct* cnemial trough, *I–V* digits, *1–4* distal tarsals, *fe* femur, *fi* fibula, *pu* pubis, *ti* tibia

head and a continuing narrow strip of the medial margin of the shaft. Both heads flare medially, giving the fibula a moderately concave medial margin and a slight lateral bowing. The impression of the ventral aspect of the distal end of the right fibula (Fig. 5.8b) indicates a broad, flattened, triangular surface. The fibula is slightly longer than the tibia.

The astragalus and calcaneum are best exemplified by their dorsal exposure in the partial right pes (Figs. 5.2, 5.8b), where they are essentially complete, articulated, and well preserved except for some erosion along the distal

margin of the calcaneum. Partial impressions of the dorsal and ventral surfaces of the left astragalus and the dorsal surface of the right (Figs. 5.2, 5.3, 5.7, 5.8a) provide no additional information. The stoutly constructed astragalus has the standard sharply angled L-shape outline, with the length of the short vertical arm (0.6 cm) being about 24 % of the total 2.5 cm of the total proximodistal length of the element. The astragalus-calcaneum contact is slightly bowed medially for most of its proximal length, with the remainder of the contact being straight except for a notch-like interruption near its distal end for the perforating artery.

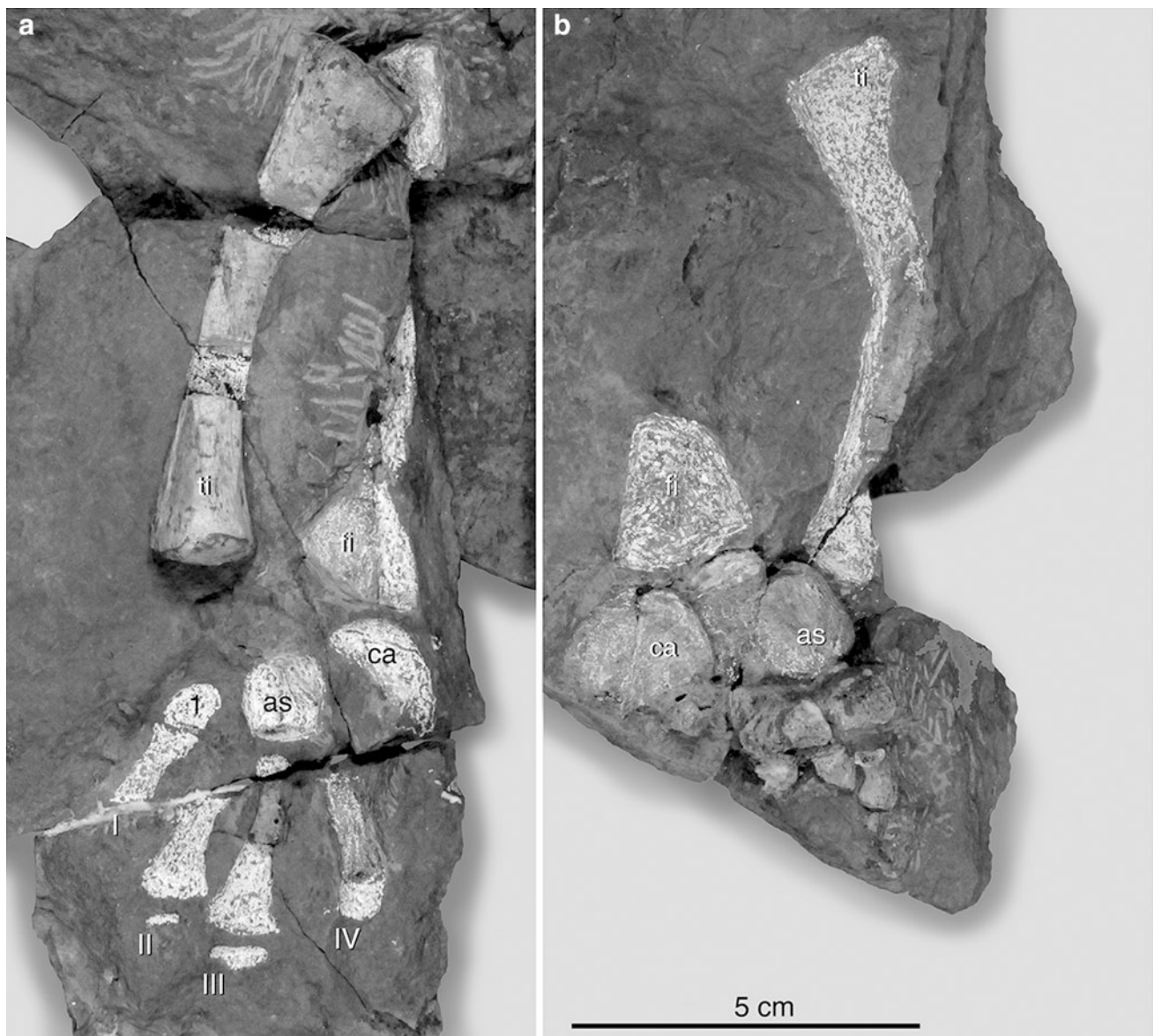


Fig. 5.8 *Tambacarnifex unguifalcatus*, holotype, MNG 10596. **a, b** Counterparts of partial right hindlimb and pes as exposed in Figs. 5.2 and 5.3, respectively. *as* astragalus, *ca* calcaneum, *I–IV* digits, *I* distal tarsal, *fi* fibula, *ti* tibia

The dorsal surface of the astragalus is smoothly finished and relatively flat except for where it rises along the contact margins with adjacent elements. The proximal articular facet of the vertical arm for the fibula is well developed, slightly convex, and transversely oval except for a slight lateral narrowing, whereas the horizontal arm ends in a prominent, well-developed, transversely convex, condyle-like articular facet for the tibia. The proximodistal length of the astragalus is subequal to that of the calcaneum, with the proximal and distal margins of both elements ending at approximately the same transverse planes. The dorsally exposed calcaneum of the right pes is nearly complete, whereas in the left pes (Figs. 5.2, 5.8a) only the distal half is

well preserved in ventral view, but the outline of the dorsal surface impression of the proximal half is accurately depicted. The calcaneum has in general a proximodistally elongate, oval outline with a thinning in thickness toward the lateral margin. It thickens toward the facets on the convex proximomedial and medial margins, and the straight distal marginal contacts with the fibula, astragalus, and fourth distal tarsal.

