Journal of Vertebrate Paleontology 29(1):103–122, March 2009

ARTICLE

POSTCRANIAL ANATOMY OF THE RAUISUCHIAN ARCHOSAUR *BATRACHOTOMUS KUPFERZELLENSIS*

DAVID J. GOWER*[,1] and RAINER R. SCHOCH[2]
[1]Department of Zoology, The Natural History Museum, London SW7 5BD, UK, d.gower@nhm.ac.uk
[2]Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart, Germany, schoch.smns@naturkundemuseum-bw.de

ABSTRACT—*Batrachotomus kupferzellensis* is an upper Middle Triassic (Late Ladinian) rauisuchian archosaur. The postcranial skeleton of this species is well-represented by fossil material, including the holotype, from the localities of Kupferzell, Crailsheim and Vellberg-Eschenau in southern Germany, and is described here in detail for the first time. All postcranial elements are known except the interclavicle and parts of the carpus, manus, tarsus, pes and some osteoderm and axial elements. *B. kupferzellensis* is now one of the best-known rauisuchians and will be important in advancing understanding of the group's biology. A period of new anatomical and taxonomic work since 2000 has improved understanding of rauisuchians. Renewed effort in rauisuchian phylogenetics will benefit from these new data, but will also require a careful and detailed approach to character formulation.

INTRODUCTION

Many aspects of modern terrestrial ecosystems emerged from the major faunal transitions that occurred during the Triassic and Jurassic (Padian, 1986; Fraser and Sues, 1994; Irmis et al., 2007). Throughout much of the Middle and Late Triassic, including the beginning of the dinosaurian radiation, the top terrestrial predators were rauisuchians—non-dinosaurian archosaurs that arose in the Early or Middle Triassic (Gower, 2000). Knowledge of rauisuchian biology is important to the understanding of Triassic-Jurassic macroevolutionary patterns, but thus far little is actually known. A recent review (Gower, 2000) summarized work suggesting that rauisuchians are a possibly unnatural (para- or even polyphyletic) diverse assemblage of suchian crurotarsan archosaurs. Gower (2000) suggested that the many unresolved issues in rauisuchian morphology, taxonomy and phylogeny, the foundation for all other biological understanding, would be best solved by a renewed effort in the basic, detailed documentation and interpretation of morphology. Some of this work has since been undertaken (e.g., Alcober, 2000; Gower, 1999, 2002; Gebauer, 2004; Nesbitt, 2005, 2007; Sulej, 2005; Gower and Nesbitt, 2006; Nesbitt and Norell, 2006; Peyer et al., 2008; Weinbaum and Hungerbühler, 2007).

Among the taxonomically less problematic rauisuchians for which reasonable material is available, the late Ladinian *Batrachotomus kupferzellensis* (Gower, 1999) is currently one of the outstanding taxa. It was discovered in the 1977 excavation at Kupferzell (southern Germany), which also yielded thousands of temnospondyl bones, including complete skeletons, as well as other vertebrates (Wild, 1980; Schoch, 1997, 1999; Schoch and Wild, 1999). *Batrachotomus kupferzellensis* is known from well-preserved partial skeletons of several individuals of different size. Much of the morphology of the cranium and mandible (Gower, 1999) and the braincase (Gower, 2002) of *B. kupferzellensis* has already been described in detail. The aim of this paper is to provide the first detailed description of the postcranial skeleton.

The term Archosauria is used here in its traditional sense (see Benton in Benton & Clark, 1988; Benton, 1999; Juul, 1994), with members of Archosauria sensu Gauthier (1986; equivalent to Avesuchia of Benton, 1999) being referred to as 'crown-group archosaurs'. Rauisuchia is also employed throughout in a traditional sense (see Gower, 2000) — including all taxa usually classified in the Rauisuchidae, Prestosuchidae, Poposauridae, and Chatterjeeidae, even though rauisuchians are probably not monophyletic (Gower, 2000; Nesbitt, 2005; Gower and Nesbitt, 2006). Rauisuchia has alternatively (Parrish, 1993) been applied to a hypothesized monophylum composed of Crocodylomorpha, Poposauridae, and Rauisuchidae (sensu Parrish, 1993). Limb bone orientation follows Gower (1996, 2003:55). A list of material examined and institutional abbreviations is given in Appendix I. All specimen numbers refer to SMNS material unless otherwise stated.

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope, 1869–1870 sensu Benton in Benton and Clark, 1988

CRUROTARSI Sereno and Arcucci, 1990

SUCHIA Krebs, 1974 sensu Benton and Clark, 1988

BATRACHOTOMUS Gower, 1999

BATRACHOTOMUS KUPFERZELLENSIS Gower, 1999

Revised Diagnosis—Gower (1999) provided a "diagnosis" for *Batrachotomus* (the same as for the type and only species, *B. kupferzellensis*) but this was an abbreviated description and was not differential, although differential characteristics were discussed in a "Remarks" section. A revised, differential diagnosis is given here.

A rauisuchian (sensu Gower, 2000) suchian with three sacral vertebrae. Differs from all other rauisuchians with three sacral vertebrae (*Bromsgroveia* and *Arizonasaurus*) in having relatively long, strongly ventrally deflected sacral ribs, having a subvertical instead of anterodorsally trending (onto anterior iliac process) rugose iliac ridge above the acetabulum, lacking a waisted ilium (sensu Nesbitt, 2005), and lacking coossification

---

*Corresponding author.

among sacral vertebrae. Many rauisuchians are known from very incomplete and/or incompletely documented material and the sacrum is not well known for some genera. Among these, differs from *Rauisuchus* in having a much shorter and less slender posterior process of the premaxilla; from *Teratosaurus* in having a kinked anterodorsal maxillary border that contributes to the border of the naris; from *Lotosaurus* in having teeth and lacking greatly elongated dorsal neural spines; from *Luperosuchus* in having a shorter, less slender posterior premaxillary process, a kinked anterodorsal maxillary border, and a shorter, broader dorsal part of the prefrontal.; from *Fasolasuchus* in having a much shorter and less slender posterior premaxillary process, a concave instead of convex anterodorsal edge of the axial neural spine, and a shorter posterodorsal maxillary process; from *Arganasuchus* in having a smaller pubic contribution to the acetabulum, and a maxillary palatal process that is much further from the ventral edge of the maxilla.

DESCRIPTION

Vertebrae, Ribs, and Hemal Arches

Most of the vertebrae and ribs are described from the smaller Kupferzell specimens because the larger holotype includes only three dorsal, a single sacral, and three caudal vertebrae. Some articulated vertebrae are known among the Vellberg-Eschenau material (MHI 1895). Except for SMNS 80310 and 80339, and two caudal vertebrae of SMNS 52970, all of the SMNS vertebrae of *Batrachotomus kupferzellensis* occur as isolated elements. Because multiple individuals are present among the 1977 Kupferzell material (see Gower, 1999), it is impossible to be confident about the number of vertebrae in most regions of the column except for the sacrum, which comprises three vertebrae. The position of isolated vertebrae in the column is interpreted by comparison with other Triassic archosaurs, including rauisuchians (e.g., *Ticinosuchus*). Vertebral centra are short (relative to height) and constricted, platycoelus to amphiplatyan, especially in the presacral region. The dorsal neural arches are excavated by possibly pneumatic pits (see Gower, 2001, but also O'Connor, 2006 and Wedel, 2007 for arguments that these features are not pneumatic). There is no evidence of intercentra. The distal ends of the neural spines are often expanded transversely, and dorsal osteoderms were present probably along the whole column. Probable ventral osteoderms are also known. Preservational distortion makes it difficult to be confident about exact proportions of individual vertebrae.

Axis (Epistropheus)—SMNS 80322 is a complete, well-preserved axis (Fig. 1A, B) and another example is known in SMNS 80323. The centra of both examples are a little taller than long, but both are slightly laterally crushed. Excluding a short, conical odontoid projecting from the anterior articular surface, they were probably about as long as they were high and wide. The centrum is constricted between the articular ends. The posterior of the arched ventral surface bears a well-developed, narrow keel. Laterally, the anterodorsal corner of the centrum bears a small area not finished with compact bone that extends back from the anterior articular surface. This might correspond with the location of the neurocentral suture.

The neural arch of the axis is approximately triangular in lateral outline, with an extended, tapering posterodorsal process. The spine is thin and blade-like except for thickenings along the anterior and posterior edges. The anterodorsal tip of the spine is rugose. Laterally, the anteroventral area of the spine bears a small, neatly circumscribed and slightly raised oval facet for articulation with the neural arch of the atlas. Prominent, anteriorly projecting zygapophyses are absent. A short postzygapophysis is present. No clear facets for articulation with a rib can be located. The axis SMNS 80322 was mistakenly interpreted by Wild (1978a, 1979) as a caudal vertebra, with the pitted area lacking compacta (and two small pits on the neural spine) believed to represent a bite mark possibly from the capitosaur temnospondyl *Mastodonsaurus*, an interpretation that is not followed here.

The axis of *B. kupferzellensis* is distinct from those of other rauisuchians in having a lower anterior part of the neural spine with a less steeply sloping, largely concave dorsal edge in lateral view. Other rauisuchians have a slightly concave or straight and steeply sloping edge (*Fasolasuchus tenax* – Bonaparte, 1981; *Rauisuchus tiradentes* – Huene, 1942: plate 26, fig. 6; *Teratosaurus silesiacus* – Sulej, 2005; *Tikisuchus romeri* – DJG, pers. obs.) or strongly convex edge (*Ticinosuchus ferox* – Krebs, 1965: fig. 17). Some rauisuchians, such as *Arizonasaurus babbitti* and some other taxa restricted to Nesbitt's (2005) Group X, have much more elongate axis and cervical centra.

Cervical Vertebrae—SMNS 80283 and 80284 (Fig. 1C, D) are among the anteriormost cervical vertebrae of the smaller Kupferzell individuals. The centra are slightly laterally crushed, but each is similar in proportions to that of the axis. The middle part of the centrum is strongly transversely constricted. The posterior half of the arched ventral surface bears a well-developed narrow midline keel with a rugose ventral surface. The parapophyses are low down on the anteroventral corner of the centra. The diapophyses are a short distance behind the anterior surface of the centra, and lie close to the probable site of the neurocentral suture. The tall, narrow neural spine of 80238 is at its base about as long (anteroposteriorly) as it is wide (transversely). The distal end is oval-shaped and not notably expanded.

SMNS 80285 is probably from a slightly more posterior position. The centrum is of similar proportions to that of more anterior cervicals, but the dorsal and ventral edges of the posterior articular surface lie slightly ventral to their counterparts on the anterior articular surface. The posteroventral midline keel is marginally less prominent and lacks a rugose, flatted ventral edge. The parapophysis is in the same position as in SMNS 80283, but the diapophysis is further back from the anterior edge of the centrum. It is also directed postero-lateroventrally rather than laterally, and it slightly overhangs the lateral excavation of the body of the centrum. The neural spine is similar to that of SMNS 80283, but slightly longer (anteroposteriorly). The distal end of the spine is slightly transversely expanded, more anteriorly than posteriorly. SMNS 80286 and 80287 are similar to SMNS 80285. The distal tips of the spines of these examples show a slightly increased anterior lateral expansion relative to posterior expansion, so that they are triangular in dorsal view.

SMNS 80288 (Fig. 1E) is interpreted as a mid-cervical and differs in several respects from the anterior cervicals described previously. The centrum is a little shorter relative to its height, and the ventral keel is much less well developed, especially posteriorly. The diapophysis is about half way along the centrum, on a short process that overhangs a deeper lateral excavation. The anterior articular surface of the centrum is positioned barely above the level of the posterior surface. The neural spine is relatively longer and more blade-like. The dorsal surface of the distal end is triangular, with a thicker anterior margin. This thick anterior margin extends onto the lateral surface of the distal end of the spine. In anterior view, the top of this distal expansion is flat and broad, so that the top of the spine is somewhat T-shaped. The corresponding expansion in the more anterior cervicals is more gently tapering.

SMNS 80290 and 80291 (Fig. 1F) show some differences to SMNS 80288 and are probably mid-posterior cervical vertebrae. The diapophysis is on a longer process and the dorsal edge of this process extends up onto the base of the postzygapophysis, harboring a posteroventral concavity. A low ridge extends posteroventrally along the lateral surface of the base of the prezygapophysis. These ridges are the first substantial indications of a

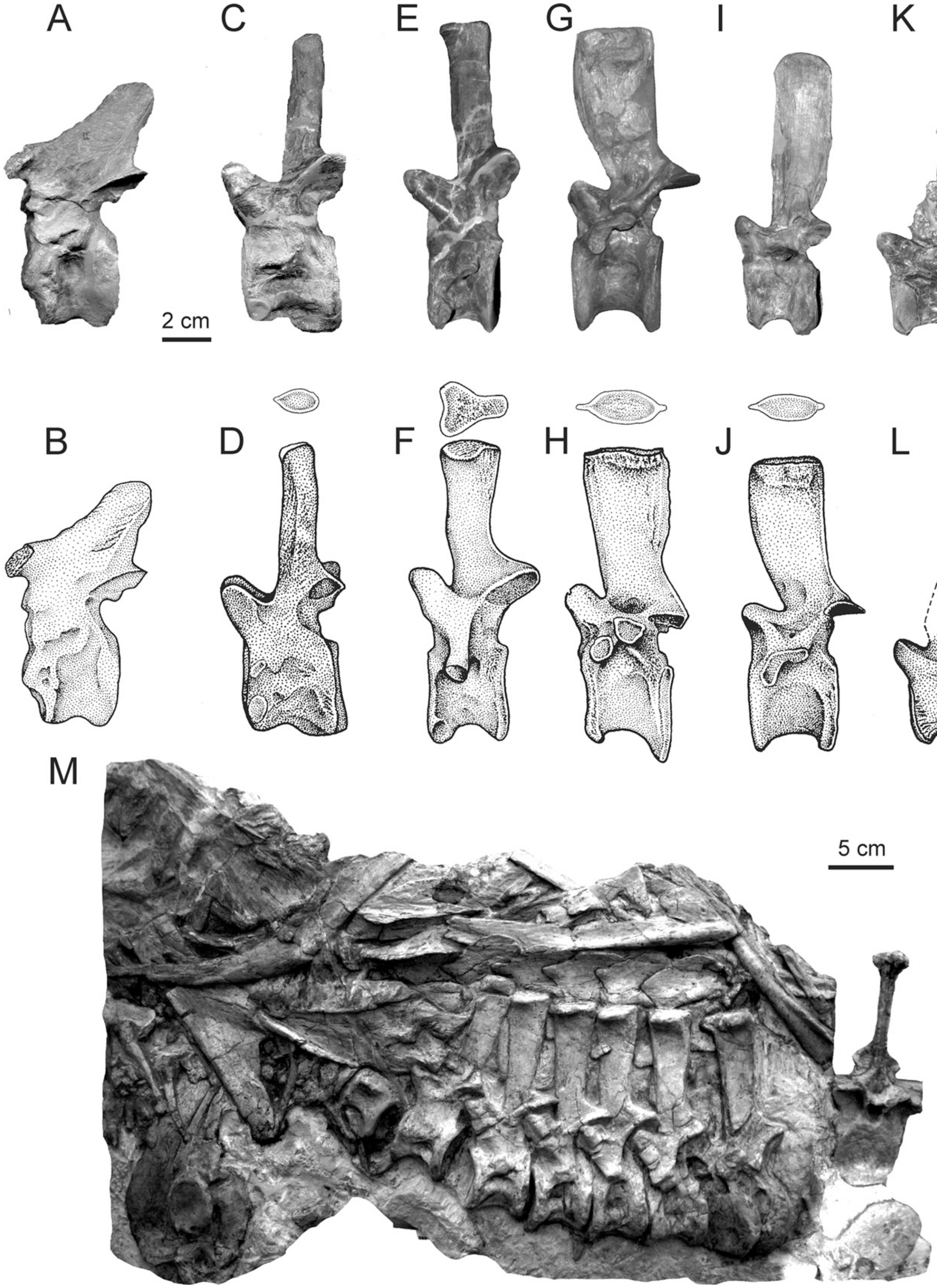

FIGURE 1. Vertebrae and paramedian dorsal osteoderms of *Batrachotomus kupferzellensis*. **A**, **B**, Left lateral view of axis SMNS 80322. **C**, **D**, Left lateral view of anterior cervical vertebra SMNS 80284. **E,** Left lateral view of mid-cervical vertebra SMNS 80288. **F,** Left lateral view of mid/posterior cervical vertebra SMNS 80291. **G, H**, Left lateral view of anterior/mid dorsal vertebra SMNS 80321. **I**, Left lateral view of caudal vertebra SMNS 80337. **J,** Left lateral view of dorsal vertebra SMNS 80306. **K, L**, Left lateral view of one of two mid/posterior caudal vertebrae of SMNS 80339. **M,** Part of MHI 1895 showing articulated cervical vertebrae and paramedian dorsal osteoderms. Drawings D–L show dorsal views of neural spines above lateral views of vertebrae.

system of lamellae and associated cavities that become increasingly prominent as far as the mid-dorsal vertebrae. The triangular distal end of the neural spine bears a central longitudinal tract finished in compact bone flanked by lateral unfinished surfaces. The expanded end is flatter and thinner than in SMNS 80288, so that the T-shaped tip seen in anterior view is more pronounced. The antero- and posteroventral edges of the centrum are slightly bevelled, but probably not strongly enough to indicate the presence of intercentra in life. Other presumed mid-posterior cervicals show exaggeration of some of the features seen in 80290. For example, the diapophyseal facet is larger and more laterally facing; an additional lamella extends posteroventrally from the diapophysis to the posterior surface of the centrum; the centra are shorter relative to their height; the strongly laterally expanded part of the distal end of the neural spine becomes longer (longitudinally) and its extension onto the lateral surface of the spine increases.

