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The cranial and mandibular osteology of a new rauisuchian archosaur from the Middle Triassic of southern Germany

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With 24 figures

Abstract

Batrachotomus kupferzellensis, a new genus and species of rauisuchian suchian archosaur, is diagnosed on the basis of incomplete, disarticulated, but well-preserved remains of at least five individuals recovered from Lettenkeuper (Longobardian, late Ladinian) deposits of the Lagerstätte Kupferzell-Bauersbach, in the Hohenlohe region of northern Baden-Württemberg, southern Germany. A familial assignment is not made because of the instability of rauisuchian taxonomy, caused by an incomplete understanding of morphology and phylogeny. The cranial and mandibular osteology of the new taxon, excluding the braincase, is described in detail and compared with that of known rauisuchians and other archosaurs.

The skull of *B. kupferzellensis* is characterized by at least two potential autapomorphies – naris larger than antorbital fenestra; depression on the ventrolateral surface of the postorbital. Other apparently derived features are shared with *Postosuchus kirkpatricki* (interlocking premaxilla-maxilla articulation surrounding a small opening; rugose ridge on dorsolateral elements of the dermatocranium), more than one other rauisuchian species (tongue-like medial process of the articular; kinked postorbital bar; anteriorly-arched nasal), and basal crocodylomorphs (e.g. laterally-overhanging postorbital-squamosal bar; topography of the dorsal surface of the skull roof). In the absence of wider tests of these hypotheses of homology and a consideration of other taxa and characters in an explicit analysis, a precise hypothesis of the phylogenetic relationships of *B. kupferzellensis* is not made.

Small differences between larger and smaller specimens (e.g. more robust and rugose ridge along dorsolateral edge of skull in the larger material) are interpreted as potential ontogenetic differences. The presence and form of soft-tissues of the antorbital region are inferred through comparisons with data from recent studies of extant and extinct archosaur anatomy. Although many of the articulations between individual elements appear to have been potentially mobile, a consideration of the skull and mandible as a whole suggests that adults of *B. kupferzellensis* lacked significant cranial or mandibular kinesis.

The good preservation of the Kupferzell specimens of *B. kupferzellensis* will probably make this fossil material important for the future resolution of rauisuchian and suchian phylogeny, and the improved understanding of the evolution of crocodilian-line archosaurs.

Zusammenfassung

Batrachotomus kupferzellensis, eine neue Gattung und Art aus der Verwandtschaft der Rauisuchier (Archosaurier: Suchia), wird anhand disartikulierter, aber sehr gut erhaltener Reste von zumindest fünf Individuen vorgestellt und beschrieben. Das Material stammt aus dem Lettenkeuper (Longobardium: Oberladin) von Kupferzell-Bauersbach (Hohenlohe, Nordwürttemberg). Eine Familienzuordnung wird vermieden, da sich die Taxonomie der Rauisuchier aufgrund der unzureichenden Kenntnis ihrer Morphologie und Phylogenie gegenwärtig in einem sehr instabilen Zustand befindet. Die Schädelosteologie der neuen Gattung wird mit Ausnahme des Hirnschädels detailliert beschrieben und mit dem anderer Rauisuchier und Archosaurier verglichen.

Der Schädel von *B. kupferzellensis* ist durch mindestens zwei Autapomorphien gekennzeichnet: die Naris ist länger als das Antorbitalfenster, und auf der ventrolateralen Oberfläche des Postorbitale befindet sich eine Vertiefung. Weitere, offenbar abgeleitete Merkmale hat die neue Form mit *Postosuchus kirkpatricki* gemeinsam: eine verzahnte Sutur zwischen Praemaxillare und Maxillare, die ein kleines Foramen einschließt, und eine aufgerauhte Leiste, die sich über die posterioren Elemente des Dermatocraniums erstreckt. Weitere Merkmale treten auch bei verschiedenen anderen Rauisuchiern auf: ein zungenförmiger medianer Vorsprung des Artikulare, eine gebogene Postorbitalspange, und ein vorn überdachtes Nasale. Mit basalen Crocodylomorphen schließlich hat *B. kupferzellensis* die lateral überlappende Postorbitale-Squamosum-Spange und die Proportionierung des Schädeldachs gemeinsam. Definitive Aussagen über verwandtschaftliche Beziehungen können erst unter Einbeziehung weiterer Taxa und Merkmale, sowie nach gründlicherer Prüfung einiger Homologie-Hypothesen gemacht werden.

Gewisse Unterschiede zwischen den verschieden großen Exemplaren werden als ontogenetische Veränderungen gedeutet, so z.B. die robustere und stärker aufgerauhte Oberfläche am hinteren Schädelrand. Schließlich wird ein Bild von der Organisation der Weichteilstrukturen in der Antorbitalregion entworfen, gestützt auf Vergleiche mit verschiedenen rezenten und fossilen Archosauriern. Trotz der potentiell beweglich gehaltenen Suturen scheint *B. kupferzellensis* über keine nennenswerte Schädel- oder Mandibelkinetik verfügt zu haben.