The medial and lateral centrales are not represented, but the space they occupied between the astragalus and distal tarsals 1–3 is well defined in the ventral view of the left pes (Figs. 5.2, 5.7b). Distal tarsal 5 is not represented, but 1–4 are in the left pes (Fig. 5.7b), with the first and second

preserved as impressions of their dorsal surfaces and the third and fourth exposed in ventral view. Distal tarsal 1 is roughly kidney-shaped in outline, with a notch-like indentation on its medial margin. The outline of the second distal tarsal, smallest of the four, describes a proximodistally elongated rectangle with a slightly convex lateral margin. The first and second distal tarsals have slightly convex distal articular margins, which match the concave proximal margins of their respective metatarsals. The third distal tarsal has roughly the outline of a proximodistally elongated ellipse with a slightly concave medial margin that contacts the greater proximal portion of the medial margin of the second distal tarsal, and a convex lateral margin that fits snugly into a complementary concave medial margin of the fourth distal tarsal. The strongly convex distal margin of the third distal tarsal is opposed by a slightly convex proximal margin of the metatarsal. The fourth distal tarsal, the largest of the series, is pentagonal in outline with a broad, flat contact with the calcaneum, a small projection of its proximomedial margin that likely contacted the distolateral corner of the astragalus, a concave medial margin that received the lateral margin of the third, and broad, mutually flat contacts with metatarsals IV and V that meet at an oblique angle.

Metatarsals I–IV increase serially in length, with that of the fifth being 79 % of the fourth. Metatarsal I, the shortest, is about 52 % of the length of the fourth. Only the fourth and fifth digits are preserved well enough to exhibit the standard phalangeal counts of five and four, respectively. The fourth and only preserved ungual of the pes is complete and exposed in ventral view. In contrast to the unguals in *Aerosaurus*, *Varanops*, *Varanodon*, and *Watongia* it has a morphology identical to those of the manus in *Tambacarnifex* in being: (1) much more strongly recurved than the unguals of the other taxa; (2) longer than the combined lengths of its respective penultimate and antepenultimate phalanges by 29 %; (3) extremely slender dorsoventrally and mediolaterally distal to the flexor tubercle, with a depth of about 4 mm and a width of about 5 mm, respectively; (4) and the medial and lateral surfaces converge dorsally to a narrow, rounded ridge.