A few vertebrae (e.g., SMNS 80294, Fig. 2A) identified as the posteriormost cervicals or anteriormost dorsals (‘pectorals’ sensu Gower, 2003), exhibit a number of distinctive features. The centrum is distinctly shorter (anteroposteriorly) than high and the articular surfaces are nearly circular in outline, in contrast to the essentially oval-shaped surfaces in most of the preceding cervicals. The concave ventral surface is broad and smooth with no keel. The parapophysis is still low down on the anterior edge of the centrum, but it is now a vertically elongated oval rather than subcircular. Almost the entire distal end of the neural spine is greatly expanded, with the lateral edges now thickened and slightly ventrally deflected, so that it is more rectangular in dorsal view. The distal surface is rugose with only a midline tract completed in compacta. SMNS 80295 has shortened prezygapophyses.

The general form of the cervical vertebrae of *B. kupferzellensis* is similar to that of several other rauisuchians, although the proportionately much longer vertebrae of “*Chatterjeea elegans*” (Long and Murry, 1995), *Sillosuchus longicervix* (Alcober and Parrish, 1997) and *Arizonasaurus babbitti* (Nesbitt, 2005) stand out as obviously distinct. Features shared by *B. kupferzellensis* and other taxa include neural arch lamellae and pits, single midline ventral keels (*Tikisuchus romeri* – DJG, pers. obs.; *Postosuchus* - Peyer et al., 2008), the form of the distal expansion of the neural spine (*Postosuchus alisonae* - Peyer et al., 2008), and the overall morphology of the posteriormost cervicals (*Fasolasuchus tenax* – Bonaparte, 1981).

Cervical Ribs—A few fragmentary, disarticulated anterior cervical ribs are present among the SMNS Kupferzell material. The best preserved of these (SMNS 91046, Fig. 2M) has two heads and a short, tapering flattened blade with a pointed anterior process. It resembles the cervical ribs of several other crurotarsan archosaurs, including the rauisuchians *Ticinosuchus ferox* (Krebs, 1965: fig. 30) and *Postosuchus alisonae* (Peyer et al., 2008) and the crocodylomorphs *Crocodylus* (Mook, 1921) and *Dibothrosuchus elaphros* (Wu and Chatterjee, 1993:fig. 9).

The isolated rib SMNS 91044 (Fig. 2N) presents clear evidence of being three-headed, similar to those described for some proterosuchids and erythrosuchids (Huene, 1960; Gower and Sennikov, 1997; Gower, 2003) and some rauisuchians (Gower and Sennikov, 2000; Long and Murry, 1995; Nesbitt, 2005; Weinbaum and Hungerbühler, 2007). As in these other taxa, SMNS 91044 is most probably from the posterior cervical or ‘pectoral’ region. The accessory head is much smaller than the others and is closely associated with (or is a subdivision of) the tuberculum. Where their anatomical distribution is best understood, three-headed ribs of archosaurs seem to be restricted to only one or two vertebrae, so it is not entirely surprising that none of the SMNS vertebrae preserves the accessory apophysis.

Dorsal Vertebrae—SMNS 80321 (Figs. 1G, H) and 80296 (Fig. 2D) are interpreted as anterior (possibly mid-) dorsal vertebrae distinct from the transitional cervical-dorsal (‘pectoral’) vertebrae. The centrum is clearly shorter than it is tall, with subcircular articular surfaces. The parapophysis is on the anteroventral edge of the arch and the diapophyseal facet is on a transverse process that extends laterally from the main body of the arch, above the level of the prezygapophysis. Several lamellae extend from the transverse process, to the parapophysis, the posterodorsal edge of the centrum, and onto the bases of the anterior and postzygapophyses. Concavities between each of these lamellae are present in other rauisuchians (e.g., *Postosuchus kirkpatricki* – Chatterjee, 1985; *Arizonasaurus babbitti* – Nesbitt, 2005) and archosaurs more widely (Wedel, 2007). The neural spine is broad and blade-like in lateral view. It becomes longer (anteroposteriorly) distally. The distal end is laterally expanded, but less so than the cervicals, and is oval in dorsal view. The expanded region extends down on to the dorsolateral surfaces of the spine. Only the midline tract of the distal surface is covered in compact bone.

Several changes occur during the transition to the mid- and mid-posterior dorsal vertebrae. The centra become longer in both absolute length and in proportion to their height. The para- and diapophyses become a little closer together. The lamellae extending from the transverse process become less prominent. The neural spine becomes increasingly anteroposteriorly long and transversely broad, and takes on a characteristic shape with a straight posterior margin and strongly convex anterior margin (in lateral view) and a shorter base than distal end (Fig. 1D). The distal transverse expansion of the neural spine becomes wider (still not as marked as in the posterior cervicals) and extends further down onto the lateral surface. The articular surfaces of the zygapophyses become extremely non-planar. For example, in SMNS 80296 (Fig. 2D), the postzygapophyses are very strongly arched in posterior view, with the near-vertical ventral ends together fitting into a narrow slit between the correspondingly shaped prezygapophyses of the following vertebra. Thus, there is development in this part of the column of hypantra and hyposphenes, though these are generally a gradual continuation of the zygapophyseal articular surfaces.

In the mid-posterior to posterior dorsals (e.g., SMNS 80300, 80301, 80306, Figs. 1J, 2B) the diapophyseal and parapophyseal facets are nearly or actually confluent. The lamellae and concavities associated with the transverse process are greatly reduced. The neural spine remains broad with laterodistal rugosities and an oval-shaped distal end, sometimes with a more narrowly tapered posterior edge. Some of the posterior dorsal vertebrae (e.g., SMNS 52970, Fig. 2C) have relatively shorter, taller centra. A narrow, low, ventral keel is more commonly present in the mid-posterior dorsals than more anterior dorsals. The centra and bases of the neural arches of *B. kupferzellensis* are generally similar to those of a wide range of Triassic archosaurs (see Nesbitt, 2005:34).

Dorsal Ribs—Several incomplete dorsal ribs (e.g., Fig. 2O) are known. The right side of one of the dorsal vertebrae of SMNS 52970 preserves a short proximal section of a dorsal rib, firmly attached (perhaps partly fused) to the vertebra (Fig. 2C), but all other SMNS examples are disarticulated. The dorsal ribs are all double headed, although the facet of the capitulum and tuberculum may contact each other posteriorly. Some probably mid-dorsal ribs bear a low ridge or flange (see also Parrish, 1993: character S30) on the anterior surface, just behind the capitulum and tuberculum. Most of the dorsal rib shafts comprise a central rod flanked by more laminar edges dorsally and ventrally, the dorsal edge being more extensive. The anterior faces of the shafts are fairly flat, but posteriorly the junction between the rod and lamellar parts form elongate concavities. This pattern of a rod, lamellae and concavities is seen in the dorsal ribs of other rauisuchians, including *Tikisuchus romeri* (DJG, pers. obs.), although the ribs of many taxa are poorly known.

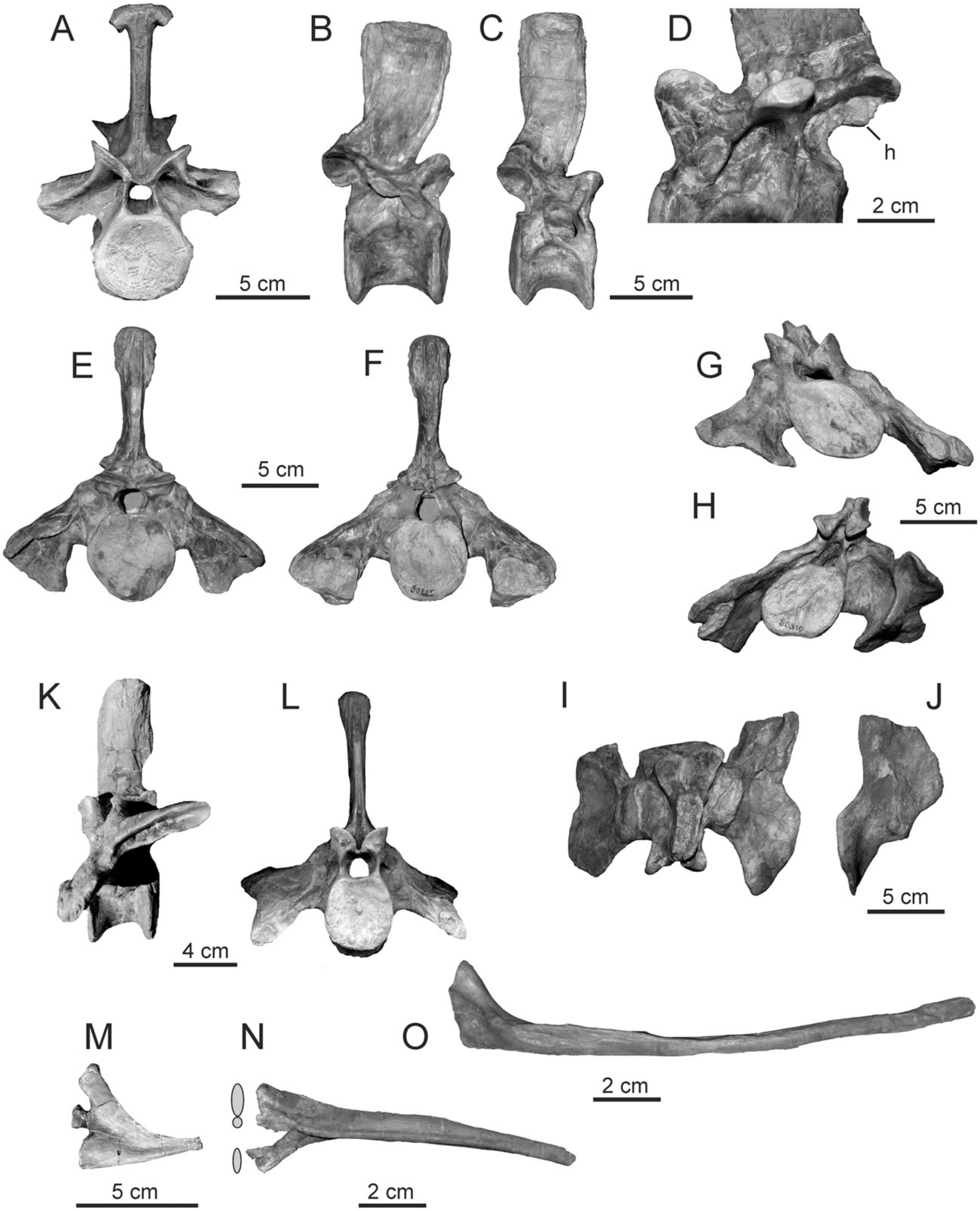

FIGURE 2. Vertebrae and ribs of *Batrachotomus kupferzellensis.* **A**, Anterior view of 'pectoral' vertebra SMNS 80294. **B, C,** Right lateral views of mid/posterior dorsal vertebrae of SMNS 80300 and 52970, respectively. **D,** Left lateral view of neurocentral region of anterior/mid dorsal vertebra SMNS 80296. **E, F,** First sacral vertebra and ribs of SMNS 80325 in anterior and posterior views, respectively. **G–I,** Second sacral vertebra and ribs of SMNS 80310 in anterior, posterior and dorsal views, respectively. **J,** Distal view of right rib of second sacral vertebra SMNS 80310. **K, L,** Left lateral and anterior views of third sacral vertebra and ribs of SMNS 80310. **M,** Lateral view of left anterior cervical rib SMNS 91046. **N,** Anterolateral view of left 'pectoral' rib SMNS 91044 with diagram showing the position of the three articular facets. **O,** Anterolateral view of left dorsal rib SMNS 91043. **Abbreviation: h**, hyposphene.

Sacral Vertebrae—Based on evidence from the medial surface of the ilia (see below) as well as vertebral and rib remains (Fig. 2), the sacrum of *B. kupferzellensis* incorporates three vertebrae. The three centra are about as tall as they are long (taller in the first and third sacrals, as with the one of the posteriormost dorsals, SMNS 80298) and they have subcircular articular surfaces. Otherwise, the three vertebrae differ among themselves and from the dorsals in several features. The first sacral centrum of SMNS 80325 (Fig. 2E, F) has a low ventral keel. The prezygapophyseal facets are short and wide, transversely aligned ovals. The neural arch lacks the well-developed pits present in the dorsal vertebrae The spine is shorter (anteroposteriorly) than in the preceding dorsals, and its distal end is laterally expanded to form a broad oval in dorsal view. The expanded and roughened laterodistal edges extend more than a quarter of the way down the spine. The second sacral of SMNS 80310 (Fig. 2G–I) is similar to the first, but the centrum is a little longer. Its neural spine is not preserved. It has a large pit on the lateral surface of the neural arch, and an additional smaller, but distinct pit below the postzygapophysis and above the centrum, close to the attachment of the rib. The distal end of the spine of the third sacral of SMNS 80310 (Fig. 2K, L) is subcircular in outline, with the thickened lateral edges extending onto the laterodistal surface of the spine. The ventral surface of the centrum is broad and smooth. The articulated second and third sacral vertebrae of SMNS 80324 are fairly complete, but heavily distorted.