Die hervorragende Erhaltung des Kupferzeller Materials macht *B. kupferzellensis* zu einem wichtigen Bezugstaxon in der phylogenetischen Erforschung der Rauisuchier und Suchier allgemein, und läßt ein vertieftes Verständnis der Evolution innerhalb der Krokodilier-Linie erwarten.

Contents

1. Introduction

Despite recent consensus on many areas of basal archosaur phylogeny, one of the most outstanding areas of current uncertainty and disagreement is the relationships of the rauisuchians (in the sense used here – Gower & Wilkinson 1996; Gower in review). Pre-cladistic studies (e.g. Chatterjee 1985; Galton 1985) grouped together taxa previously recognized as members of the Rauisuchidae, Prestosuchidae, and Poposauridae into the Sub- or Infraorder Rauisuchia. Gauthier (1986) employed Rauisuchia as a terminal taxon, but subsequent cladistic analyses have hypothesized that this group is paraphyletic, with poposaurids being more closely related to Crocodylomorpha than to rauisuchids or prestosuchids (e.g. Benton & Clark 1988; Parrish 1993). The subset of non-poposaurid rauisuchians employed in recent cladistic analyses has usually been restricted to the best known and/or described forms, *Ticinosuchus ferox* and *Saurosuchus galilei* (although there has been disagreement as to whether these taxa are 'rauisuchids' or 'prestosuchids'). Recently, Parrish (1993) has presented findings of the only cladistic phylogenetic analysis to include a wider range of rauisuchians as coded terminal taxa, and he hypothesized that the rauisuchians fall into three monophyletic families, none the sister group to each other. The only area of consensus that had emerged, regarding rauisuchian phylogeny, was that poposaurids were more closely related to crocodylomorphs than to other rauisuchians (Gower & Wilkinson 1996). There is, however, a potentially major problem with this hypothesis because the taxon almost exclusively used to represent poposaurids (*Postosuchus kirkpatricki*) has recently (Long & Murry 1995) been claimed to have been based on a mixture of material that represents three recognizable genera belonging to three distinct families, and that the majority of the material (*Postosuchus kirkpatricki* in the sense of Long & Murry 1995) is rauisuchid rather than poposaurid. Long & Murry's (1995) study was essentially restricted to alpha taxonomy, so that while one can interpret their position as recognizing a monophyletic Rauisuchia, they did not present an explicit phylogenetic analysis or hypothesis.

Amid this rampant phylogenetic confusion, there have been relatively few recent additions to our knowledge of the morphology of these forms. Rauisuchians are often recognized as an important group represented by an assemblage of poorly-preserved and/or documented taxa (e.g. Benton & Gower 1997; Gower in review), and this long-standing situation has undoubtedly contributed to the instability of hypotheses of relationships.

This paper focuses on the description of a new rauisuchian taxon, represented by abundant and well-preserved material from Kupferzell in southern Germany. The aim of this paper is to name and diagnose the new taxon, and to provide a detailed description of most of the cranial and mandibular osteology. Preliminary considerations of the relationships and significance of this new Kupferzell taxon are also presented. Detailed descriptions of the braincase and postcranial material, which are largely also well-preserved, are in preparation and will be presented elsewhere.

Archosauria is used here in its traditional sense (see Juul 1994), with members of Archosauria *sensu* Gauthier (1986) being referred to as 'crown-group archosaurs'. Rauisuchia is also employed throughout in a traditional sense (see Gower in review) – including all taxa usually classified in the Rauisuchidae, Prestosuchidae, Poposauridae, and Chatterjeeidae, even though rauisuchians might not be monophyletic. It should be noted that Rauisuchia has recently (Parrish 1993) been applied to a hypothesized monophylum composed of Crocodylomorpha, Poposauridae, and Rauisuchidae (*sensu* Parrish 1993).

Institution collections have been abbreviated as follows:

BMNH: 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, Calcutta
MNHN: Museum national d'Histoire naturelle, Paris
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
UFRGS: Department of Paleontology and Stratigraphy, Federal University of Rio Grande do Sul, Porto Alegre
WARMS: Warwickshire Museum, Warwick

2. Geological setting

All of the specimens used for the following description are derived from the Lagerstätte Kupferzell-Bauersbach, in the Hohenlohe region of northern Baden-Württemberg, southern Germany (Fig. 1). The locality was discovered by J. G. Wegele in 1977 after the fossiliferous strata were exposed during construction of the