Gastralia

Remarkably, the abdominal ribs or gastralia are preserved nearly intact and complete, on both counterpart blocks (Figs. 5.2, 5.3), but they have shifted to the right side of the trunk region. Their shape and arrangement are best exemplified at the anterior end of the structure (Fig. 5.9), where they are arranged in tightly packed, chevron-shaped rows with the sharply angled apices directed anteriorly.

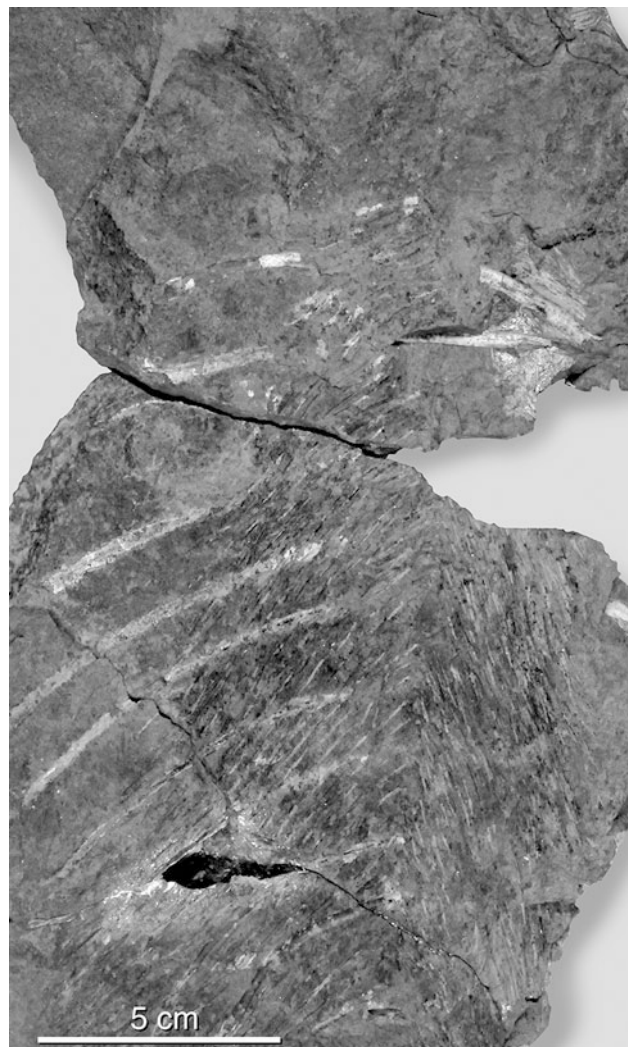


Fig. 5.9 *Tambacarnifex unguifalcatus*, holotype, MNG 10596. Gastralia superimposed on ribs as exposed in Fig. 5.3. Anterior is towards the top of the figure

Individual elements are slender, forming an approximately one centimeter long rod that is sharply pointed at both ends. The anterior end of each element anteriorly overlaps the distal end of the medially adjacent element.

Phylogenetic Analysis

In a redescription of the varanopid *Elliotsmithia longiceps*, Reisz et al. (1998) were the first to recognize that the varanopids consist of two distinct clades, one consisting of *Mesenosaurus* Efremov, 1938 (Reisz and Berman 2001) and *Mycterosaurus* Williston, 1915 (Berman and Reisz 1982) and a second consisting of *Elliotsmithia*, *Aerosaurus*, *Varanodon*, and *Varanops*. However, they did not assign them formal systematic designations. Subsequently, in a