The number of sacral vertebrae varies among rauisuchians (see Gower, 2000) from the plesiomorphic archosaurian condition of two in, for example, *Postosuchus* (Long and Murry, 1995), *Prestosuchus chiniquensis* (Huene, 1942), and *Stagonosuchus nyassicus* (Gebauer, 2004) to three, as in *B. kupferzellensis* (e.g. *Teratosaurus suevicus* – Galton, 1985; *Bromsgroveia walkeri* – Galton and Walker, 1996; Benton and Gower, 1997; *Arizonasaurus babbitti* – Nesbitt, 2005), or more (e.g., *Poposaurus gracilis* – Long and Murry, 1995; *Sillosuchus longicervix* – Alcober and Parrish, 1997; *Effigia okeeffeae* – Nesbitt, 2007). Although *B. kupferzellensis* is derived in having three sacrals, it differs from all members of Nesbitt's (2005) Group X in that these vertebrae are not coossified. Ontogenetic variation in the number of sacral vertebrae is unknown in any Triassic archosaur to the best of our knowledge.

Sacral Ribs—The (mostly distorted) sacral ribs are strongly ventrally directed and overlap and articulate with one another. The first has a centrally excavated anterior surface (Fig. 2E), and the anteriorly projecting ridges above and below this excavation articulate with the border of the anterior waist at the base of the iliac blade (Fig. 5D). The articular surface of the rib for the ilium is directed almost ventrally (Figs. 2E–H), so that the corresponding part of the ilium is held subhorizontally (about 25°). The ventral end of the posterior surface of the first sacral rib bears a large subtriangular facet (Fig. 2F) that articulates with the second sacral rib. The corresponding facet on the second sacral rib (Fig. 2G) is comprised of two discrete regions on both left and right of 80310. The second sacral rib is the most robust of the three and has the largest distal facet for the ilium. This facet (Fig. 2J) tapers posteriorly, where it bears a groove that articulates with the anterior end of the ridge on the medial surface of the ilium (Fig. 5D). Posteriorly, the second sacral rib bears an excavation that extends dorsomedially into an overhung concavity on the neural arch of the vertebra. Distally, the ventral end of the posterior surface of the second sacral rib bears a facet for articulation with the anterior edge of the third sacral rib (seen clearly only on the left of SMNS 80310, Fig. 2H). The second rib also overlaps and contacts the anterodorsal surface of the third. The matching areas of the third rib bear clear facets (Fig. 2L). A roughened area on the anterodorsal surface of the third rib of SMNS 80310 behind this main facet for the second sacral rib indicates that a less well-defined inter-rib articulation occurred in this area. The whole third sacral rib is anterodorsally-posteroventrally compressed, and most of its narrow distal surface is grooved for articulation with the medial iliac ridge (Fig. 2K). Anteriorly, the third sacral rib articulates mostly with the underside of the iliac ridge, and posteriorly mostly with its upper surface.

The plesiomorphic archosaurian and crurotarsan condition is two sacral vertebrae with ribs that are directed laterally or slightly ventrolaterally (e.g., *Crocodylus* – Mook, 1921; *Erythrosuchus africanus* – Gower, 2003; *Stagonolepis robertsoni* – Walker, 1961; *Parasuchus hislopi* – Chatterjee, 1978). In many rauisuchians, the (often more than two) sacral ribs are strongly downturned, so that the ilia are held subhorizontally (e.g., *B. kupferzellensis*), though in others the sacral ribs do not appear to be downturned; instead it is a modification of the ilium that causes the acetabulum to face largely ventrally (e.g., *Poposaurus gracilis* and *Chatterjea elegans* – Long and Murry, 1995). Nesbitt (2005: 43, character 5) argued that rauisuchians in his Group X have a derived condition in which the proximal ends of the sacral ribs are relatively short (anteroposteriorly), but the sacral ribs of *Batrachotomus kupferzellensis* (not in Nesbitt's Group X) are also relatively short, certainly considerably shorter and more gracile than those of the sacrum referred to *Postosuchus kirkpatricki* by Long and Murry (1995:fig. 136). The specific identification of the latter has yet to be demonstrated conclusively, complicating taxonomic comparisons. Similarly, Bonaparte (1984) refers sacra with three vertebrae to *Saurosuchus* sp. and *Prestosuchus* sp. but the systematics of these taxa and the referral of incomplete material to each of them is also currently potentially problematic (e.g., Alcober and Parrish, 1997; Gower, 2000). In addition to seemingly having only two sacrals, the centra of *Ticinosuchus ferox* are relatively longer than in *B. kupferzellensis* (DJG, pers. obs.).

Caudal Vertebrae—SMNS 80335 and 80313 are among the most anterior caudal vertebrae. As with the third sacral, the centrum of each is taller than it is long, with subcircular articular surfaces. The dorsal and ventral margins of the posterior articular surface are positioned lower than the corresponding margins of the anterior surface, much as in the anteriormost cervicals. There is no ventral keel, or bevelling to articulate with a hemal arch. The neural arch bears lateral pits similar to those in the dorsal vertebrae. The spine is broad in lateral view, particularly distally. The distal tip is approximately oval-shaped, with the thickened lateral edges extending down onto the laterodistal surfaces of the spine for about one quarter of its height. Two anterior caudal vertebrae belonging to the holotype (SMNS 52970) are pathologically ankylosed together.

One isolated holotype vertebra is from the anterior caudal region. There is no midline ventral keel, but instead a midline concavity bordered by a pair of ridges aligned with the paired facets for the hemal arch on the bevelled ventral edge of the posterior articular surface. As in SMNS 80335 and 80313, the neural arch bears a deep lateral pit. The neural spine is straight edged and rectangular in lateral view, shorter (anteroposteriorly) than the spine of SMNS 80313 and the posterior dorsals. The distal tip is polygonal to subcircular in dorsal view and its thickened lateral edges extend for only a short distance onto the laterodistal surfaces of the spine.

More posterior caudals differ in several regards. The centra are relatively longer and less tall, less laterally constricted, and the articular surfaces more oval in shape. The lateral pits on the neural arch persist, the distal tip of the spine becomes much less expanded laterally, with the roughened area on the adjacent lateral surface weakly developed or absent. Most of the caudal neural spines are too incomplete proximally to ascertain with complete certainty whether the small, subsidiary anterior processes seen in *Ticinosuchus ferox* (Krebs, 1965:fig. 29) and *Teratosaurus silesiacus* (Sulej, 2005) are present throughout, but one is clearly indicated in both vertebrae of SMNS 80339 (Fig. 1K).

Caudal Ribs—The ribs of the anterior caudal vertebra 80313 is very firmly attached and probably at least partly fused to the arch. They abruptly taper from a broad base, but distally are incomplete. The ribs of the ankylosed anterior caudals of 52970 also have broad proximal ends, and taper strongly to form thin, subhorizontal blades with slightly spatulate distal ends. The ribs of the posterior caudals are fused to the arches, and are present as very short processes with small oval transverse sections.

Hemal Arches—A few, mostly incomplete hemal arches are preserved, including SMNS 91047 (Figs. 7N, O), but all are disarticulated from the caudal vertebrae. The proximal ends consist of a pair of incompletely fused, subcircular facets presenting hourglass shaped surfaces for articulation with the centra. Below these facets, each arch encloses a large opening for the passage of blood vessels. The distal end of each arch forms a transversely compressed blade. The hemal arches of *B. kupferzellensis* generally resemble those of many archosaurs, including non-crown-group taxa (e.g., Gower, 2003) and extant crocodilians (e.g., Mook, 1921).

Pectoral Girdle and Limb

Scapula—Both scapulae of SMNS 80271 are well preserved (left figured by Parrish, 1993:fig. 5c) (Fig. 3). Several other incomplete scapulae are known (Appendix 1). The long axis of the element is bowed so that the lateral surface is convex and the medial surface concave. It has a clear waist with strongly expanded dorsal and ventral ends, so that both the anterior and posterior edges are concave in lateral view. Towards the ventral end, it bears a very weak acromion 'process', detectable as a small bump on the lateral surface, close to the anterior edge. At about the same level, the posterolateral surface has a clearly defined, roughly pitted, posteroventrally directed projection. A roughened muscle scar is present in a comparable area on the scapula of *Crocodylus* (e.g., Mook, 1921), and the phytosaur *Nicrosaurus* (e.g., present as a small nubbin in SMNS 4060) and is interpreted in *B. kupferzellensis* as the attachment site of the scapular head of M. triceps. The medial surface of the waisted region of the left scapula of SMNS 80271 bears a low ridge towards its anterior edge, possibly associated with muscle attachment (Fig. 3H). A less well-defined, roughened area on the medial surface of the dorsal expansion of the same specimen may also be associated with muscle attachment, but a comparable texture is absent on its opposite member as well on the incomplete scapulae of SMNS 80274.

As a whole, the scapula is thin, although the roughened ventral surface is thickened for articulation with the coracoid. The posteroventral edge is also bevelled to form the dorsal part of the glenoid for articulation with the head of the humerus.

Coracoid—The approximately semicircular coracoid is much smaller than the scapula (Fig. 3). It is also best preserved in SMNS 80271 (left figured by Parrish, 1993: fig. 5c). The inner surface is strongly concave and the lateral surface convex. The foramen for the passage of the supracoracoid nerve lies entirely within the coracoid, set within a fossa on both the ventrolateral and dorsomedial surfaces. The coracoid forms most of the postero-ventrolaterally open glenoid. While the upper, scapular portion of the glenoid is composed of a single simple surface, the lower, coracoid part is formed from two partially discrete areas. The largest of these lies posteriorly, and generally mirrors the scapular portion in facing posterolaterally, its ventral edge is raised above and overhangs the lateral surface of the main body of the coracoid. The smaller surface is a thin, more laterally directed strip along the anteroventral margin of the glenoid. Apart from the glenoid region and a laterally roughened region ventromedial to this on the outer surface, the coracoid is thin and smooth. Although the posterior end of the glenoid region forms a raised lip, it is debatable whether this renders the region posteromedial to the lip a much smaller homologue of the posterior coracoid process seen in crocodylomorphs (as indicated by Parrish, 1993: fig. 5) and *Effigia* (Nesbitt, 2007). None of the known *B. kupferzellensis* coracoids is well enough preserved to know whether there was an anterior notch close to the contact with the scapula.

Clavicles and Interclavicle—SMNS 91050 (Fig. 3I, J) is a possible right clavicle of *B. kupferzellensis* (S. J. Nesbitt, pers. comm.). Identification of this element is tentative because clavicles of rauisuchians are poorly known. Evidence for the presence of clavicles in *B. kupferzellensis* also comes from the weak acromion process and textured surface on the anterolateral edge of the scapulae (e.g., right scapula of SMNS 80271). The distal end of 91050 is fairly flat and finely striated on both main surfaces, especially towards the anteromedial edge. About one third the length from the distal end, the clavicle is at its most circular in cross section. Between here and the flat distal end, the clavicle is concave on its inner surface. The central portion of the element bears a very finely rugose surface, especially along the posterolateral edge. The proximal end is incomplete, but has thicker margins joined by a thinner web of bone. Nesbitt (2007:45) considered the clavicle of *Effigia okeeffeae* to be proportionately larger than that of *B. kupferzellensis*, but this is unclear from Nesbitt's description of *Effigia* and the isolated element described here. No indisputable interclavicles of *B. kupferzellensis* are known.

Humerus—The humerus is a little longer (c. 118%) than the forelimb epipodials (Fig. 4), with the forelimb pro- and epipodials being about 70% of the length of that of the hindlimb pro- and epipodials (estimated from SMNS 80275-278). The relative length of pro- and epipodials, and of fore- and hindlimbs is not known in most rauisuchians, which are represented largely by incomplete, often fragmentary material. The right humeri of 80275 and the only slightly smaller SMNS 80276 (225 vs 235 mm length, a photograph of which is presented by Wild, 1978b:192) are well preserved. The expanded proximal and distal ends are joined by a short shaft that has an approximately oval transverse section. The ventral surface of the proximal end bears a well-defined deltopectoral crest (Fig. 4C, D). At its apex, the edge of this curved (in lateral view) crest has an expanded free end. This surface is not finished with compact bone and it extends onto and along the whole of the proximal articular surface. Most of this articular surface is terminal, with restricted expansion onto the proximodorsal and proximoventral edges. On the dorsolateral surface of the proximal end of the humerus, the supinator ridge extends about half of the way up the length of the deltopectoral crest. An oval-shaped area with a roughly pitted surface extends from the area where the supinator ridge begins to fade up to the proximal end of the element, this is more clearly defined in SMNS 80276 (Fig. 4A, C). In texture, this surface (interpreted as the attachment site of the humeral head of M. triceps) resembles that on the posterolateral projection on the scapula above the glenoid fossa. The two lie in reasonably close proximity when the humerus is articulated in the glenoid, supporting the hypothesis that they represent points of origin for different heads of the M. triceps.

The distal end of the humerus is slightly less expanded than the proximal end. The entepicondylar (medial) side is larger than the ectepicondylar (lateral) side, so that the medial edge of

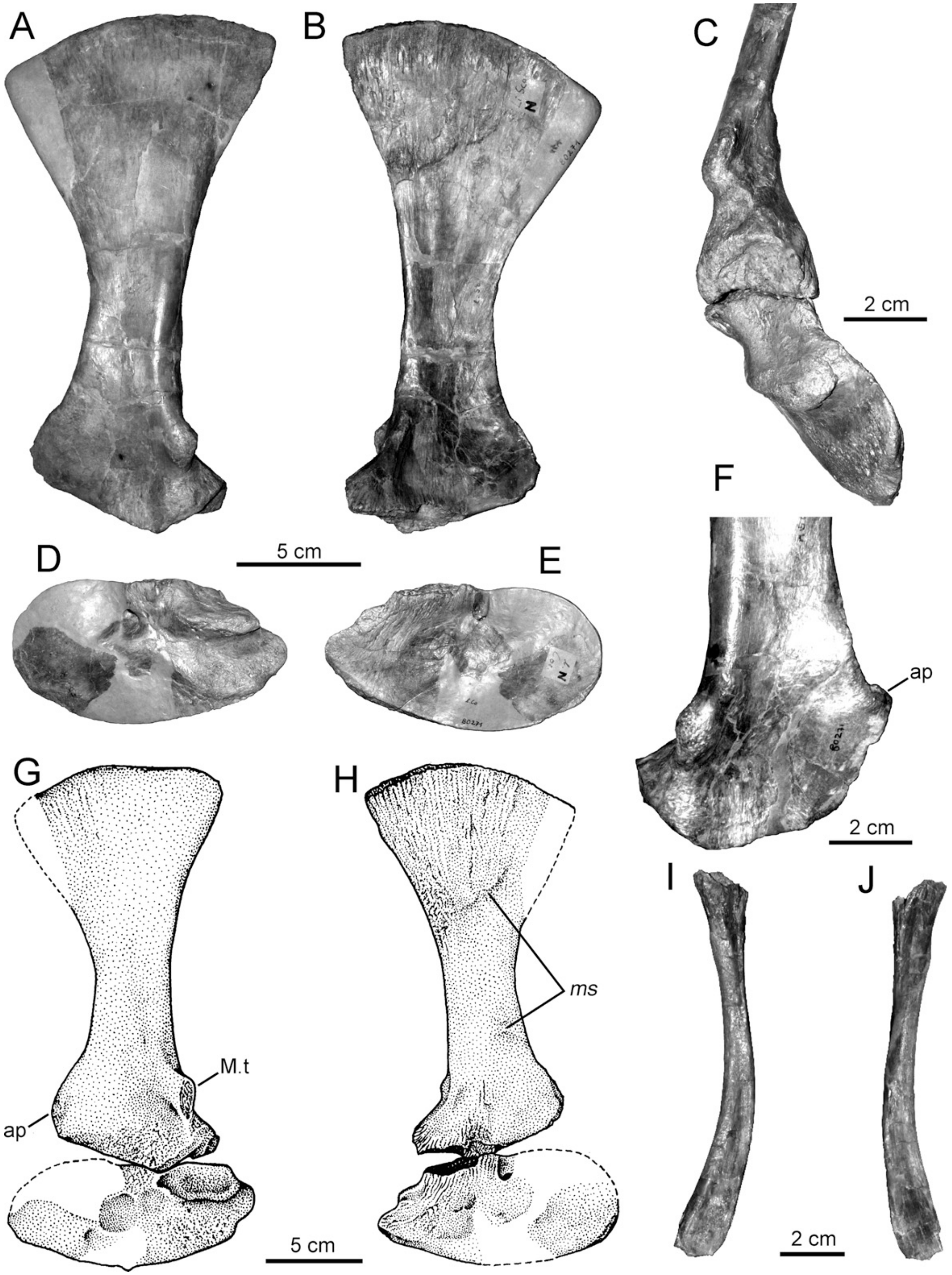

FIGURE 3. Pectoral girdle of *Batrachotomus kupferzellensis*. **A**, **B**, Lateral, medial views of left scapula. **C**, Posterior view of left glenoid region. **D**, **E**, Lateral, medial views of left coracoid. **F**, Lateral view of proximal end of right scapula. **G**, **H**, Lateral, medial views of left scapula and coracoid. **I, J**, Internal, external views of right clavicle?. All scapula and coracoid figures are of SMNS 80271; clavicle? is SMNS 91050. **Abbreviations: ap**, acromion process; **ms**, possible muscle attachment scar; **M.t**, surface for origin of M. triceps.