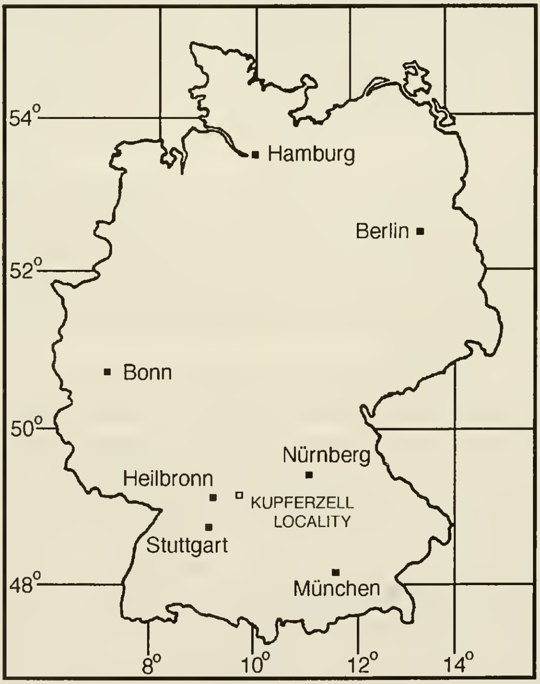

Fig. 1. Map of Germany, indicating position of the Kupferzell-Bauersbach locality.

Autobahn between Nürnberg and Heilbronn (Bundesautobahn A6, between km 674.5 and 674.8). The stratigraphy and sedimentology of the locality have been outlined by MUNDLOS & WEGELE (1978) and URLICHS (1982). The fossils were recovered from a yellowish-green marl of variable thickness (approximately 30 cm thick at Kupferzell). This marl lies in the middle of several discrete beds that represent the Untere Graue Mergel at Kupferzell. These sediments represent the Upper Lettenkeuper and are Longobardian (late Ladinian) in age. The rich vertebrate fauna has mostly yet to be studied in detail, but it includes dipnoan (SCHULTZE 1981) and actinopterygian fishes, two genera of plagiosaurid amphibians (*Gerrothorax* and *Plagiosuchus*), four genera of stereospondyl amphibians (the capitosaurids *Kupferzellia wildi,* SCHOCH 1997 and *Mastodonsaurus giganteus,* SCHOCH 1999, and a new trematosaurid and a new metoposaur-like taxon, SCHOCH & WERNEBURG in press), a nothosaur, the basal archosauromorph *Tanystropheus* sp., and a possible cynodont (for preliminary overviews see also WILD 1978a, b, c, 1980a, b, 1981; HAGDORN in press).

3. Material and methods

All of the material of the new taxon described here originates from the 1977 Kupferzell-Bauersbach excavation, and is stored at the Staatliches Museum für Naturkunde, Stuttgart. The material is almost entirely disarticulated, three-dimensionally preserved, and generally little distorted. The elements were prepared from the matrix mechanically.

Comparative data on basal 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*
GPIT	*Stagonosuchus nyassicus*
ISI	*Tikisuchus romeri*
MNHN	unnamed Moroccan form (see DUTUIT 1979)
PIN	largely fragmentary material referred to several taxa (see review by GOWER & SENNIKOV in press)
PIMUZ	*Ticinosuchus ferox*
SMNS	*Teratosaurus suevicus* (material referred by GALTON 1985)
TMM	*Postosuchus kirkpatricki*; *Poposaurus gracilis*; *Lythrosuchus langstoni* (see LONG & MURRY 1995)
TTU	*Postosuchus kirkpatricki*; *Chatterjeea elegans*
UFRGS	specimen referred to *Prestosuchus chiniquensis* by BONAPARTE (1978)
WARMS	*Bromsgroveia walkeri*

4. Systematics

Diapsida Osborn, 1903
Archosauria Cope, 1869
Crurotarsi Sereno & Arcucci, 1990
Suchia Krebs, 1974

Batrachotomus gen. nov.

Type species: *Batrachotomus kupferzellensis* gen. et sp. nov.

Derivation of name: From the Greek *batrachos* (frog) and *tome* (cutting, slicing). The name refers to reconstructions of the Kupferzell locality (Wild 1978c, 1919, 1980a, b, 1981) in which rauisuchians are shown preying on the capitosaurid *Mastodonsaurus* (formerly classified in the Batrachia) – 'slicing' refers to the tall and narrow form of the skull, and laterally-compressed, serrated teeth.

Diagnosis. – As for the type species (by monotypy).

Batrachotomus kupferzellensis sp. nov.