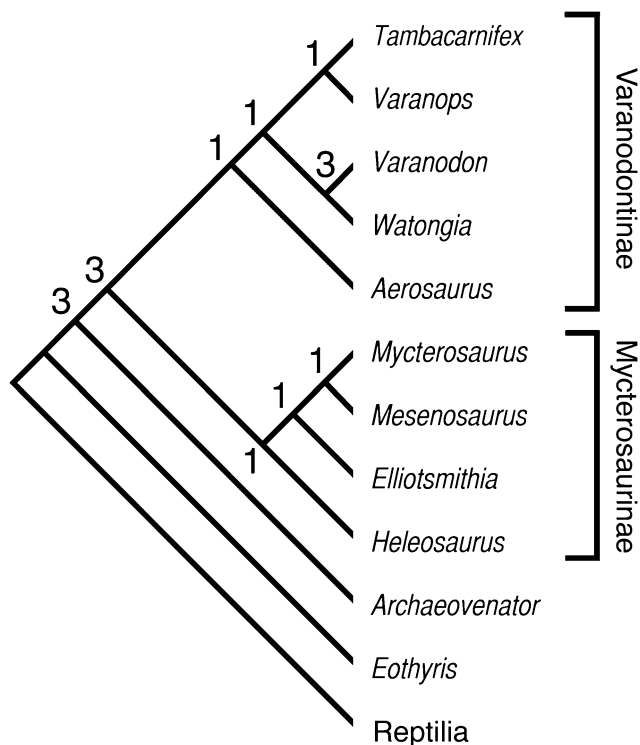


Fig. 5.10 Hypothesized relationships of varanopids based on a single most parsimonious tree (Tree Length = 87). Bremer decay values are given next to nodes

redescription of the varanopid *Mesenosaurus romeri*, Reisz and Berman (2001) proposed the formal designations Mycterosaurinae and Varanodontinae, respectively, for the two varanopid clades, which have been accepted by later authors with some alterations (although see Kammerer and Angielczyk 2009). A fifth species of varanodontine, *Watongia meieri*, based originally on a single specimen described by Olson (1974) as a gorgonopsian therapsid, was reassigned to Varanodontinae in a redescription by Reisz and Laurin (2004). Modesto et al. (2001) assigned a second specimen, BP/1/5678 (Bernard Price Institute for Palaeontological Research), to *E. longiceps* and, using a composite character coding based on it and the holotype, reassigned BP/1/5678 to Mycterosaurinae. Reisz and Dilkes (2003), however, suspected that the new specimen may pertain to a different species based on their differing interpretations from those of Modesto et al. (2001) on certain characters inferred to be present in the holotype. In a subsequent reconsideration of the affinities of BP/1/5678, however, Botha-Brink and Modesto (2009) cautioned that none of the autapomorphies of the mycterosaurines are determinable in BP/1/5678 and suggested that it may be referable to *Heleosaurus scholtzi* Broom, 1907. *H. scholtzi*, described originally as a diapsid by Broom (1907), was recently reclassified by Reisz and Modesto (2007) to Mycterosaurinae. With the discovery of an aggregation of five

specimens of *H. scholtzi*, Botha-Brink and Modesto (2007, 2009) were able to provide significant new anatomical information that not only provided a greatly expanded diagnosis of the species, but also established its mycterosaurinae affinities in a revised phylogenetic analysis of the varanopids. It should be noted also that their analysis did not use BP/1/5678 to code either *E. longiceps* or *H. scholtzi*. Modesto et al. (2011) reported an additional fragmentary mycterosaurine specimen from the rocks assigned to the *Pristerognathus* Assemblage Zone in the Karoo Basin, but did not name it. Lastly, two new species of varanopids, *Archaeovenator hamiltonensis* and *Pyozia mesenensis*, were recently described by Reisz and Dilkes (2003) and Anderson and Reisz (2004), respectively. Neither species, however, was assigned to either the Varanodontinae or Mycterosaurinae clades, but rather, in a cladistic analysis by Anderson and Reisz (2004), *Pyozia* and *Archaeovenator* were resolved as successive sister taxa.

In order to evaluate the phylogenetic relationships of *Tambacarnifex unguifalcatus* within Varanopidae, three recently published cladistic analyses were utilized. Maddin et al. (2006) were the first to offer a comprehensive data matrix based on 60 characters in their evaluation of the phylogenetic position of a varanopid from the Lower Permian fissure-fill deposits of the Richards Spur locality near Fort Sill, Oklahoma. Their analysis of isolated cranial and postcranial elements of three specimens, which were described by them as virtually indistinguishable from *Varanops brevirostris* of the Lower Permian of Texas, resolved the unnamed Richards Spur varanopid as the sister taxon of *V. brevirostris*.