---

the humerus is the more concave viewed dorsally/ventrally. Viewed distally, however, the articular surfaces of the ent- and ectepicondyles are of approximately the same size, although a precise comparison is prevented by some dorso-ventral crushing of both known examples. Distolaterally, the supinator process lies clear of the distal end of the ectepicondyle. Dorsolaterally, the process flanks a clearly visible ectepicondylar groove for the radial nerve and blood vessels.

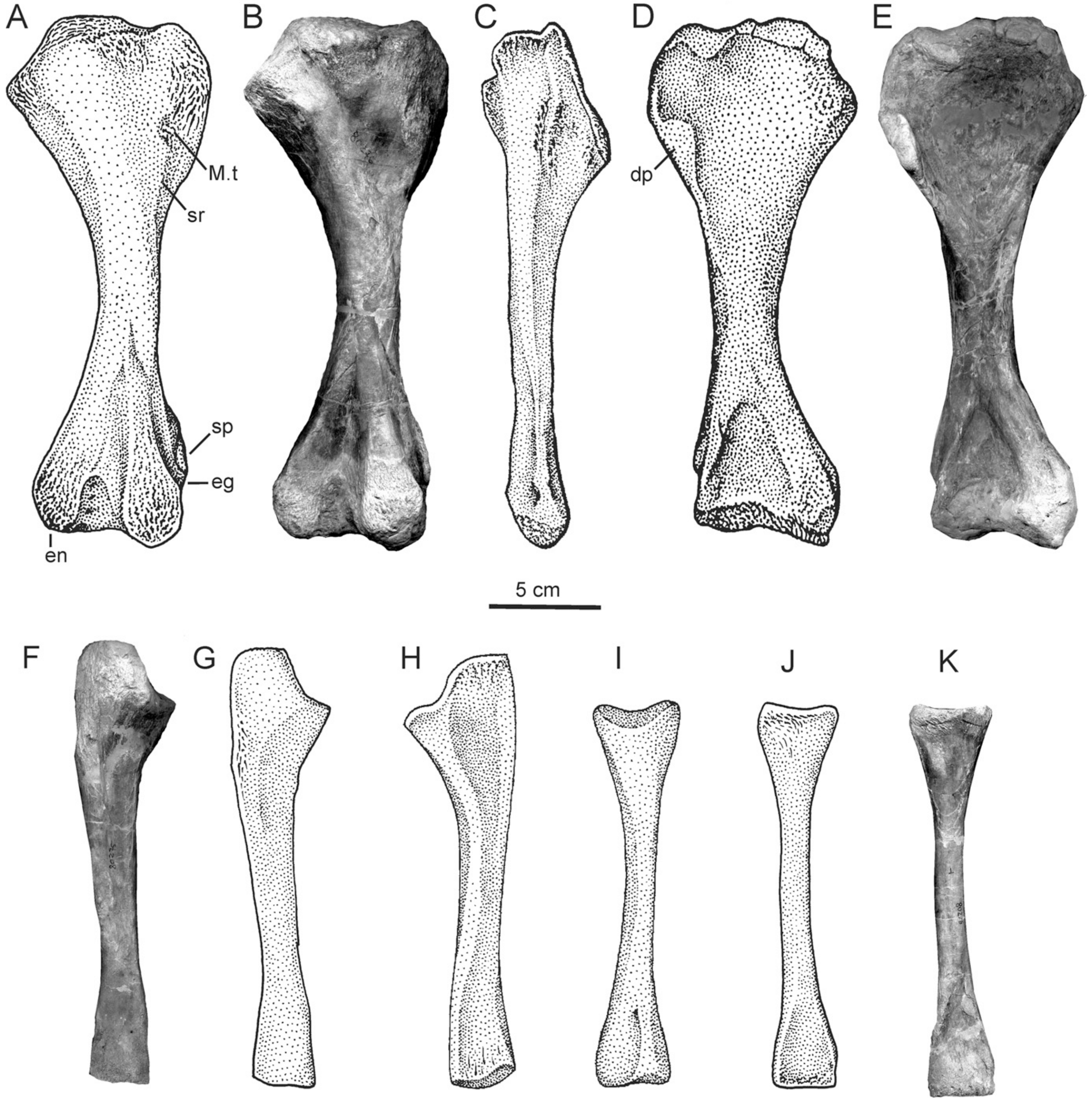

FIGURE 4. Right forelimb pro- and epipodials of *Batrachotomus kupferzellensis*. **A**–**C**, Dorsal and lateral view of humerus of SMNS 80276. **D**, **E**, Ventral view of SMNS 80275. **F–H,** Ulna of SMNS 80275. **I–K,** Radius of SMNS 80275. **Abbreviations: dp**, deltopectoral crest; **eg**, ectepicondylar groove; **en**, entepicondyle; **M.t**, surface for origin of M. triceps; **sp**, supinator process; **sr**, supinator ridge.

Krebs (1965) reported that the humerus of *Ticinosuchus ferox* is 105% the length of the scapula. A comparison with *B. kupferzellensis* is not possible because the known scapulae and humeri are not known to belong to any one individual, but it is clear that the humerus is considerably shorter than the scapula in this species.

Ulna and Radius—The slender forelimb epipodials (Fig. 4) are known from one example of each element found close to the right humerus of SMNS 80275 (R. Wild, pers. comm.) and catalogued under the same number. The ulna is of about the same length as the humerus whereas the radius is somewhat shorter (85% length of humerus). The proximal end of the ulna has a strong olecranon process, with a subterminal and strongly concave articular surface positioned on the proximal corner of the flexor (dorsal sensu Gower, 2003) surface of the element. The extensor (ventral sensu Gower, 2003) surface of the olecranon process is roughened for attachment of M. triceps. Both the radius and ulna bear a few other roughened areas, but both preserved elements are somewhat crushed and none of these areas is clearly defined enough to be interpreted confidently as muscle attachment scars. Both the radius and ulna of *Ticinosuchus ferox* are estimated to be a little longer than the humerus (Krebs, 1965),

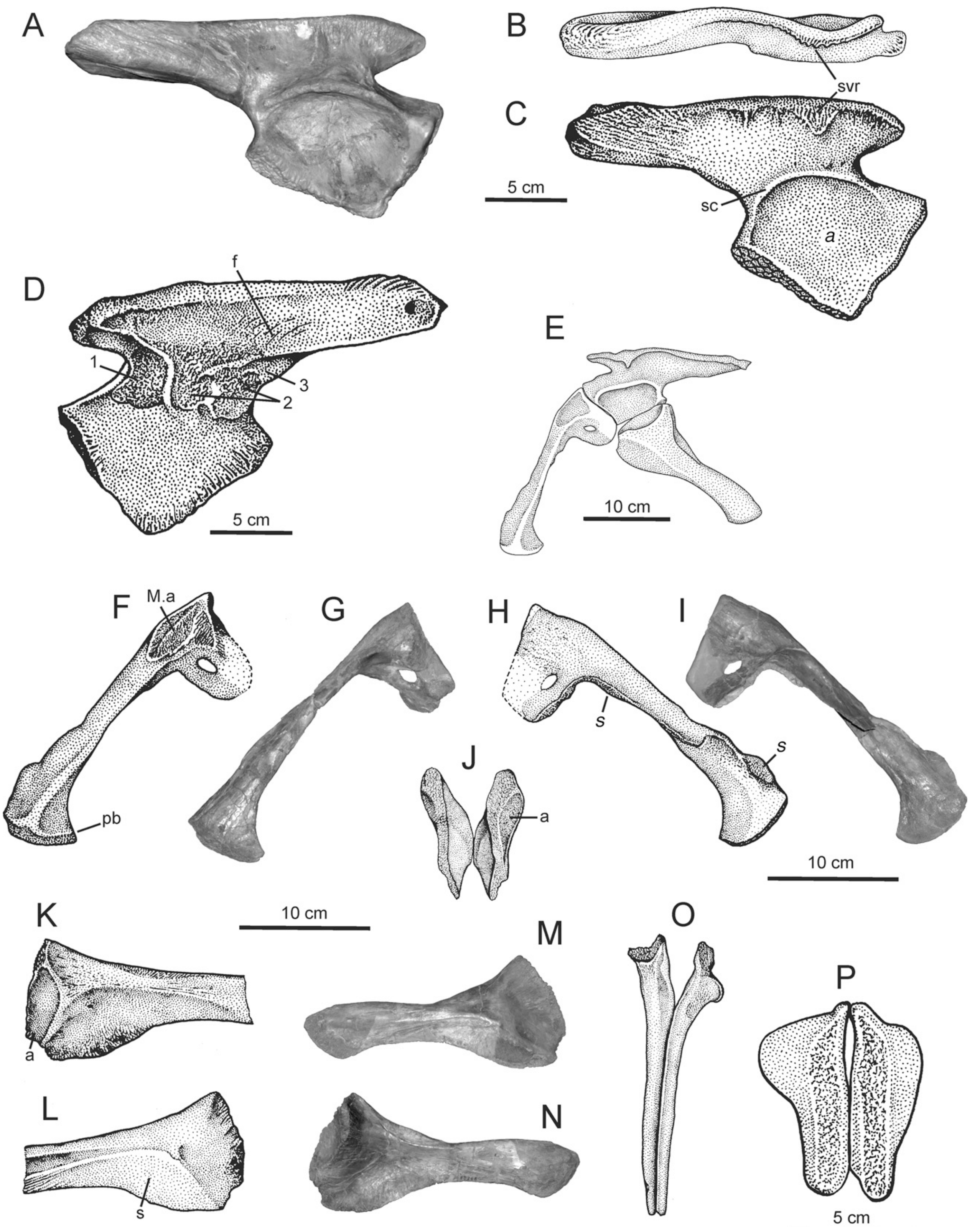

FIGURE 5. Pelvis of *Batrachotomus kupferzellensis*. **A–C**, 'Lateral' and 'dorsal' views of right ilium of SMNS 80269. **D**, 'Medial' view of right ilium of SMNS 80270. **E**, 'Lateral' view of left pelvis to show relative sizes of elements, based on SMNS 80270. **F**, **G**, Lateral view of left pubis of SMNS 80270. **H**, **I**, Medial view of left pubis of SMNS 80270. **J**, Anterodorsal view of articulated ischia of SMNS 80280. **K**, **L**, Lateral, medial views of left ischium of SMNS 52970. **M**, **N**, Medial, lateral views of left ischium of SMNS 80268. **O**, Dorsal view of ischia of SMNS 80280. **P**, Distal view of pubic boot of SMNS 52970. **Abbreviations: a**, acetabulum; **f**, fossa; **M.a**, attachment site of M. ambiens; **pb**, pubic boot; **s**, symphyseal surface; **sc**, supraacetabular crest; **svr**, rugose subvertical ridge; **1**, **2**, **3**, facets for first, second and third sacral ribs.

but this material is heavily crushed and the forelimb epipodials are shorter than the propodial in other rauisuchians, where known (e.g., *Postosuchus* sp. nov., Peyer et al., 2008).

Carpus and Manus—SMNS 90018 includes two fragments of probable right metacarpals, distinctly smaller than the metatarsals of the same specimen. Two other elements, one of which is distorted, are interpreted as phalanges of the manus, but little further information can be gained. No unequivocal carpal elements are known, but a small ovoid bone preserved as part of SMNS 90018 (which includes probable metacarpals/phalanges of the manus) may represent one, if it is not a distal tarsal, which are otherwise unknown.

Pelvic Girdle and Limb

Ilium—The ilium (Fig. 5) is one of the best represented elements among the SMNS Kupferzell material, with several examples being well preserved, notably the right ilium of the holotype SMNS 52970 (Galton, 1985:fig. 1A), and left and right ilia of the smaller SMNS 80269, 80270, and 80272. The ilium of *B. kupferzellensis* exhibits several characteristics seen in other rauisuchians, chiefly a thickened and subvertical rugosity region on the lateral surface of the iliac blade (Fig. 5A–C), articulation with three sacral ribs (Fig. 5D), and the subhorizontal inclination of the whole element when articulated with the sacral ribs. Although held subhorizontally, the consequently ventrolateral surface is here described as 'lateral' to facilitate comparison with the homologous surface of a wider range of non-rauisuchian archosaurs.

The dorsal blade of the ilium has a short anterior and long posterior process. Its dorsolateral edge bears a series of closely packed rugose ridges with their long axes extending toward a central point in the vicinity of the apex of the supra-acetabular crest. The rugosities are particularly concentrated at the anterior and posterior ends of the blade, but they are most conspicuous at a point above the apex of the supra-acetabular crest. Here, the rugose surface is raised above the lateral surface of the main body of the iliac blade. In some examples this raised area assumes the form of a rugose, subvertical ridge perpendicular to the dorsal edge of the blade. The rugose area is constant among different specimens, but the ridge varies in its distinctiveness.

A waist lies between the blade of the ilium and the ventrally expanded acetabular region. The acetabulum is a shallow concavity, but the supra-acetabular crest is prominent. The antero- and posteroventral edges of the acetabular region of the ilium are bevelled, at greater than 90° to the lateral surface of the element and allowing the subhorizontal ilium to articulate with the pubis and ischium, both of which are held in a position much more comparable with non-rauisuchian archosaurs. The region between the articular surfaces for the pubis and ischium is not waisted as in members of Nesbitt's (2005) Group X.

The areas of the ilium that articulate with the sacral ribs can be detected on the medial surface of the waisted region between the expanded blade and the acetabular region (Fig. 5D). The first has anterodorsal and anteroventral arms that extend along the anteroventral edge of the blade and anterodorsal edge of the acetabular region respectively. The second extends from approximately halfway along the waisted region to the anterior end of a narrow longitudinal ridge that lies toward the lower edge of the base of the dorsal blade of the ilium. The third sacral rib articulates with a short (dorsal-ventral) area on and either side (only the underside, anteriorly) of the medial ridge. This third area is largely restricted to the blade of the ilium posterior and slightly dorsal to the waist. The facets for the three ribs are confluent and not always clearly identifiable as discrete regions, especially the separation of the second and third facets.