1978a räuberischer Thecodontier – Wild: 188, 3 plates (pp. 190–192).
1978b Thecodontier – Wild: 5, 1 plate (p. 5).
1978c *Ticinosuchus* nahestehender Thecodontier – Wild: 794, 796–797, 1 plate (p. 797).
1979 Scheinkrokodil – Wild: 43,44,45, 2 plates (p. 45).
1980a *Ticinosuchus*-like rauisuchid – Wild: 16.
1980b Kupferzeller Rauisuchier – Wild: 113–115, figs. 7, 8.
1981 Rauisuchier – Wild: 50–51, fig. 9.
1985 rauisuchid thecodontian – Galton: fig. 1A-C.
1985 Thecodontier, Familie Rauisuchidae – Hagdorn & Simon: fig. 62.
1986 undescribed rauisuchid – Benton: 295.
1993 Kupferzell rauisuchid – Parrish: 301, figs. 1, 5C, 8, table 2.
1995 rauisuchid indet. – Benton: table 1.
1995 cf. *Ticinosuchus* – Benton & Wild in Benton: 35.
1997 rauisuchian – Gower: 82.
1998 *Kupferzellia* – Dyke: fig. 1C [nomen nudum, also preoccupied by *Kupferzellia* Schoch 1997]

Holotype: SMNS 52970, substantial but incomplete and disarticulated cranial and postcranial remains, apparently from a single individual. Rauisuchian elements recovered from the main Kupferzell excavation in 1977 can be referred to individuals belonging to either of two broad size classes. The smaller size class (skull length approximately 400 mm) is represented by remains of what must have been at least four individuals (four small left and four small right ilia), but there is no evidence that there was more than a single larger individual (skull length approximately 500 mm). Additionally, many cranial elements of the large size class can be shown to fit together precisely, and excavation records show that this material was relatively restricted and largely separate from the other recovered material (R. Wild, pers. comm.). SMNS 52970 is therefore interpreted as representing a single, large individual.

Type locality: N 49° 12' 52", E 9° 40' 52", Autobahn near Kupferzell-Bauersbach, Hohenlohekreis, Baden-Württemberg, Germany.

Type horizon: Untere Graue Mergel, Upper Lettenkeuper. Longobardian, Upper Ladinian, Middle Triassic (Brunner 1973, 1977, 1980; Urlichs 1982).

Derivation of name: The specific name refers to the type locality. *B. kupferzellensis* has been previously known informally as the "Kupferzell rauisuchian" (e.g. Gower 1997).

Referred material: SMNS 80260–80339 all numbers inclusive, mostly disarticulated remains of at least four individuals. See Appendix I for detailed list.

Diagnosis. – Rauisuchian suchian archosaur with skull length up to at least 500 mm. Naris larger than anteriorly-tapered antorbital fenestra; interlocking articulation between premaxilla and maxilla surrounds a small opening between these elements; posterior process of premaxilla short and maxilla contributes to naris; nasal arched anteriorly and depressed posteromedially; rugose ridge present on dorsolateral elements of dermatocranium; frontal with medial sagittal ridge and surrounding depressions; postfrontal present; postorbital bar kinked; postorbital with ventrolateral depression; bar between lower and upper temporal fenestrae low and broad and formed by postorbital overlapping the squamosal; raised medial part of parietals holds shallow depression; dorsal fossa on palatine extensive; dentary with mild anterior expansion and probably three posterior processes; articular with robust tongue-like medial process pierced by foramen; small mandibular symphysis; teeth laterally compressed, serrated, and variable in size and shape – 4 premaxillary, 11 maxillary, and 11 or 12 dentary teeth; braincase with undivided metotic foramen and lateral exoccipital ridge posterior to foramen for exit of hypoglossal nerve; three sacral vertebrae; ilium held subhorizontally and with rugose, vertical supraacetabular ridge; pubis with moderate foot; paired dorsal osteoderms subquadrangular, flexed, mildly sculptured, and with anterior underlapping processes.

Remarks. – The material described here has been known in the literature for more than twenty years (e.g. WILD 1978), usually being referred to as a rauisuchid (e.g. GALTON 1985; BENTON 1993), comparable with *Ticinosuchus ferox* (e.g. WILD 1978). A more detailed consideration was given by PARRISH (1993), who scored various characters for the "Kupferzell rauisuchid" based on his observations of some of the material. PARRISH (1993) hypothesized that the material represented a taxon belonging to his concept of the Rauisuchidae, a clade also including *Rauisuchus tiradentes, Fasolasuchus tenax,* and *Lotosaurus edentus*. PARRISH (1993: 301) further suggested that the Kupferzell taxon "might possibly be referred to *Rauisuchus*". This proposal was lent support by PARRISH's (1993: 301) interpretation that the two taxa "share one notable synapomorphy", the "presence of two prominent ridges on the anterior face of the distal end of the fibula". However, I interpret the ridges present in this area (KREBS 1973: fig. 1) on the holotype fibula of *Rauisuchus tiradentes* (BSP AS XXV-90) to be preservational artefacts. Surface preservation of this specimen is poor, with each of the known elements being distorted and/or cracked. This interpretation aside, it is also clear that the known fibulae (SMNS 52970 and 80277) of the Kupferzell taxon certainly lack any closely comparable feature. Furthermore, there is a morphological difference between the Kupferzell taxon and *Rauisuchus tiradentes* (the latter has a relatively longer and more slender posterior process of the premaxilla: HUENE 1942; pers. obs.) and several close similarities between the Kupferzell taxon and many other rauisuchians (see below).