In a more recent analysis of the varanopids, Botha-Brink and Modesto (2009) used a slightly altered version of the character data matrix of Maddin et al. (2006) in a phylogenetic assessment of the mycterosaurine *Heleosaurus scholtzi* Broom, 1907. The analysis, the first to include *H. scholtzi*, was prompted by the discovery of five additional, closely associated, articulated specimens from the Middle Permian of South Africa (Botha-Brink and Modesto 2007). Changes made to the Maddin et al. (2006) data matrix by Botha-Brink and Modesto (2009) were limited to the addition of two characters, 61 (character 59 here, absence or presence of squamosal tubercle) and 62 (character 60 here, absence or presence of osteoderms). Interestingly, their analysis resolved *Elliotsmithia* from the Middle Permian of South Africa within the Mycterosaurinae as the sister taxon of *Heleosaurus*. Most recently, Campione and Reisz (2010) provided a comprehensive revision of *Varanops brevirostris* based on a large, well-preserved, nearly complete, articulated skeleton from the Lower Permian of Texas. Their cladistic analysis also adopted in great part the characters used by Maddin et al. (2006), with the following alterations: (1) inclusion of *Heleosaurus*; (2)

exclusion of *Pyozia* from the Middle Permian of Russia, as it is based on a specimen they believed does not exhibit the diagnostic characters of Varanopidae; (3) removal of the Richards Spur varanopid as separate taxon from *V. brevirostris*, but still utilizing it to score the amended data matrix (characters 36 and 39, the morphology of the parasphenoid); (4) removal of characters 45 (presence of a lateral temporal fenestra) and 60 (length to distal width ratio of femur) as uninformative; and (5) the addition of new information provided by the specimen described by Campione and Reisz (2010) that they used to recode *V. brevirostris* (characters 3, presence or absence of tooth serrations, and 22, morphology of postorbital). Furthermore, in the data matrix of Campione and Reisz (2010) three of the five outgroups used by Maddin et al. (2006) (Reptilia, the eothyridid synapsid *Eothyris*, and the ophiacodontid synapsid *Archaeothyris*) were eliminated, but the caseid *Cotylorhynchus* and ophiacodontid *Ophiacodon* were retained.

In evaluating the phylogenetic relationships of *Tambacarnifex unguifalcatus* within Varanopidae, the data matrix of Maddin et al. (2006) was used with the alterations listed above by Botha-Brink and Modesto (2009) and Campione and Reisz (2010). The data matrix of the latter was not used, because of numerous transcription errors. In addition, Reptilia and *Eothyris* are the only outgroups of Maddin et al. (2006) retained in the data matrix used here. Unfortunately, *Tambacarnifex* could be coded only for eight of the 60 characters of Botha-Brink and Modesto (2009) and Campione and Reisz (2010), as all but 11 are cranial. The applicable characters include 1, 3, 49–51, and 55–57, which were coded 1, 0, 1, 2, 1, 0, 0, and 1, respectively. MacClade 2.0 (Maddison and Maddison 1992) was used to construct the data matrix, consisting of 12 taxa (Fig. 5.10), and a cladistic analysis utilizing the branch-and-bound algorithm of PAUP (Swofford 1993) was conducted to determine the most parsimonious tree(s). All the characters were equally weighted, and multiple, derived states were unordered. Delayed transformation (DELTRAN) was used to optimize characters. The analysis produced only one most parsimonious tree with a length of 87 steps, a Consistency Index of 0.782, a Retention Index of 0.810, and a Rescaled Consistency Index of 0.633. The robustness of each varanopid clade was determined using the Bremer (1994) decay analysis.