The ilia of many other rauisuchians are distinctive, often bearing pronounced rugose regions on the anterodorsal part of the iliac blade, although this is absent in, for example, *Stagonosuchus nyassicus* (Gebauer, 2004). The anterior process of the iliac blade of *B. kupferzellensis* is relatively longer than in non-crown-group archosaurs (e.g., *Erythrosuchus africanus* – Gower, 2003) and phytosaurs (e.g., *Parasuchus hislopi* – Chatterjee, 1978), but shorter than in sphenosuchian crocodylomorphs (e.g., *Terrestrisuchus gracilis* – Crush, 1984) and aetosaurs (*Stagonolepis robertsoni* – Walker, 1961). Among rauisuchians, the iliac blade of *B. kupferzellensis* closely resembles that of material referred to *Postosuchus kirkpatricki* by Long and Murry (1995). It is distinct from the ilia of those rauisuchians with a more arched anterolateral rugosity and often expanded blades (e.g., *Bromsgroveia walkeri* – Galton and Walker, 1996; Benton and Gower, 1997; *Poposaurus gracilis* – Long and Murry, 1995). The acetabulum of *B. kupferzellensis* is clearly imperforate, possibly unlike some other rauisuchians (e.g., *Poposaurus*, Long and Murry, 1995; Weinbaum and Hungerbühler, 2007). The ilium of *B. kupferzellensis* differs from that of *Ticinosuchus ferox* in that, in the latter taxon (DJG, pers. obs. of right ilium of holotype), the area on the medial surface of the ilium for articulation with the first sacral rib does not seem to expand so far onto the anterior extension of the iliac blade. This anterodorsal extension of the facet for the first sacral rib is even more pronounced in members of Nesbitt's (2005) Group X.

Pubis—The slender pubes (Fig. 5) form a narrow, elongated and strongly downturned pubic apron ending in a posteroventrally deflected distal foot/boot. Proximally, the anterodorsal part of the pubis is expanded, while the posteroventral part is thin and plate-like. The proximal face of the anterodorsal expansion generally matches the corresponding surface on the ilium, except that it is broader transversely and so also forms the anteroventral rim of the acetabulum. The posteroventral edge of the plate-like part of the pubis also articulates with the ischium.

A single, large obturator foramen lies at the junction between the expanded and plate-like parts of the proximal end of the pubis, close to the edge that articulates with the ilium. Distal to the proximal expansion, the pubis is essentially a thin medial sheet with a thick, rounded lateral ridge. Proximally, the dorsolateral edge of the plate, just in front of the edge of the acetabulum, is further expanded and roughened, probably for attachment of the M. ambiens (Fig. 5F, G). This scar is fairly constant across all known specimens. It is approximately oval in outline, with the long axis of this oval aligned with the long axis of the pubic plate. A longitudinal groove divides the oval into a smaller anterodorsal and larger posteroventral region. The latter is sharply demarcated by a low ridge from the smoothly surfaced bone posteroventral to it, as Weinbaum and Hungerbühler (2007:fig. 5C) documented for *Poposaurus*.

The medial edge of the pubic plate is slightly thickened for midline symphysis with its antimere (Fig. 5H, I). The distal boot is laterally compressed (probably at least partly crushed in all SMNS specimens) and essentially vertically oriented, and is thicker than the rest of the plate, especially along its anteroventral edge. The boot also met its antimere along a midline symphysis (Fig. 5P), although the slightly thickened, rugose, and convex distalmost edge is free (Fig. 5H).

The moderate pubic boot of *B. kupferzellensis* resembles that of *Postosuchus kirkpatricki* (material referred by Long and Murry, 1995) and *Tikisuchus romeri* (DJG, pers. obs.), and is notably shorter than in *Shuvosaurus inexpectatus* (Long and Murry, 1995) or *Effigia okeeffeae* (Nesbitt, 2007). A distinct pubic boot is absent in non-rauisuchian crurotarsans including phytosaurs (e.g., Chatterjee, 1978), aetosaurs (e.g., Walker, 1961) and sphenosuchian (e.g., Crush, 1984) and crocodyliform (e.g., Mook, 1921) crocodylomorphs. The lateral edges of the articulated pubes converge anteriorly to a narrow pubic plate. In this regard *B. kupferzellensis* differs from, for example, *Erythosuchus africanus* (Gower, 2001) in which the medial and lateral edges of each pubis are subparallel.

Ischium—The ischium (Fig. 5) of *B. kupferzellensis* is generally thin and flat, and more plate- than rod-like. As with the articular surfaces of the other pelvic girdle elements, the proximal edge has a coarsely rugose surface for articulation with the ilium and pubis. Contact with the pubis is along a short, barely expanded anteroventral surface, but articulation with the ilium is via a more expanded edge. The lateral surface of the proximal end of the ischium bears a gently concave semi-oval area that forms the posteroventral limit of the acetabulum. More distally, the ischium tapers in lateral view. About one third of the way along its length, the thickened dorsolateral edge of the ischium bears a roughened suboval muscle scar with a longitudinal groove, present in all specimens. The ischium tapers to a minimum about two-thirds along its length, before ending in a moderately expanded distal end.

The medial surface of the ischium can be divided roughly into anterodorsal and posteroventral regions. The medial surface is convex overall, with the apex of this convexity lying along the division between these two regions. The anterodorsal region lies at a shallow angle to the horizontal and forms a freestanding dorsomedially-facing inner surface. The posteroventral region forms a subvertical surface that forms the midline symphysis with its antimere. The nature of this symphysis varies throughout this region. The most intimate union between the opposite ischia is formed by the anteroventral edge, immediately behind the proximal edge of the ischium that articulates with the pubis, and the posterior edge. The bone surface of the large area between these edges is lightly striated and not obviously specialized for a very tight contact.

In being essentially plate-like in form (albeit more slender than in e.g., *Erythrosuchus africanus* – Gower, 2003), the ischia of *B. kupferzellensis* resemble the plesiomorphic archosaurian condition, and differ from the more rod-like elements of *Arizonasaurus babbitti* (Nesbitt, 2005), *Stagonosuchus nyassicus* (Gebauer 2004), *Shuvosaurus inexpectatus* (Long and Murry, 1995) and *Effigia okeeffeae* (Nesbitt, 2007). The dorsal groove is a widespread feature, at least among rauisuchians, although its form varies.

Femur—The best-preserved SMNS Kupferzell femora of *B. kupferzellensis* are the left element of SMNS 52970 (holotype, Fig. 6A–E) and 80278 (Wild, 1978b: photograph on p. 192). Although almost complete, they are somewhat crushed in parts and few indisputable muscle scars can be identified. Other specimens (all SMNS) include the proximal end of SMNS 52970 (Fig. 6F–H) and 90508 (both right), 90509 (almost complete but heavily crushed left femur), 54833 (right distal end), and 90018 (crushed left distal end). The femur is smoothly sigmoidal in dorsal and ventral views. Much of this sigmoidal appearance is a result of the gradually inturned proximal end and associated strongly concave proximomedial edge. There is also a slight sigmoid curve to the femur seen in lateral and medial views, with the distal articular surface being a little downturned. The long axes of the articular surfaces are offset and therefore show some torsion about the shaft, although distortion prevents an accurate measurement of this angle. The terminal ends are rugose, concave, have longitudinal grooves, and were likely capped by a substantial layer of cartilage in life.

The proximal articular surface (Fig. 6H) is clearly demarcated medially where it forms the main femoral head, but laterally it narrows and merges gradually with the greater trochanter (sensu e.g., Hutchinson 2001:178) on the proximolateral edge of the femur. The proximoventral surface bears a low central ridge that recedes as it extends away from the femoral head. The fourth trochanter is identifiable as a slightly raised, elongate, roughened region between one third and one quarter of the length of the femur from the proximal terminus. A short distance distal to the fourth trochanter, a small, localized part of the ventrolateral edge of the femur is slightly thickened. This small thickening, a probable muscle attachment site, is present on both of the nearly complete femora of SMNS 52970 (Fig. 6E) and 80278 as well as 90508, and marks the proximal limit of a low crest that forms the ventrolateral edge of much of the more distal part of the femur.

The dorsal surface of the femur bears two probable muscle scars: a weakly developed roughened (but not raised) area lies on the dorsal surface of the greater trochanter, clearly seen on the right femur of SMNS 52970 (Fig. 6B, D), is probably for the insertion of the M. puboischiofemoralis externus (see Hutchinson, 2001), and a second scar (a small, subtly raised area) located a short distance distal to this, close to the lateral edge and in a very slightly more proximal position than the proximal end of the fourth trochanter on the ventral surface (Fig. 6D, E). The central portion of the femoral shaft is approximately oval in transverse section, apart from the more angulate ventrolateral edge. The distal articular surface is partially subdivided into lateral and medial condyles, with a broad popliteal space extending from between them up the ventrodistal surface of the femur. The lateral (fibular) condyle also has a groove extending away from it up the ventrolateral edge of the femur.

Tibia and Fibula—The left hindlimb epipodials of the holotype (SMNS 52970) are essentially complete (Fig. 6). In addition, there is a well-preserved distal end of a tibia from Crailsheim (SMNS 54840) and a nearly complete right fibula (SMNS 80277) from one of the smaller Kupferzell individuals. The tibia and fibula are of about the same length and, in the holotype, they are about 60% the length of the femur. The stout tibia has an approximately cylindrical shaft with a more expanded proximal than distal end. Approximately one quarter of the way from the proximal end, a partly crushed medial pit perhaps represents the insertion site of the M. puboischiotibialis. Localized crushing and an inconsistently preserved surface prevents confident identification of other possible muscle scars. The distal articular surface of the tibia, best seen in SMNS 54840 (Fig. 6I, J), is distinctly non-planar for articulation with an astragalus of similar form to that known in other suchian archosaurs.

The proximal and distal ends of the fibula are not much expanded relative to the shaft. The articular surfaces are suboval, that of the distal end is planar, and that of the proximal end apparently more flexed, but the latter is not especially well preserved in either example. The dorsolateral trochanter for the M. iliofibularis lies about one third to one half the way from the proximal end of the fibula. The shaft is essentially subcylindrical, but the ventromedial surface is markedly concave transversely, with the concavity flanked by a pair of longitudinal ridges. This concavity is absent in non-crown-group archosaurs (e.g., *Erythrosuchus africanus* – Gower, 2003) but is seen in other rauisuchians such as *Postosuchus* (Long and Murry, 1995:fig. 140), *Prestosuchus chiniquensis* (Huene, 1942:plate 20), and *Arganasuchus dutuiti* (Dutuit, 1979; Jalil and Peyer, 2007). Parrish (1993) suggested that *B. kupferzellensis* and *Rauisuchus tiradentes* share a notable synapomorphy of two prominent ridges on the anterior (dorsal here) surface of the fibula, but the ridges described above in *B. kupferzellensis* are on the ventral, not dorsal surface, and are similar to those of other rauisuchians. Furthermore, the ridges in *R. tiradentes* do not appear to be natural (Gower, 1999:7).

Tarsus and Pes—The partial left tarsus and pes (Fig. 7A–G) of a large specimen (similar in size to the holotype) were recovered from a dolomitic horizon at the Vellberg-Eschenau quarry (part of SMNS 90018). Because of the close association of these finds with a distal end of the femur, gastralia and osteoderms, the tarsal and pedal material can be referred to *B. kupferzellensis*. The preserved tarsus consists of a complete, but crushed calcaneum and a much smaller, bean-shaped element that is possibly

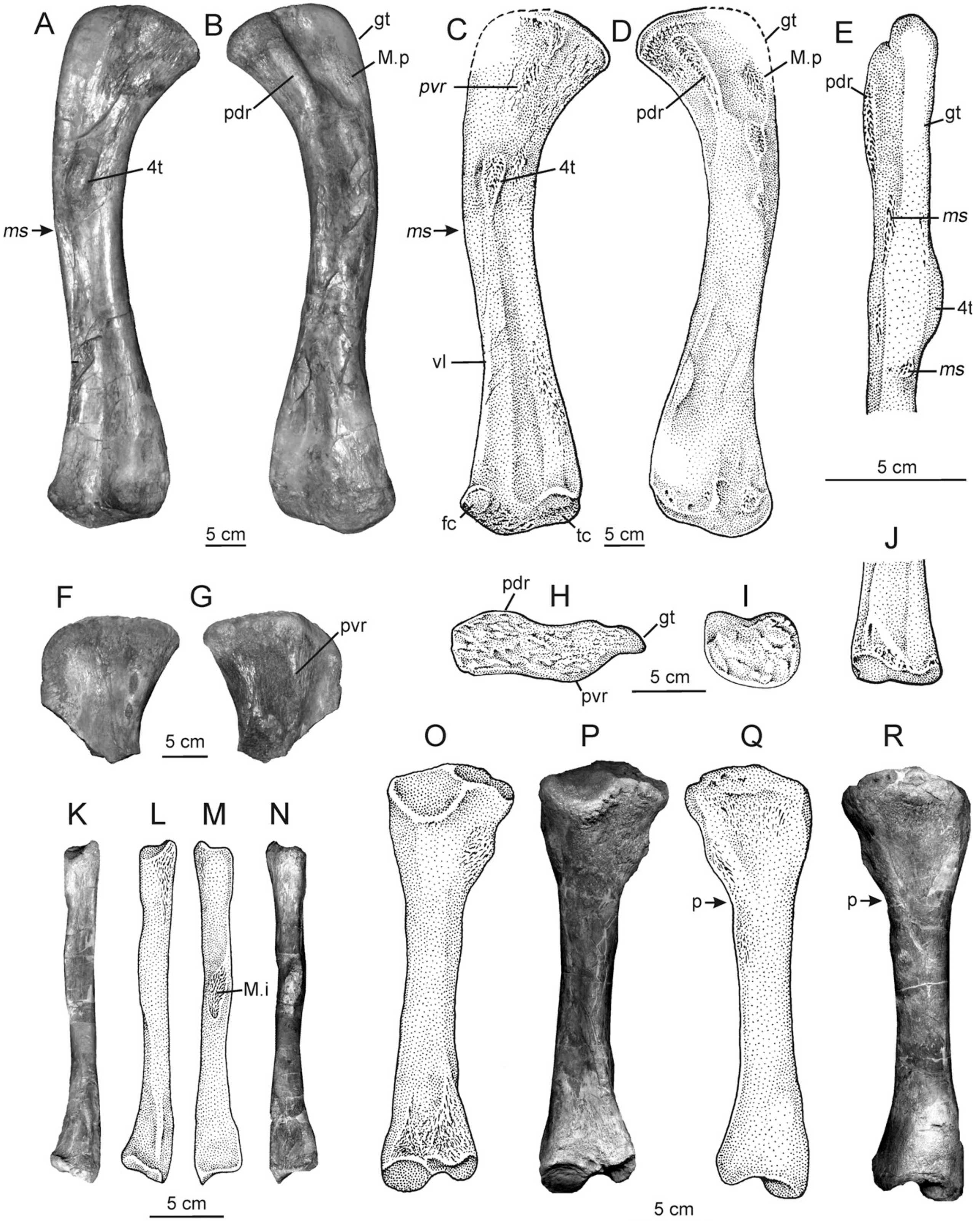

FIGURE 6. Hindlimb pro- and epipodials of *Batrachotomus kupferzellensis*. **A**–**D**, Ventral and dorsal views of left femur of SMNS 52970. **E**, Lateral view of proximal end of left femur of SMNS 52970. **F**–**H**, Dorsal, ventral, and proximal views of proximal end of right femur of SMNS 52970. **I**, **J**, Distal and ventral view of tibia of SMNS 54840. **K**–**N**, Ventral and dorsal views of right fibula of SMNS 80277. **O**–**R**, Dorsal and ventral views of left tibia of SMNS 52970. **Abbreviations: fc**, condyle for fibula; **gt**, greater trochanter; **M.i**, trochanter for M. iliofibularis; **M.p**, attachment site of M. puboischiofemoralis externus; **ms**, muscle attachment scar; **p**, pit; **pdr**, proximodorsal ridge; **pvr**, proximoventral ridge; **tc**, condyle for tibia; **vl**, ventrolateral edge; **4t**, fourth trochanter.