The morphology of the well preserved rauisuchian material from Kupferzell can be compared with, and be shown to differ clearly from, that of other described rauisuchians. *Ticinosuchus ferox* was found geographically and stratigraphically close to *Batrachotomus kupferzellensis*. *T. ferox* is known from an essentially complete holotype (KREBS 1965) and additional, incomplete specimens (KREBS 1965; PINNA & ARDUINI 1978), but the former is very strongly crushed, making detailed comparisons of three-dimensional morphology difficult, especially for cranial elements. Among the few detailed comparisons that can be made, there are some clear differences between the morphology of the Kupferzell taxon and that of *Ticinosuchus ferox* (pers. obs.). For example, relative to the height of the centra, the neural spines of the anterior cervical and anterior caudal vertebrae are shorter (anteroposteriorly) in *B. kupferzellensis*; the axis neural spine is smaller and more triangular; and the ilial facet for articulation with the first sacral rib is more extensive anteriorly. Clear, if not numerous, morphological differences are also seen between *B. kupferzellensis* and other known rauisuchian taxa, some of which are mentioned briefly here.

Teratosaurus suevicus (Galton 1985; Benton 1986; pers. obs.) has an ilium (material referred by Galton 1985) with a more anterodorsally-inclined supraacetabular 'buttress' and a longer anterodorsal process, and a maxilla with a straighter and steeper anterior margin than that of *B. kupferzellensis. Poposaurus gracilis* (Mehl 1915; Colbert 1951; Long & Murry 1995) has an ilium with a more anterodorsally-inclined supraacetabular 'buttress' and a longer anterodorsal process, and the same features are present in *Bromsgroveia walkeri* (Galton 1985; Galton & Walker 1996; Benton & Gower 1997; pers. obs.) and *Lythrosuchus langstoni* (Long & Murry 1995; pers. obs.). *Stagonosuchus nyassicus* and *Prestosuchus chiniquensis* (Huene 1938, 1942; pers. obs.) have only two sacral vertebrae, and their ilia lack a supraacetabular rugosity. The skull referred to *P. chiniquensis* by Barberena (1978) has a longer posterior process of the premaxilla, and the maxilla is excluded from the naris. *Saurosuchus galilei* (Reig 1959; Sill 1974) has a significantly longer posterior process of the premaxilla, a relatively smaller naris, an elongate opening between the premaxilla and maxilla, and only two sacral ribs. *Luperosuchus fractus* (Romer 1971) has a more extensive posterior process of the premaxilla, a maxilla excluded from the naris, and an elongate opening between the premaxilla and maxilla. The documented material of *Fasolasuchus tenax* (Bonaparte 1981) is very incomplete, but it includes a premaxilla with a longer posterior process than seen in *B. kupferzellensis. Heptasuchus clarki* (Dawley *et al.* 1979; but see Wroblewski 1997) has only three premaxillary teeth, the maxilla is excluded from the naris, and the opening between the premaxilla and maxilla is perhaps larger. *Postosuchus kirkpatricki* (Chatterjee 1985; Long & Murry 1995; pers. obs.) has a much taller basisphenoid with a posteroventral trough, possible quadratojugal-postorbital contact, and the maxilla is excluded from the naris. *Tikisuchus romeri* (Chatterjee & Majumdar 1987; pers. obs.) has a taller basisphenoid with a posteroventral trough, and a more simple anterior margin of the maxilla. *Chatterjeea elegans* (Long & Murry 1995; pers. obs.) and *Sillosuchus longicervix* (Alcober & Parrish 1997) have much more strongly triradiate pelves, relatively more expanded ilial blades, more overhanging dorsal acetabular borders, and more elongate vertebral centra.

Clearly these differences are not numerous, and some might not be very significant, but this might be a function of the reduced number of comparisons that can be made between *B. kupferzellensis* and any of the other, less completely known, rauisuchian taxa. *B. kupferzellensis* shares similarities with many of the existing rauisuchian taxa, but to which one it shows the strongest derived affinity is currently unknown because of incomplete preservation and insufficient knowledge of the distribution of shared features within Suchia. The Kupferzell taxon could be named as a new species and assigned arbitrarily to one of the known genera to which it shows greatest affinity based on limited comparisons, e.g. *Postosuchus* or *Fasolasuchus*. A preferred, alternative resolution is the referral of the Kupferzell rauisuchian to a new genus as well as a new species. A robust revision of rauisuchian taxonomy might argue that the limited nature of some of the comparisons that can be made between the good Kupferzell material and less well known taxa suggests that most of the other rauisuchian genera and species should be considered *nomina dubia*. This course of action would be fairly drastic and, even if these taxa are eventually shown to be based on undiagnostic material, it would currently not help to achieve the immediate goal of a stable, meaningful, and useful taxonomy.