The resultant cladogram (Fig. 5.10) resolves *Tambacarnifex* as nested within the varanodontines as the sister taxon to *Varanops* in a terminal dichotomy, which in turn forms a sister clade to the terminal dichotomy of *Varanodon*+*Watongia* from the Middle Permian of Oklahoma. The position of *Aerosaurus* from the Lower Permian of New Mexico as the basal taxon of Varanodontinae is unaltered from previous analyses. Within Mycterosaurinae, *Mycterosaurus* from Lower Permian of Texas and *Mesenosaurus* from the Middle Permian of Russia form a terminal

dichotomy, with *Elliotsmithia* and *Heleosaurus* as successive basal sister taxa. This relationship, therefore, supports Modesto et al.'s (2001) contention that *Elliotsmithia* is a mycterosaurine. In this regard, it is worth noting that in the cladistic analysis of Campione and Reisz (2010) *Elliotsmithia* is poorly supported as a varanodontine, yet it is also poorly supported as a mycterosaurine in their stratocladistic analysis. The position of *Archaeovenator* from the Upper Pennsylvanian of Kansas as a basal taxon to the clade Varanodontinae+Mycterosaurinae is unaltered here from previous analyses. In the present analysis, however, relatively high Bremer support values of three are obtained only for those nodes that include *Varanodon*+*Watongia*, Varanodontinae+Mycterosaurinae, and *Archaeovenator*+all other varanopids, whereas the remaining varanopid nodes are supported by a low value of one. Importantly, the analysis implies that *Tambacarnifex* is the only varanodontine known outside of North America. This is not totally unexpected, however, considering the strong taxonomic commonality between the vertebrates of the Bromacker locality and those of the Early Permian of North America.

Environmental and Biological Uniqueness of the Bromacker Locality

General

The Bromacker locality is distinguishable from all other well-known Early Permian terrestrial vertebrate-fossil sites in its paleoenvironmental and paleobiological features (Eberth et al. 2000; Berman et al. 2000a, 2001), which for the first time fully document a paleoecosystem in the Early Permian that represents an initial stage in the evolution of the modern terrestrial vertebrate trophic system or food chain. The small, internally-drained Tambach Basin and its Bromacker locality currently document the best example of an Early Permian assemblage from a rarely encountered upland terrestrial setting, and the strictly terrestrial Bromacker vertebrate assemblage is dominated by large herbivores that greatly outnumbered the apex predators in diversity and abundances. Because of their diversity and abundance, the large herbivorous tetrapods played a vital role in sustaining the ecosystem by providing a major link between primary producers and a greatly reduced number and variety of apex predators, a situation that contrasts that of the well-known, lowland, paralic, mixed terrestrial-aquatic assemblages of comparable age. It is not until nearly 50 million years later in the Early Triassic that modern terrestrial vertebrate herbivore-based ecosystems appear, but then as fully developed and typifying most terrestrial vertebrate communities. Together, both aspects of the

Bromacker locality have provided the unique opportunity to assess the mutual influences of the environmental and biological components of community assembly and structure in an Early Permian upland terrestrial paleoecosystem.

Paleoenvironmental Features

Deposition of the Bromacker sediments and their associated vertebrate fossil assemblage in the Tambach Basin was interpreted as representative of a rarely encountered paleoenvironment of a 'truly upland' terrestrial setting (Eberth et al. 2000; Berman et al. 2000a, 2001). This was defined as far removed and up-dip from regional-scale drainage systems of extensive coastal or alluvial plains bordering non-coal-forming wetlands, which constitute the overwhelming source of Late Pennsylvanian-Early Permian terrestrial vertebrates. All of the hundreds of vertebrate specimens collected from the Bromacker locality, ranging from isolated elements to partial and complete articulated skeletons, were recovered from two massive, red-brown, very fine-grained sandstone and siltstone sheetflood (non-channelized) deposits separated by 50 cm that occur in a stratigraphic interval of 1.2 m within the massive siltstones to very-fined-grained-sandstones of the 50–100 m thick 'Tambach Sandstone' (the informal name given to the middle unit of the tripartite division that separates a lower and upper conglomerate unit of the Tambach Formation). Collectively, the Tambach Sandstone consists of alluvial paleochannel and sheetflood facies and lacustrine suspension deposits. The beds of the Bromacker locality are interpreted as having been deposited on an upland alluvial plain with minor stream channels under seasonal-to-subseasonal cycles of flooding in an ephemeral setting of a savanna-type climate. The sheetflood deposits containing the vertebrates were interpreted as representing meteoric flooding events, and they were undoubtedly the agents of death of the vertebrates.