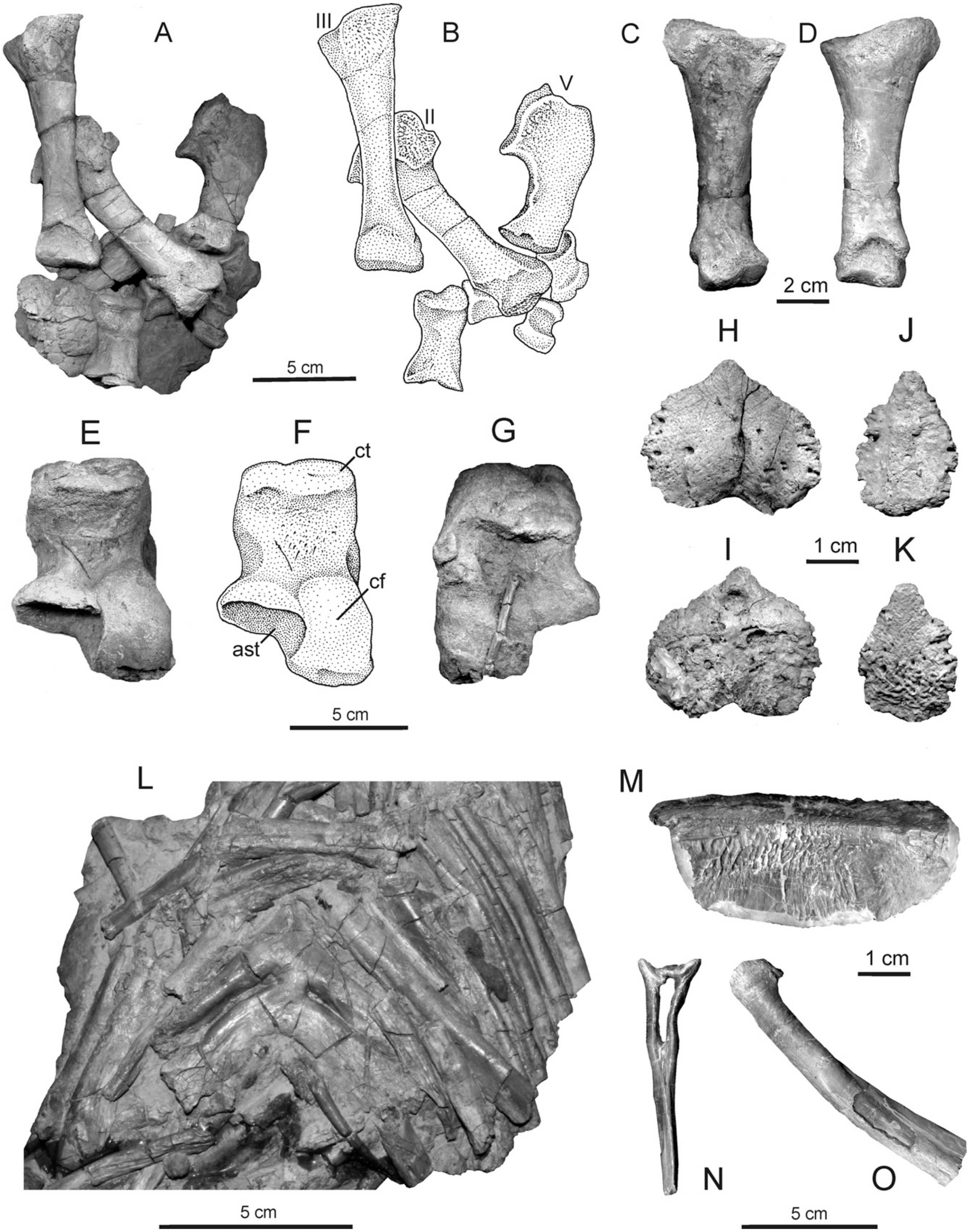

FIGURE 7. Assorted postcranial elements of *Batrachotomus kupferzellensis*. **A**, **B**, Associated metacarpals and phalanges of right pes of SMNS 90018, mostly in ventral view. **C**, **D**, Metatarsal (first?) of SMNS 90018. **E–G**, Dorsal and ventral views of left calcaneum of SMNS 90018. **H**, **I**, Tail osteoderm of SMNS 90018. **J**, **K**, Possible flank, belly, limb, or tail osteoderm of SMNS 90018. **L**, articulated fragmentary gastralia of SMNS 90018. **M**, Lateral view of left paramedian dorsal osteoderm. **N, O**, Hemal arch in anterior, left lateral views. **Abbreviations: ast**, 'socket' for articulation with astragalus; **cf**, condyle for articulation with fibula; **ct**, calcaneal tuber; **II** and **III**, metatarsals (possibly second and third); **V**, fifth metatarsal.

a distal tarsal. The heavily constructed calcaneum is similar to that of the aetosaur *Desmatosuchus haplocerus* (Long and Murry, 1995:fig. 97; DJG, pers. obs. of SMNS cast of UCMP A269) and perhaps *Prestosuchus chiniquensis* (Huene, 1942: plate 21; Parrish, 1993:fig. 3), more so than to the more elongate calcanea of *Postosuchus* (Long and Murry, 1995; Peyer et al., 2008) and *Saurosuchus galilei* (material figured by Sill, 1974: plate 4). However, the degree of similarity to *D. haplocerus* needs to be checked when less crushed material becomes available. Posterior to the hemicylindrical facet for the fibula (clearly indicative of a rotary, crocodilian-like joint between astragalus and calcaneum), the calcaneum shaft is wider than long, with lateral and ventral concavities, and a flared (apparently on all sides), distally convex tuber. The distal face of the tuber might bear a gentle concavity, but it is too crushed to be certain that this is not an artefact.

In the pes, four metatarsals, several phalanges and a few distally incomplete unguals are preserved. However, none of the digits is complete, and the only element that can be identified with precision is the robust and strongly hooked fifth metatarsal (Fig. 7A, B), which is quite similar to those of *Prestosuchus chiniquensis* (Huene, 1942) and *Saurosuchus galilei* (material referred by Sill, 1974) but perhaps more strongly hooked than *Postosuchus* (Long and Murry, 1995; Peyer et al., 2008). The other three metatarsals (Fig. 7A–D) are 110, 120, and 130 mm long (perhaps suggesting that they are the first/fourth, second and third metatarsals, through comparison with other rauisuchians [e.g., Sill, 1974; Peyer et al., in press]), considerably longer than the fifth (85 mm). The various phalanges and unguals cannot be identified with precision, and some might even belong to the manus.

Gastralia

SMNS 90018 preserves a range of abdominal ribs in partial articulation (Fig. 7L). In addition, there are several isolated gastral elements (SMNS 91045 and unnumbered material) from the 1977 Kupferzell excavation. Some asymmetrical, almost V-shaped elements are notable in being fused to each other along the tip and inside angle of the V. The articulated elements are very closely spaced and the apparatus as a whole appears to have been largely immobile.

Osteoderms

Evidence from articulated and isolated osteoderms, and comparisons with other crurotarsans, indicate that *B. kupferzellensis* was characterized by a dorsal series of plates that were paired, paramedian elements along most of the precaudal vertebral column (Fig. 8). The SMNS Kupferzell material includes several isolated presacral dorsal osteoderms. Although a few of these are associated with specific vertebrae (i.e. stored in the same container, sometimes under the same accession number), they were found only in close proximity to vertebrae rather than in life position. In addition, none was found in articulation with other osteoderms. In contrast, one specimen (MHI 1895, Fig. 1M) shows a series of paramedian osteoderms in articulation and closely associated with a series of articulated cervical vertebrae, clearly in a 1:1 alignment. All of the available paramedian dorsal osteoderms share the same general morphology and this lack of differentiation and comparison with *Ticinosuchus ferox* (Krebs, 1965) suggests that none of the anterior- or posteriormost examples has been preserved.

Each paramedian dorsal osteoderm (e.g., Fig. 7M) is composed of two main plate-like parts, a horizontal plus an angled, ventrolateral plate. Each plate is longer than it is wide and the angle between the two is marked by a longitudinal dorsal thickening. The horizontal, dorsal plate is approximately rectangular in outline. Its medial edge is thick and flattened, but has a minutely rough texture for articulation with its antimere along the vertebral midline. The anterior edge bears a short tapering process that articulates with the preceding osteoderm by underlying its slightly embayed posterior edge of the dorsal plate. This is facilitated by a shallow, gentle concavity on the posterior end of the ventral surface of the dorsal plate. The ventrolateral plate probably lies at an internal (ventral) angle of about 100–130° to the horizontal plate. Its free lateral edge is gently tapered and somewhat irregular. The outline of the ventrolateral plate is more semi-elliptical than rectangular, with a less straight lateral edge than in *Ticinosuchus ferox* (Krebs, 1965). The outer surface of each osteoderm is sculptured with a largely irregular series of small pits, grooves, and rugosities. The texturing is at its most noticeable on either side of the slightly arched and narrow longitudinal ridge between the dorsal and ventrolateral plates, and toward the anteromedial border of the dorsal plate. The most conspicuous and seemingly fairly constant of the small grooves lies in the central part of the anterior end of the dorsal plate. It is branched, but its major axis is approximately parallel to the long axis of the osteoderm. The rugosities occasionally form short ridges and furrows that are transversely oriented. Apart from the depression that articulates with the dorsal surface of the lappet of the following osteoderm of the series, the inner surface is not notably contoured. Its surface is not finished in as smooth a layer of compact bone as is the outer surface.

Presumed caudal osteoderms (Fig. 7H, I) are known from a few disarticulated, isolated examples associated with SMNS 90018. Evidence that these formed a single median series comes from their flat, nearly symmetrical, heart- or leaf-shape, and lack of articular surfaces for antimeres. The presumed tail osteoderms are much smaller than the precaudal series, and more than one osteoderm may have been associated with each caudal vertebra. As in *Ticinosuchus ferox* (Krebs, 1965), these caudal osetoderms might have been arranged along the ventral as well as dorsal surfaces of the tail. Several isolated, even smaller, less regularly shaped osteoderms were found attached to the gastral apparatus of SMNS 90018 (Fig. 7J, K), and these may have been associated with the tail, flank, belly or limbs.

The phylogenetic significance of the number of paramedian dorsal body osteoderms in relation to the vertebrae among archosaurs has been debated (e.g., Sereno and Arcucci, 1990, Sereno, 1991; Parrish, 1993). Sereno and Arcucci (1990) and Sereno (1991) argued that a 1:1 relation between dorsal body osteoderm and vertebral segments is a synapomorphy of Crurotarsi, but Parrish (1993), although including three osteoderm characters in his phylogenetic analysis, chose to exclude Sereno's character *a priori* because of evidence of homoplasy. Parrish (1993) contrasted the presence of one pair of dorsal body osteoderms in some non-crown-group archosaurs with more than one pair in some crurotarsans, including *Prestosuchus* and *Ticinosuchus*, and this is supported by the known material (e.g., Huene, 1942: plate 19; DJG, pers. obs.; Krebs, 1965). Archosaur phylogeny and osteoderm anatomy is too inadequately understood currently to draw firm conclusions, but we see no reason to exclude Sereno's character from future analyses. A possibly important caveat is that regional (and perhaps ontogenetic) variation is very poorly understood but should perhaps be taken into account. For example, the 1:1 alignment in *B. kupferzellensis* is known with certainty only from the cervical region, and a 2:1 alignment in *Prestosuchus chiniquensis* has been documented only from the sacral region (Huene, 1942:plate 19).

DISCUSSION

Following documentation of the cranial and mandibular osteology (Gower, 1999, 2002), this report of the postcranial anatomy completes the basic description of *Batrachotomus kupferzellensis.*

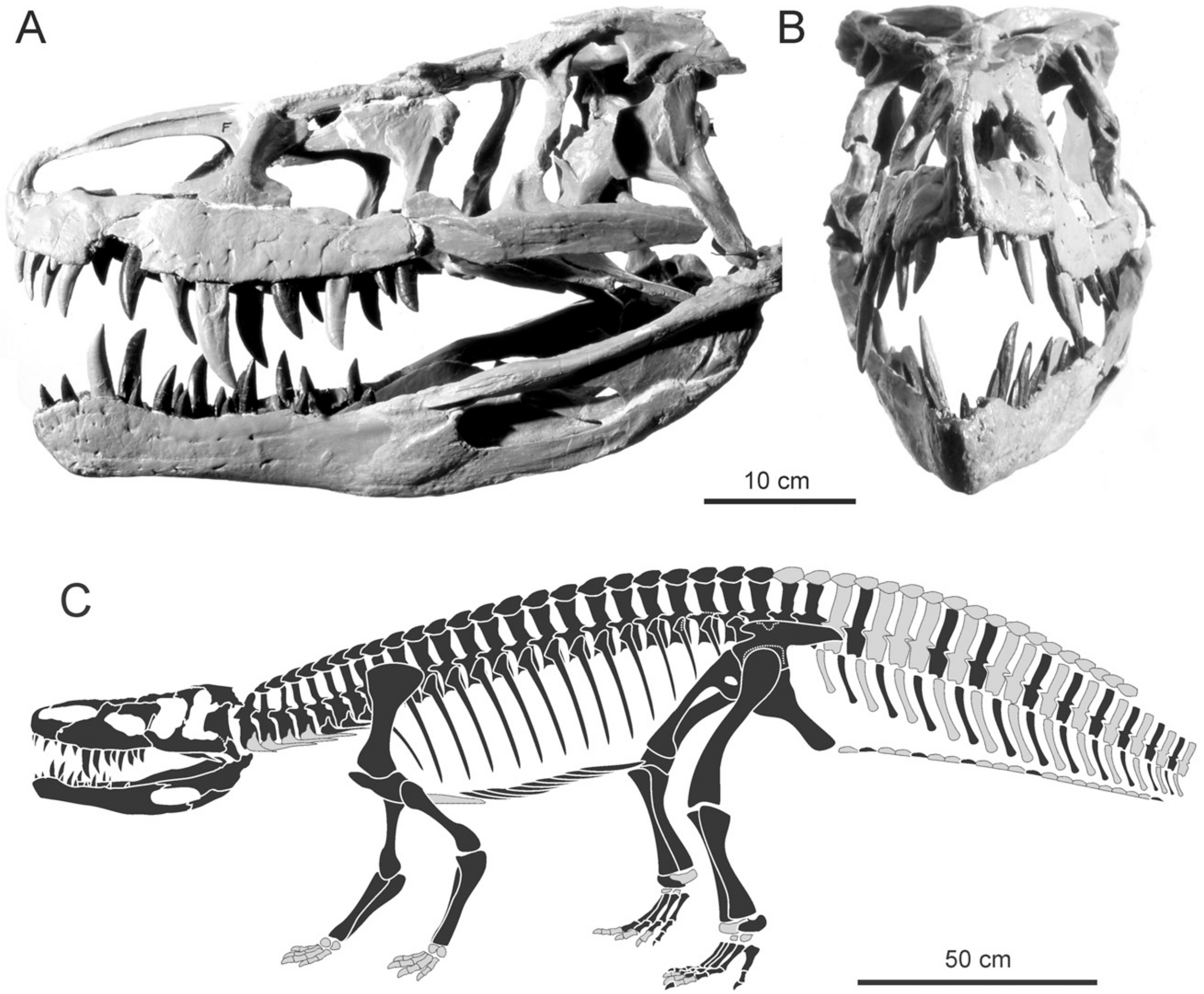

FIGURE 8. Skeletal reconstructions of *Batrachotomus kupferzellensis*. **A**, **B**, Skull reconstruction based on assembly of cast, retrodeformed elements of SMNS 80260. **C**, Partial skeletal reconstruction based on three-dimensional mount of cast and modelled elements, showing known (black) and unknown (grey) bones.