5. Description of skull and mandible

5.1. Reconstruction

To date, there has been no attempt to reconstruct or model the skull of *B. kupferzellensis* three-dimensionally. The skull reconstruction presented in Fig. 2 is an estimate composed from separate drawings of individual elements, or small groups of elements arranged in articulation, and is therefore preliminary in certain respects. The main aim of this reconstruction is limited to conveying approximate proportions and sutural patterns. The description should be consulted for information on the degrees of certainty of particular sutural arrangements. This reconstruction was drafted from information from skulls of different sizes, and it incorporates many unavoidable uncertainties and potential inaccuracies. It is strongly recommended that this figure is not used as the only source of information for the coding of phylogenetic data in character-taxon matrices.

5.2. Dermal bones of the skull roof

Premaxilla (Figs. 3, 5A)

Four premaxillae are preserved; the left and right antimeres of both SMNS 52970 and 80260. The main body of the premaxilla is strongly laterally compressed and, in lateral view, it is subquadrangular, being a little longer (anterior-posterior) than high (dorsal-ventral). In no example is the anterior ascending process complete. The lateral surface of the premaxilla bears several nutrient foramina, of which an anteroventral pair are recognizably constant. The external naris is remarkable for its large size. Its anteroventral margin is bordered by a shallow fossa.

The articulation between premaxilla and maxilla is of particular interest in terms of the diagnostic and phylogenetic importance previously assigned to the presence of a premaxilla-maxilla opening and/or kinetic premaxilla-maxilla joint among rauisuchians (e.g. Benton & Clark 1988; Parrish 1993; see Gower in review). Parrish (1993: fig. 8) has recently figured the right premaxilla and maxilla of SMNS 52970 to indicate the nature of the articulation and the presence of a "subnarial fenestra" in *B. kupferzellensis*. The posterior part of the premaxilla has a relatively (by comparison with rauisuchians such as *Rauisuchus tiradentes*, *Saurosuchus galilei*, and *Postosuchus kirkpatricki*) short, lobe-like posterodorsal process, with longitudinal striations on its medial surface. The posterior edge of the premaxilla is smooth for a short distance immediately ventral to the base of this process. A roughened posterolateral depression extends from the lower boundary of this smooth section to the ventral edge of the premaxilla. The anterior edge of the maxilla consists correspondingly of two specialized articulatory regions separated by a smooth notch. An area below the notch laterally overlaps the roughened depression on the premaxilla,