Ample sedimentological and taphonological evidence was provided (Eberth et al. 2000) to support the conclusion that the Bromacker assemblage is representative of a single community living within the Tambach Basin. The sheetflood deposits containing the vertebrates occur as two, discrete, massive units, representing two, closely spaced, catastrophic flooding events of very short duration over a very wide area. They probably originated at the basin margin and when of sufficient magnitude spread across the low relief at the center of the basin and the Bromacker locality. The thickness of the fossiliferous sheet-flood deposits indicate a magnitude of deposition sufficient to have had the potential of preserving individuals much larger than those recovered to date or possessing a cursorial ability

to escape entrapment. In many instances death and burial were apparently coeval events, sometimes including small groups of partial-to-complete articulated specimens, with some being preserved in natural poses, with the limbs extended away from the body and the elbows pointed posteriorly and the knees pointed anteriorly. Size ranges of the different taxa do not differ depending on whether they are represented by isolated elements or partial-to-complete skeletons. The excellent state of preservation of the fossil vertebrates indicates that subaerial exposures were either lacking or of short duration, and reworking and transport were limited or in some instances absent. The location of the Bromacker locality near the center of a lowland topography of the Tambach Basin was undoubtedly a critical factor in the superb preservation of the many articulated specimens.

Paleobiological Features

All the taxa from the Tambach Formation are highly terrestrial, but most remarkably, all are otherwise unique to Europe yet share a strong commonality with those of the mixed terrestrial-aquatic assemblages of the well-documented, lowland terrestrial environments of the Early Permian of the southwestern United States (Sumida et al. 1996; Eberth et al. 2000). The uniqueness of the Bromacker vertebrate assemblage is most profoundly expressed in the composition of its constituents and the relative abundances of its members. Palaeoniscoid fish, xenacanth sharks, and dipnoan lungfish are completely absent, as are aquatic and semi-terrestrial amphibians. Instead, amphibians are limited to the highly terrestrial trematopids *Tambachia trogallas* (Sumida et al. 1998) and *Rotaryus gothae* (Berman et al. 2011), the amphibamid *Georgenthalia clavinasica* (Anderson et al. 2008), the ostodolepidid microsauro *Tambaroter carrolli* (Henrici et al. 2011), *Seymouria sanjuanensis* (Berman et al. 2000a), and the diadectomorphs *Diadectes absitus* (Berman et al. 1998) and *Orobates pabsti* (Berman et al. 2004b). The abundance and variety of herbivores is unusually high and includes *Diadectes absitus* and *Orobates pabsti* (Berman et al. 1998, 2004b), an as yet undescribed, primitive basal caseid synapsid (Berman et al. 2009; Reisz et al. 2010), and the bolosaurid parareptile *Eudibamus cursoris* (Berman et al. 2000a). In contrast, the abundance and variety of apex predators is unusually low, including only two primitive basal synapsids: several specimens of the diminutive-sized *Dimetrodon teutonis*, weighing about 24 kg (compared to 37–259 kg for previously described species) (Berman et al. 2001, 2004b) and the relatively large-sized varanodontine varanopid *Tambacarnifex unguifalcatus*, first reported but undescribed by Berman et al.

(2009). On the basis of these paleobiological features it was hypothesized (Eberth et al. 2000) that the Bromacker assemblage documents an initial stage in the evolution of the modern terrestrial trophic ecosystem based on herbivory, in which herbivorous tetrapods represented a significant source for the direct introduction of plant food into the animal food chain.

The relative abundances of the Bromacker locality taxa were originally estimated by preliminary, albeit rough, specimen counts (Eberth et al. 2000). In the time since that report, relative abundances were continually tracked using minimum number of individuals counts during continued excavation of the Bromacker locality. These data clearly indicate that collectively the four herbivores outnumbered the apex predators by a ratio of at least 8 to 1. Using the same census, the combined numbers of individuals counts of the herbivores and carnivores for the entire assemblage is about 50 and 6 %, respectively. In addition, documentation of the great abundance of herbivores is also revealed by the superb vertebrate trackways preserved in paleochannel sandstones subadjacent to the Bromacker locality. Of the five recognized ichnospecies, a track-trackmaker association was firmly established between the ichnospecies *Ichniotherium cottae* (Pohlig 1885) and *I. sphaerodactylum* (Pabst 1895) and the skeletal fossils of *Diadectes absitus* and *Orobates pabsti*, respectively (Voigt et al. 2007). Collectively, the *Ichniotherium* species comprise about 95 % of the more than 600 collected tracks or trackways (Voigt et al. 2007).