Through comparative description and/or character scoring and discussion in phylogenetic considerations, the anatomy of *B. kupferzellensis* has also been commented on by Galton (1985), Parrish (1993), Gower (2000, 2001), Gebauer (2004), Nesbitt (2005, 2007), and Weinbaum and Hungerbühler (2007).

Intraspecific Variation

The known ilia indicate that the SMNS Kupferzell postcranial material of *B. kupferzellensis* is from at least four modest sized individuals. Additional material pertaining to at least one larger individual is catalogued with the larger cranial elements comprising the holotype (SMNS 52970). Thus, an investigation of ontogenetic variation in the postcranial skeleton is necessarily restricted to a few pairwise comparisons for only a few elements, and even then it is not possible to distinguish this from possible sexual dimorphism or background individual variation.

The pubes of the larger SMNS 52970 have proportionally longer and more robust (less concave inner edge in lateral view) boots than the smaller specimens (e.g., SMNS 80270). The smaller ilia have slightly less well developed rugosities on the dorsal blade. The limb bones of the smaller specimens are slightly more slender with less well-developed trochanters, especially notable for the fibulae. None of these variations is marked enough to challenge the hypothesis that all of the referred material represents a single species.

Phylogeny

Rauisuchian phylogenetics is currently a series of mostly open questions but some progress has been made since Gower's (2000) review. Current evidence favors the non-monophyly of Rauisuchia (Parrish, 1993; Gower, 2000; Nesbitt, 2005; Gower and Nesbitt, 2006; Weinbaum and Hungerbühler, 2007). There is a new body of evidence from sacral, pelvic, femoral and osteoderm characters for the monophyly of Nesbitt's (2005) Clade X that includes *Arizonasaurus, Bromsgroveia, Effigia, Poposaurus, Shuvosaurus* (=*Chatterjeea*), and *Sillosuchus* (see also Alcober and Parrish, 1997; Nesbitt, 2007; Weinbaum and Hungerbühler, 2007), and perhaps *Lotosaurus* and 'ctenosauriscids' (Nesbitt, 2005, 2007). Incompleteness of material means that many of the linking characters are not comparable across all these taxa and so the conclusions are necessarily tentative, but the obviously derived sacrum, pelvis, cranial (especially lack of teeth in some species) and dorsal neural spine characters indicate that these taxa might represent a distinct crurotarsan lineage (Alcober and Parrish, 1997; Nesbitt, 2005, 2007; Weinbaum and Hungerbühler, 2007), and there is some evidence from braincase data that it is not closely related to the majority of other rauisuchians (Gower and Nesbitt, 2006). The main challenge to the reality and possible composition of Clade X is that the limited anatomical data reveal a complex distribution of some important characters. For example, it is clear that several taxa (e.g. *Poposaurus, Effigia*) do not possess the elongated dorsal neural spines that are so characteristic of *Arizonasaurus* and other potential members such as *Lotosaurus* and 'ctenosauriscids'. Additionally, the ilium referred to *Teratosaurus* by Galton (1985) is similar in its derived anterodorsal blade and lateral rugosity to those of Clade X taxa but the known cranial material (Galton, 1985; Sulej, 2005) is clearly dissimilar to that of *Shuvosaurus* and *Effigia*. Some perceived incompatible character state combinations might be caused by problematic taxonomy and incorrect referral of material rather than homoplasy. Other rauisuchians that apparently show no immediate affinity to Clade X present an even greater phylogenetic challenge. Most (including *Fasolasuchus, Rauisuchus, Prestosuchus, Procerosuchus, Heptasuchus, Stagonosuchus, Saurosuchus*) are too poorly represented or documented and/or are plagued by problems of knowing what material can be referred to which taxa (e.g., Alcober and Parrish, 1997). There is a general similarity among many non-Clade X rauisuchians in, for example, strongly downturned sacral ribs, but evidence that any subset of genera comprise a clade is scanty and complex. For example, *Stagonosuchus* has strongly downturned sacral ribs (e.g., Gower, 2000; Gebauer, 2004) but the dorsal blade of the ilium lacks any supraacetabular rugosity. Some complete skulls (e.g., material referred to *Saurosuchus galilei* – Alcober, 2000; *Prestosuchus* – Barbarena, 1978; *Youngosuchus* – Sennikov in Kalandadze and Sennikov, 1985) are seemingly not associated with postcranial elements and although superficially similar to, for example, *Batrachotomus* and *Postosuchus*, there are no compelling synapomorphies proposed thus far that might group some taxa. Interpreting the phylogeny of rauischians among other crurotarsans based on cranial anatomy alone is complicated by the highly distinct, substantially derived form of phytosaurs, aetosaurs and crocodylomorphs, which makes distinguishing plesiomorphy from apomorphy among rauisuchians non-trivial. Phytosaurs and aetosaurs should not be scored as having the same character state as outgroups simply because they do not resemble crocodylomorphs and rauisuchians — lacking a particular derived condition is not the same as retaining the outgroup condition.

We do not believe that Parrish's (1993) interpretations of rauisuchian intrarelationships are founded on robust character data. For example, the single synapomorphies presented as uniting Parrish's distinct Prestosuchidae and the *Fasolasuchus, Batrachotomus* + *Rauisuchus* clade are the same, support levels are generally uncompelling, and the published data matrix is not that for which analytical results were reported (Gower and Wilkinson, 1996; Gower, 2000). Gower (2002) and Gower and Nesbitt (2006) analysed only braincase characters, and we consider the analyses of Nesbitt (2003), Nesbitt and Norell (2006), Nesbitt (2007), and Weinbaum and Hungerbühler (2007) to be preliminary, and we suggest that the main results to take from these studies is the proposed monophyly of Nesbitt's (2005, 2007) Groups X and Y and the lack of robust resolution of wider relationships of rauisuchians within Suchia (see also Nesbitt, 2007:60–61). Weinbaum and Hungerbühler (2007) reported how less parsimonious some suboptimal hypotheses were based on their data, and used this to suggest that stagonolepids being more closely related than rauisuchians to crocodylomorphs (Gower, 2002) is "unlikely," but they did not include the vast majority of braincase characters or the palatal character proposed by Gower (2002) to provide support for this. The most recent analyses (Nesbitt, 2007; Weinbaum and Hungerbühler, 2007) have yet to get a firm grip on the issues of homology in the potentially key characters outlined by Gower (2000). For example, Weinbaum and Hungerbühler's (2007) character formulation and ordering denies the possible homology of the rugose supraacetabular ridges on the anterolateral surface of the ilium, and Nesbitt's (2007) denies the possible homology of the foramen between the premaxilla and maxilla in *Effigia* and *Postosuchus*.

The recent effort directed at detailed anatomical documentation of rauisuchian anatomy and taxonomy instead of expanding numerical phylogenetic analyses without improving the primary data is, in our opinion, reaping rewards. Because of possible para- or polyphyly, reappraisal of rauisuchian phylogeny requires a much wider reconsideration of crurotarsan relationships, the scope of which is beyond the present study. However, based on the new data generated by anatomical studies including this one, new phylogenetic studies are needed, even if only to begin to improve character formulation and focus attention on patterns of character (in)congruence that will lead to distinguishing homology from homoplasy. We suggest that future research will profit from phylogenetic analyses that pay great attention to detailed character discussion, as well as from resolution of alpha taxonomy and completing the anatomical documentation of key taxa including *Rauisuchus, Saurosuchus, Prestosuchus, Procerosuchus*, "*Mandasuchus*" and *Postosuchus kirkpatricki*. For possible Clade X taxa, detailed (re)descriptions of the anatomy of *Shuvosaurus* and *Lotosaurus*, and discovery and documentation of good cranial material of *Poposaurus* and *Sillosuchus* are identified as priorities.

ACKNOWLEDGMENTS

We thank R. Wild for initial access to the Stuttgart material, invaluable help during time spent at SMNS, and significant contributions to the study of *B. kupferzellensis* at all stages. Local expertise, assistance, and information were provided generously by H. Hagdorn, W. Kugler, F. Ullmann, and M. Salomon. Some important *Batrachotomus* material was collected and kindly donated by W. Kugler (to the Alberti-Stiftung which runs MHI) and M. Weinert (to SMNS). N. Adorf's skilful preparation, casting, and restoration of *B. kupferzellensis* helped greatly in understanding its anatomy. Beneficial information, discussion and advice came from E.-E. Kischlat, M. Maisch, S. J. Nesbitt, S. Novak, J. M. Parrish, K. Peyer, and J. Weinbaum, and the submitted ms was carefully and constructively critiqued by P. M. Galton, S. J. Nesbitt, and JVP editors.

Study of comparative material was made possible and enjoyable with the help of S. Chapman (BMNH); P. Wellnhofer (BSP); S. Bandyopadhyay, S. Roy, T. Roy-Chowdhury and D. Sengupta (ISI); N.-E. Jalil (MNHN); A. G. Sennikov (PIN); W. Brinkman (PIMUZ); M. Winans, C. Brochu, J. Merck, and R. Balinsky (TMM); S. Chatterjee (TTU); K. Padian and P. Holroyd (UCMP).

DJG's time in Tübingen was supported by a Royal Society European Exchange Fellowship, warmly supported by his hosts W.-E. Reif and F. Westphal. RRS's research was supported by the Deutsche Forschungsgemeinschaft grant "Lettenkeuper-Tetrapoden." Our work was partly supported by generous awards from the Welles Fund from the University of California Museum of Paleontology, Berkeley, for which we especially thank K. Padian.

LITERATURE CITED

Alcober, O. 2000. Redescription of the skull of *Saurosuchus galilei* (Archosauria: Rauisuchidae). Journal of Vertebrate Paleontology 20:302–316.

Alcober, O., and J. M. Parrish. 1997. A new poposaurid from the Upper Triassic of Argentina. Journal of Vertebrate Paleontology 17:548–556.

Barberena, M. C. 1978. A huge thecodont skull from the Triassic of Brazil. Pesquisas 7:111–129.

Benton, M. J. 1999. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. Philosophical Transactions of the Royal Society B 1388:1423–1446.

Benton, M. J., and Clark, J. M. 1988. Archosaur phylogeny and the relationships of the Crocodylia; pp. 295–338. in M. J. Benton. (ed.), The Phylogeny and Classification of the Tetrapods, 1: Amphibians, Reptiles, Birds. Clarenden Press, Oxford, UK.

Benton, M. J., and D. J. Gower. 1997. Richard Owen's giant Triassic frogs: Middle Triassic archosaurs from England. Journal of Vertebrate Paleontology 17:74–88.

Bonaparte, J. 1981. Rescripcion de "*Fasolasuchus tenax*" y su significado en la sistemática y evolucion de los Thecodontia. Revista del Museo Argentino de Ciencias naturales Bernardino Rivadavia 3:55–101.

Bonaparte, J. 1984. Locomotion in rauisuchid thecodonts. Journal of Vertebrate Paleontology 3:210–218.

Charig, A. J. 1956. New Triassic archosaurs from Tanganyika, including *Mandasuchus* and *Teleocrater*. Unpublished PhD thesis; Cambridge (University of Cambridge, UK).

Chatterjee, S. 1978. A primitive parasuchid (phytosaur) reptile from the Upper Triassic Maleri Formation of India. Palaeontology 21:83–127.

Chatterjee, S. 1985. *Postosuchus*, a new thecodontian reptile from the Triassic of Texas and the origin of tyrannosaurs. Philosophical Transactions of the Royal Society of London B 309:395–460.

Chatterjee, S., and P. K. Majumdar. 1987. *Tikisuchus romeri*, a new rauisuchid reptile from the late Triassic of India. Journal of Paleontology 61:787–793.

Cope, E. D. 1869–1870. Synopsis of the extinct Batrachia, Reptilia, and Aves of North America. Transactions of the American Philosophical Society 14:1–252.

Crush, P. J. 1984. A late Upper Triassic sphenosuchid crocodilian from Wales. Palaeontology 27:131–157.

Dutuit, J.-M. 1979. Un pseudosuchien du Trias continental Marocain. Annales de Paléontologie (Vertébrés) 65:55–71.

Fraser, N. C., and H.-D. Sues (eds.). 1994. In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods. 435 pp. Cambridge University Press, New York.

Galton, P. M. 1985. The poposaurid thecodontian *Teratosaurus suevicus* v. Meyer, plus referred specimens mostly based on prosauropod dinosaurs, from the Middle Stubensandstein (Upper Triassic) of Nordwürttemberg. Stuttgarter Beiträge zur Naturkunde, series B 116:1–29.

Galton, P. M., and A. D. Walker. 1996. *Bromsgroveia* from the Middle Triassic of England, the earliest record of a poposaurid thecodontian reptile (Archosauria: Rauisuchia). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 201:303–325.

Gauthier, J. A. 1986. Saurischian monophyly and the origin of birds. Memoirs of the California Academy of Science 8:1–55.

Gebauer, E. V. I. 2004. Neubeschreibung von *Stagonosuchus nyassicus* v. Huene, 1938 (Thecodontia, Rauisuchia) aus der Manda-Formation (Mittlere Trias) von Südwest-Tansania. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 231:1–35.

Gower, D. J. 1996. The tarsus of erythrosuchid archosaurs (Reptilia), and implications for early diapsid phylogeny. Zoological Journal of the Linnean Society 116:347–375.

Gower, D. J. 1999. Cranial osteology of a new rauisuchian archosaur from the Middle Triassic of southern Germany. Stuttgarter Beiträge zur Naturkunde B 280:1–49.

Gower, D. J. 2000. Rauisuchian archosaurs: a review. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 218:447–488.

Gower, D. J. 2001. Possible postcranial pneumaticity in the last common ancestor of birds and crocodilians – evidence from *Erythrosuchus* and other early archosaurs. Naturwissenschaften 88:119–122.

Gower, D. J. 2002. Braincase evolution in suchian archosaurs (Reptilia: Diapsida): evidence from the rauisuchian *Batrachotomus kupferzellensis*. Zoological Journal of the Linnean Society 136:49–76.

Gower, D. J. 2003. Osteology of the early archosaurian reptile *Erythrosuchus africanus*, Broom. Annals of the South African Museum 110:1–84.

Gower, D. J., and S. J. Nesbitt. 2006. The braincase of *Arizonasaurus babbitti* – further evidence for the non-monophyly of rauisuchian archosaurs. Journal of Vertebrate Paleontology 26:79–87.

Gower, D. J., and A. G. Sennikov. 1997. *Sarmatosuchus* and the early history of the Archosauria. Journal of Vertebrate Paleontology 17:60–73.

Gower, D. J., and A. G. Sennikov, 2000. Early Archosaurs from Russia; pp. 140–159 in M. J. Benton, E. N. Kurochkin, M. A. Shishkin and D. M. Unwin (eds.), The Age of Dinosaurs in Russia and Mongolia. Cambridge University Press Cambridge, UK.

Gower, D. J., and M. Wilkinson. 1996. Is there any consensus on basal archosaur phylogeny? Philosophical Transactions Royal Society of London B 263:1399–1406.