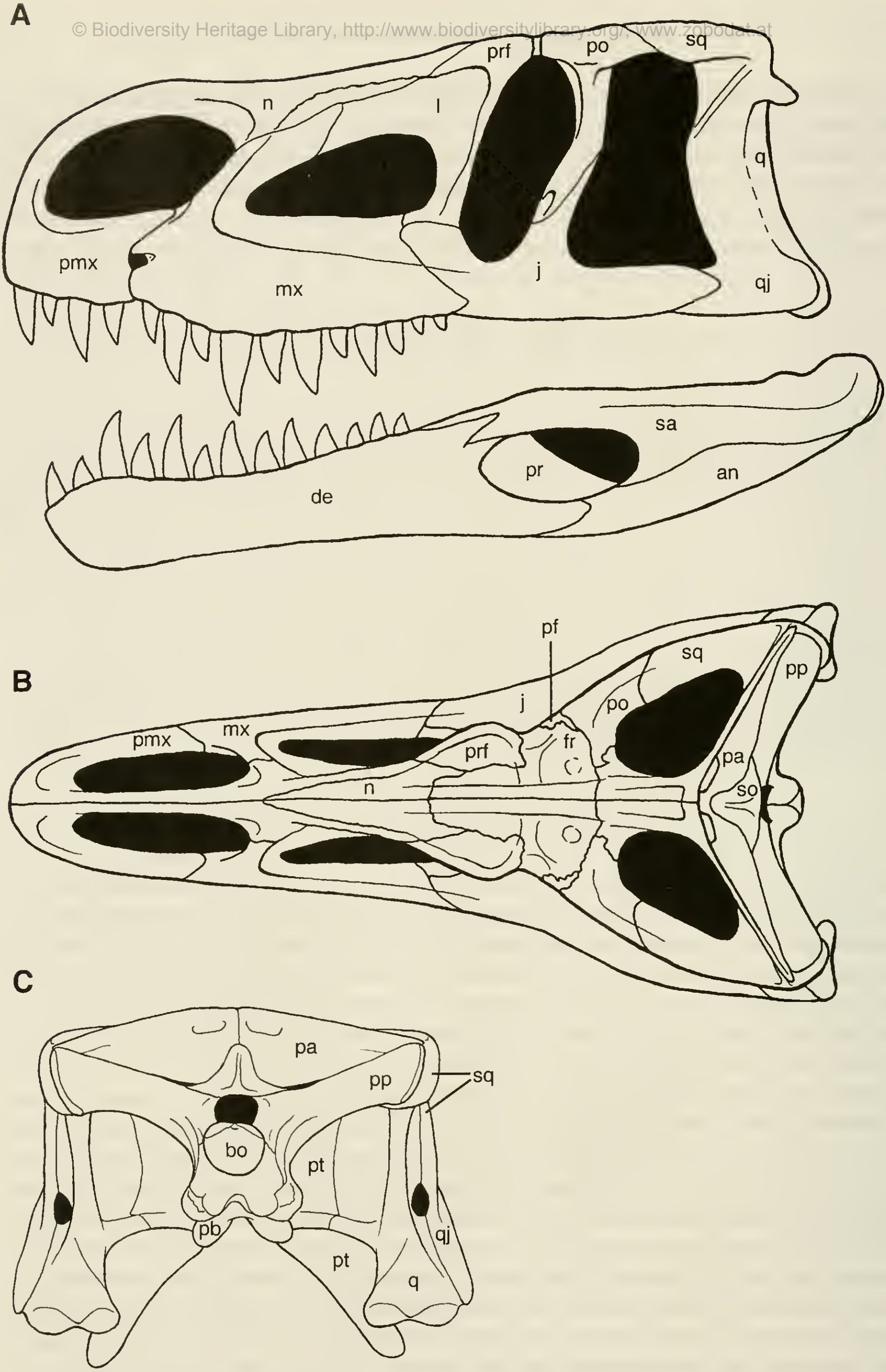

Fig. 2. Preliminary reconstructions (see text, section 5.1) of the cranium and mandible of *Batrachotomus kupferzellensis* gen. et sp. nov. A: lateral view of cranium and mandible; B: dorsal view of cranium; C: occipital view of cranium not to scale. Skull length of known specimens approximately 400–500 mm. The text should be consulted for data on the morphology of individual elements, and it is recommended that this figure is not used as a primary source of phylogenetic data. Produced with the assistance of D. M. Henderson (Bristol).

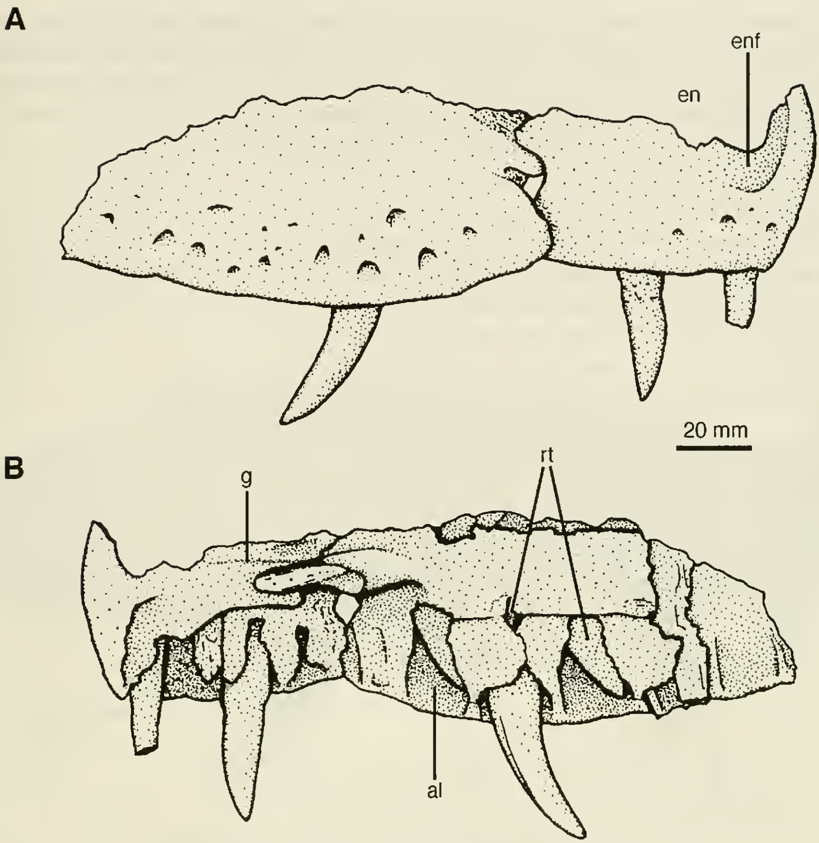

Fig. 3. Right premaxilla and part of maxilla of SMNS 80260. A: lateral; B: medial view. The posterior and dorsal parts of the maxilla, and distal ends of the dorsal and posterior processes of the premaxilla are absent.

while, dorsal to the maxillary notch, a slightly laterally raised, elongate dorsal area is itself overlapped by the posterodorsal premaxillary process (Figs. 3, 4). This is not apparent in PARRISH's (1993) figure 8, where the premaxillary process is depicted anterior to the raised area on the maxilla, rather than overlapping it laterally. Additionally, the small foramen between maxilla and premaxilla, formed mostly by the maxillary notch, is positioned lower down the posterior margin of the premaxilla than shown by PARRISH.