An equally compelling measure of whether the herbivores constituted a major standing crop capable of sustaining the apex predators would be to calculate the difference between the relative total biomasses of the two groups. Unfortunately, there is no reliable technique for accurately calculating body mass of vertebrate fossils (Laurin 2004), which is especially exaggerated by the vagaries of preservation. An alternate, although rough, method of indexing relative body masses is maximum snout-vent length (Laurin 2004). This convention, of course, ignores the fact that the large herbivores had much more rotund torsos and stockier limbs than the apex predators and snout-vent lengths would, therefore, actually tend to underestimate the herbivore biomass. Nevertheless, the snout-vent lengths of the three large herbivores (*Orobates*, *Diadectes*, and the caseid) and the two large apex predators (*Dimetrodon* and *Tambacarnifex*) fall into a narrow range of 50–60 cm. Again, preliminary minimum number of individuals counts indicates a great numerical disparity in the abundance ratio of the two groups of 22 herbivores to three apex predators, suggesting a comparable disparity between their total biomasses. Thus, as in a modern terrestrial trophic ecosystem the herbivores would appear to have substantially supported the apex predators. Undoubtedly, the apex predators did not prey solely on the large herbivores, and the food web must have also included

alternative pathways in which the apex predators preyed on the smaller carnivores and insectivores.

Until recently, Olson (1952, 1966, 1971, 1983) was the primary researcher to theorize the existence of an Early Permian upland terrestrial vertebrate community or ecosystem. Olson's (1966, 1971, 1983) evidence of an Early Permian upland terrestrial vertebrate community was based on the rare occurrences of faunal elements of what he referred to as the Caseid Chronofauna, which was characterized mainly by herbivorous species of the primitive basal synapsid Caseidae and eureptiles, and the carnivorous Varanopidae. The unexpected occurrences of these taxa were explained as "erratics," forms that originally inhabited an upland community, but were transported or introduced into a lowland, water-based vertebrate community, Olson's Permian-Carboniferous Chronofauna. Interestingly, both a caseid and a varanopid are members of the Bromacker assemblage.

Other than the Bromacker locality, our understanding of Early Permian vertebrates from an upland setting is dependent mainly on a single site, the Richards Spur locality near Fort Sill, Oklahoma, which has been widely regarded as Leonardian in age and therefore younger than the Bromacker locality. Woodhead et al. (2010), however, utilizing radiometric analysis to determine the age of a stalagmite from the cave deposits of the same locality, assessed an age of Wolfcampian, making it roughly coeval with the Bromacker locality. The vertebrates of the Richards Spur locality are preserved in clay-rich fissure fills in the Ordovician limestone of the Arbuckle Formation and represent possibly the richest late Paleozoic vertebrate locality in the world, comprising a very diverse assemblage of 25 or more taxa (Sullivan and Reisz 1999; Sullivan et al. 2000; Anderson and Reisz 2004; Kissel et al. 2002; Reisz 2005; Maddin et al. 2006; Fröbisch and Reisz 2008; Reisz et al. 2009). Carroll (1968) theorized the existence of an upland ecosystem based on a diapsid parietal he described from the Richards Spur locality, believing that it might have been transported from an upland fauna. Unfortunately, the allochthonous origin of the Richards Spur vertebrates prevents any description of the physical and climatic aspects of the environment(s) that influenced and supported this assemblage in its original paleoenvironment (Olson 1991; Sullivan and Reisz 1999). Furthermore, the vertebrates are randomly concentrated and typically disarticulated to single elements, and therefore may have been subjected to sorting biases during transport, making calculations of the relative abundances of the taxa and the determination of the trophic organization of the assemblage highly speculative at best. In dramatic contrast, the Bromacker locality provides a unique opportunity to assess the interplay between physical, climatic, and biological ecosystem components in an upland setting, and to test previously proposed hypotheses about upland paleoecosystem composition and dynamics. In this

context, the Bromacker locality offers a critical understanding of late Paleozoic tetrapod evolution and paleobiogeography, and ecosystem evolution (e.g., Vaughn 1966, 1969, 1970; Olson 1975, 1976, 1979; Eberth and Berman 1993; Sullivan and Reisz 1999).

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