Huene, F. v. 1942. Die fossilen Reptilien des südamerikanischen Gondwanalandes. 332 pp. Beck, Nördlingen.

Huene, F. v. 1960. Ein grosser Pseudosuchier aus der Orenburger Trias. Palaeontographica A 114:105–111.

Hutchinson, J. R. 2001. The evolution of femoral osteology and soft tissue on the line to extant birds (Neornithes). Zoological Journal of the Linnean Society 131:169–197.

Irmis, R. B., S. J. Nesbitt, K. Padian, N. D. Smith, A. H. Turner, D. Woody, and A. Downs. 2007. A Late Triassic Dinosauromorph assemblage from New Mexico and the rise of dinosaurs. Science 317:358–361.

Jalil, N.-E., and K. Peyer. 2007. A new rauisuchian (Archosauria, Suchia) from the Upper Triassic of the Argana Basin, Morocco). Palaeontology 50:417–430.

Juul, L. 1994. The phylogeny of basal archosaurs. Palaeontologia Africana 31:1–38.

Kalandadze, N. N., and A. G. Sennikov. 1985. Novyye reptilii iz Srednego triasia Yuzhnogo Priural'ya. Paleontologicheskii Zhurnal 1985:77–84.

Krebs, B. 1965. Die Triasfauna der Tessiner Kalkalpen. XIX. *Ticinosuchus ferox*, nov. gen. nov. sp. Ein neuer Pseudosuchier aus der Trias des Monte San Giorgio. Schweizerische Paläontologische Abhandlungen 81:1–140.

Krebs, B. 1974. Die Archosaurier. Naturwissenschaften 61:17–24.

Long, R. A., and P. A. Murry. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. Bulletin of the New Mexico Museum of Natural History and Science 4:1–254.

Mook, C. C. 1921. Notes on the postcranial skeleton in the Crocodilia. Bulletin of the American Museum of Natural History 44:67–100.

Nesbitt, S. J. 2003. *Arizonasaurs* and its implications for archosaur divergence. Proceedings of the Royal Society of London B (Suppl.) 270: S234–237.

Nesbitt, S. J. 2005. Osteology of the Middle Triassic pseudosuchian archosaur *Arizonasaurus babbitti*. Historical Biology 17:19–47.

Nesbitt, S. J. 2007. The anatomy of *Effigia okeeffeae* (Archosauria: Suchia), theropod-like convergence, and the distribution of related taxa. Bulletin of the American Museum of Natural History 302:1–84.

Nesbitt, S. J., and M. A. Norell. 2006. Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda). Proceedings of the Royal Society of London B 273:1045–1048.

O'Connor, P. M. 2006. Postcranial pneumaticity: an evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. Journal of Morphology 267:1199–1226.

Padian, K. (ed.) 1986. The Beginning of the Age of Dinosaurs: Faunal Change Across the Triassic-Jurassic Boundary. 378 pp, Cambridge University Press, New York.

Parrish, J. M. 1993. Phylogeny of the Crocodylotarsi, with reference to archosaurian and crurotarsan monophyly. Journal of Vertebrate Paleontology 13:287–308.

Peyer, K., J. G. Carter, H.-D. Sues, S. E. Novak, and P. E. Olsen. 2008. A new suchian archosaur from the Upper Triassic of North Carolina. Journal of Vertebrate Paleontology 28:363–381.

Schoch, R. R. 1997. A new capitosaur amphibian from the Lower Lettenkeuper (Triassic: Ladinian) of Kupferzell (Southern Germany). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 203:239–272.

Schoch, R. R. 1999. Comparative osteology of *Mastodonsaurus giganteus* (Jaeger, 1928) from the Middle Triassic (Lettenkeuper:

Longobardian) of Germany (Baden-Württemberg, Bayern, Thüringen). Stuttgarter Beiträge zur Naturkunde, series B 178:1–173.

Schoch, R. R. 2002. Stratigraphie und Taphonomie wirbeltierreicher Schichten im Unteren Keuper von Vellberg. Stuttgarter Beiträge zur Naturkunde, series B 218:1–29.

Schoch, R. R., and R. Wild, 1999. Die Tetrapoden-Fauna im Keuper Süddeutschlands; pp. 395–408 in N. Hauschke and V. Wilde (eds.), Die Trias – Eine Ganz Andere Welt. Pfeil, München.

Sereno, P. C. 1991. Basal archosaurs: phylogenetic relationships and functional implications. Society of Vertebrate Paleontology Memoir 2:1–53.

Sereno, P. C., and A. B. Arcucci. 1990. The monophyly of crurotarsal archosaurs and the origin of bird and crocodile ankle joints. Neues Jahrbuch für Geologie und Paläontologie Abhandlung 180:21–52.

Sill, W. D. 1974. The anatomy of *Saurosuchus galilei* and the relationships of the rauisuchid thecodonts. Bulletin of the Museum of Comparative Zoology 146:317–362.

Sulej, T. 2005. A new rauisuchian reptile (Diapsida: Archosauria) from the Late Triassic of Poland. Journal of Vertebrate Paleontology 25:78–86.

Walker, A. D. 1961. Triassic reptiles from the Elgin area: *Stagonolepis, Dasygnathus* and their allies. Philosophical Transactions of the Royal Society B 244:103–204.

Wedel, M. 2007. What pneumaticity tells us about 'prosauropods', and vice versa. Special Papers in Palaeontology 77:207–222.

Weinbaum, J. C., and A. Hungerbühler. 2007. A revision of *Poposaurs gracilis* (Archosauria: Suchia) based on two new specimens from the Late Triassic of the southwestern U.S.A. Paläontologische Zeitschrift 81/2:131–145.

Wild, R. 1978a. Massengrab für Saurier. Kosmos 74:790–797.

Wild, R. 1978b. Die Saurier von Kupferzell. Vorläufige Ergebnisse der Fossilgrabung beim Autobahnbau. Jahrbuch Württembergisch Franken 62:181–196.

Wild, R. 1979. Saurier kommen ans Licht. Sielmanns Tierwelt, 3:38–45.

Wild, R. 1980. The fossil deposits of Kupferzell, Southwest Germany. Mesozoic Vertebrate Life 1:15–18.

Wu, X.-C., and S. Chatterjee. 1993. *Dibrothrosuchus elaphros*, a crocodylomorph from the Lower Jurassic of China and the phylogeny of the Sphenosuchia. Journal of Vertebrate Paleontology 13:58–89.

Submitted October 8, 2007; accepted June 16, 2008

APPENDIX 1. Material examined.

Batrachotomus kupferzellensis

Most of the material of *Batrachotomus kupferzellensis* described here originates from the 1977 excavation of the type locality – the *fossillagerstätte* Kupferzell, situated in the Hohenlohe region of northern Baden-Württemburg in southern Germany (Gower, 1999). Some significant additional material comes from the same stratigraphical horizon at Vellberg-Eschenau and Crailsheim, about 10 and 30 km east of Schwäbisch Hall in Baden-Württemburg.

All *B. kupferzellensis* specimens derive from the Upper Lettenkeuper sequence (Lower Keuper, Erfurt Formation) that is Longobardian (late Ladinian) in age (see Gower, 1999 and Schoch, 2002 for details and further literature). The bulk of this material is stored at the Staatliches Museum für Naturkunde, Stuttgart (SMNS), with additional material housed at the Muschelkalkmuseum, Ingelfingen (MHI).

Some of the Vellberg-Eschenau material is preserved in articulation or close association. The Kupferzell material is almost entirely disarticulated but many elements were found in close proximity and often closely match in size and morphology, consistent with them deriving from particular individuals. This is the case with at least three batches of specimens (SMNS 52970, 80260, 80270), one from a larger and two from slightly smaller individuals. The specimens are throughout preserved three dimensionally, although most are distorted to varying degrees. Two important specimens come from Vellberg-Eschenau. MHI 1895 includes articulated trunk vertebrae, ribs and osteoderms, and SMNS 90018 incomplete manus, tarsus, pes, and some gastralia elements in close association. The former specimen was embedded at the base of a large dolomite block and is consequently heavily crushed, while the latter specimen is preserved in three dimensions. The Kupferzell material was largely mechanically prepared to free the specimens from the clay- and marl-bearing matrix. The Vellberg-Eschenau material derives mainly from dolomitic carbonates, which were prepared away with acid. The Crailsheim material comprises well-preserved fragmentary, isolated elements.

A list of material of *B. kupferzellensis* was given by Gower (1999), who focused on the cranial material from Kupferzell and did not provide details of some of the postcranial material or of most of the Vellberg-Eschenau or Crailsheim specimens, some of which are new finds. Since 1999, additional Kupferzell material has also surfaced and/or been catalogued at SMNS. A more complete list is given here, with specimens sharing the same number believed to represent a single individual. Unless stated otherwise, all material is from the 1977 Kupferzell excavation:

SMNS 52970 (holotype), the largest known specimen, comprising a partial and disarticulated skull (see Gower, 1999) and postcranium. The postcranial material includes isolated vertebrae and osteoderms, pectoral and pelvic girdle elements and a left femur and tibia. A proximal fragmentary right femur catalogued under this number is slightly smaller than the complete right element and questionably belongs to the same individual as the bulk of the holotypic material.
SMNS 54840, distal tibia (Crailsheim).
SMNS 80260, a smaller specimen comprising a disarticulated, fairly complete skull and mandible (see Gower, 1999 for details).
SMNS 80261, crushed occiput and part of braincase.
SMNS 80268, left ilium and both ischia; SMNS 80269, both ischia and ilia; SMNS 80270, both pubes, ischia, and ilia; SMNS 80271, both scapulae and coracoids; SMNS 80272, both ilia; SMNS 80273, right ilium; SMNS 80274, incomplete scapula; SMNS 80275, right humerus, radius, and ulna; SMNS 80276, right humerus; SMNS 80277, right fibula; SMNS 80278, left femur; SMNS 80279, left pubis; SMNS 80280, both ischia; SMNS 80281, right scapula; SMNS 80282, distal end of right pubis; SMNS 80283-6, anterior cervical vertebrae; SMNS 80287-9, middle cervical vertebrae; SMNS 80290-2, posterior cervical vertebrae; SMNS 80293-7, anterior dorsal vertebrae; SMNS 80298, mid-dorsal vertebra; SMNS 80299, anterior dorsal vertebra; SMNS 80300-9, mid-dorsal vertebrae; SMNS 80310, articulated second and third sacral vertebrae; SMNS 80311, anterior dorsal vertebra; SMNS 80312, mid-dorsal vertebra; SMNS 80313, one posterior dorsal and one anterior caudal vertebrae; SMNS 80314, mid-dorsal vertebra; SMNS 80315, mid-dorsal vertebra; SMNS 80316, anterior dorsal vertebra; SMNS 80317-9, mid-dorsal vertebrae; SMNS 80320-1, posterior dorsal vertebrae; SMNS 80322-3, two axis vertebrae; SMNS 80324, disarticulated second and third sacral vertebrae; SMNS 80325, first sacral vertebra; SMNS 80326-27, mid-caudal vertebrae; SMNS 80328, posterior dorsal vertebra; SMNS 80329-31, anterior/mid-caudal vertebrae; SMNS 80332-33, mid-caudal vertebrae; SMNS 80334-36, anterior caudal vertebrae; SMNS 80337, two mid-caudal vertebrae; SMNS 80338, sacral vertebra and two sacral ribs; SMNS 80339, two articulated mid-caudal vertebrae; SMNS 80340-1, mid-caudal vertebrae; SMNS 80342-3, two mid-dorsal vertebrae; SMNS 80344, anterior caudal vertebra; SMNS 80345, sacral vertebra; SMNS 80346, two sacral ribs; SMNS 80347, sacral vertebra and two sacral ribs; SMNS 80348-50, dorsal spines.
SMNS 90018, associated but largely disarticulated partial postcranial skeleton, including femur, tibia, calcaneum, metatarsals, several phalanges of the foot, and parts of a manus (Vellberg-Eschenau).
SMNS 90042, basisphenoid (Vellberg-Eschenau).
SMNS 91043, left dorsal rib.
SMNS 91044, left 'pectoral' rib with three heads.
SMNS 91045, fragmentary, disarticulated gastralia.
SMNS 91046, left cervical rib.
SMNS 91047, hemal arch.
SMNS 91048, isolated left paramedian dorsal osteoderm.
SMNS 91049, crushed right calcaneum (Schumann quarry, Eschenau).
SMNS 91050, right clavicle
SMNS unnumbered. There are many, mostly isolated, unnumbered specimens in the SMNS collection, including hundreds of teeth, ribs, osteoderms, gastralia, and unidentified bone fragments. Most of these are from the 1977 Kupferzell excavations.
MHI 1895, incomplete and disarticulated cranial/mandibular elements plus incomplete articulated postcranium including dorsal vertebrae, osteoderms, ribs, and limb elements (Vellberg-Eschenau).

Other rauisuchians

Comparative data on Permo-Triassic archosaurs have been compiled from the literature and, where possible, direct observation. The following comparative material of rauisuchians has been studied first-hand:

BMNH	*Teratosaurus suevicus;* East African material described by Charig (1956)
BPS	*Rauisuchus tiradentes; Prestosuchus chiniquensis; P. loricatus; Procerosuchus celer* (material described by Huene, 1942)
GPIT	*Stagonosuchus nyassicus* (material redescribed by Gebauer, 2004)
ISI	*Tikisuchus romeri* (specimen described by Chatterjee and Majumdar, 1987)
MNHN	*Arganasuchus dutuiti* (see Dutuit, 1979; Jalil and Peyer, 2007)
PIN	largely fragmentary material referred to several taxa (see review by Gower and Sennikov, 2000)
PIMUZ	*Ticinosuchus ferox* (material described by Krebs, 1965)
SMNS	*Teratosaurus suevicus* (ilium referred by Galton, 1985); *Rauisuchus* sp. (Santa María Formation, Brazil); *Arizonasaurus babitti* and other rauisuchian taxa from the Moenkopi Formation of New Mexico
TMM	*Postosuchus kirkpatricki; Poposaurus gracilis; Lythrosuchus langstoni* (see Long and Murry, 1995)
TTU	*Postosuchus kirkpatricki; Chatterjeea elegans* (see Long and Murry, 1995) – the latter taxon accepted here as a junior synonym of *Shuvosaurus inexpectatus* (see Nesbitt and Norell, 2006)
UCMP	*Arizonasaurus babitti* (material described by Nesbitt, 2005)
UFRGS	specimen referred to *Prestosuchus chiniquensis* by Barbarena (1978)
WARMS	*Bromsgroveia walkeri* (see Benton and Gower, 1997; Galton and Walker, 1996)

INSTITUTIONAL ABBREVIATIONS

BMNH: Department of Palaeontology, The Natural History Museum, London
BPS: Bayerische Staatssammlung für Paläontologie und historische Geologie, München
GPIT: Institut und Museum für Geologie und Paläontologie, Universität Tübingen
ISI: Indian Statistical Institute, Kolkata
MNHN: Museum National d'Histoire Naturelle, Paris
MHI: Muschelkalkmuseum Ingelfingen
PIN: Paleontological Institute of the Russian Academy of Sciences, Moscow
PIMUZ: Paläontologisches Institut und Museum der Universität, Zürich
SMNS: Staatliches Museum für Naturkunde, Stuttgart
TMM: Texas Memorial Museum, Austin
TTU: Texas Tech University Museum, Lubbock
UCMP: University of California Museum of Paleontology, Berkeley
UFRGS: Department of Paleontology and Stratigraphy, Federal University of Rio Grande do Sul, Porto Alegre
WARMS: Warwickshire Museum, Warwick