The medial surface of the premaxilla bears a small anterior symphyseal area. The palatal process is short. Anteriorly, the opposite palatal processes would have contacted each other along the midline. Further posteriorly, midline contact is not certain, because it is possible that the tapered anterior ends of the vomers (although not preserved – see below) would have lain between them. The posterior part of the palatal process underlaps, and articulates with, the anterior part of the maxillary palatal process. The dorsal edge of the part of the premaxilla that forms the ventral narial border bears a fine groove, seen in all preserved examples, that extends from just behind the prenarial ascending process to the point where the palatal process merges with the main body of the premaxilla.

The tooth-bearing margin is not particularly well preserved in any of the known premaxillae, although four alveoli are consistently present. In both SMNS 80260 examples, a small overhang forms a ventrally-open groove that extends from the dorsal part of the posteriormost premaxillary alveolus to the posterior edge of the premaxilla, where it borders the premaxilla-maxilla foramen.

Maxilla (Figs. 3, 4, 5)

The right maxilla of SMNS 52970 has been figured previously by GALTON (1985, fig.1) and PARRISH (1993, fig. 8). The left maxilla from the same specimen is also preserved, as are the left and right maxillae of SMNS 80260. The main body of the maxilla is tall and laterally compressed and the ventral margin, seen in lateral view, is notably convex. The lateral surface of the maxilla, particularly ventrally, bears a number of nutrient foramina distributed in a radiating pattern. The maxilla forms most of the

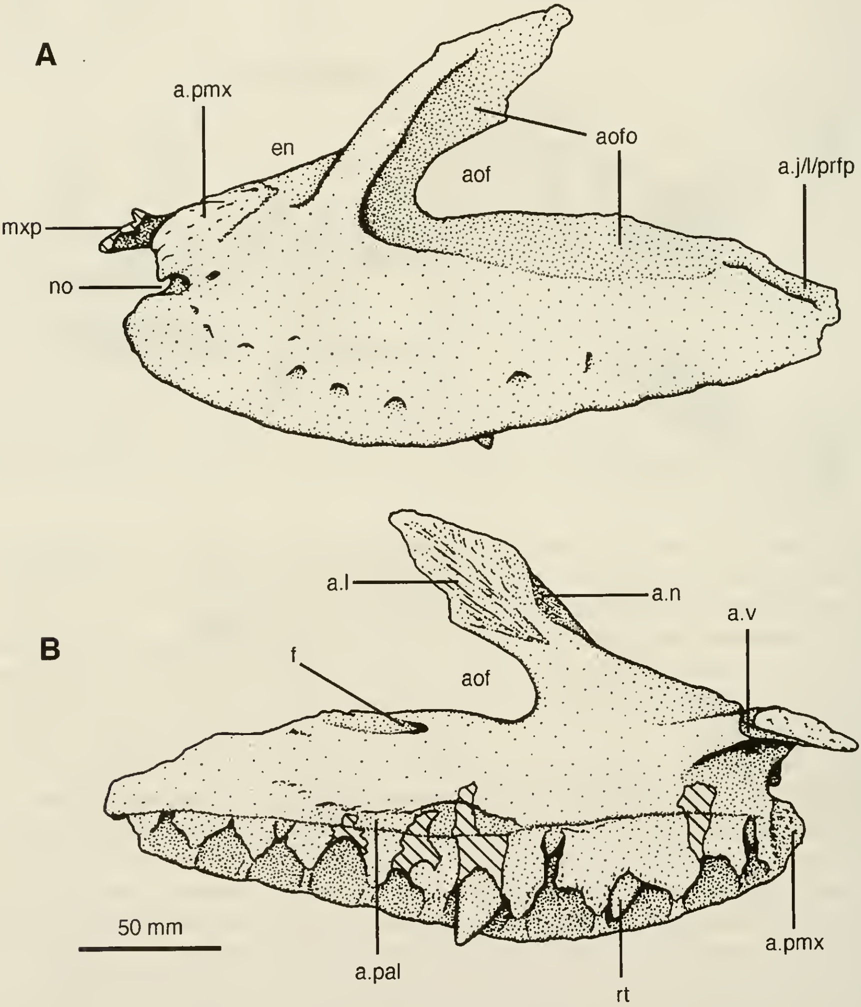

Fig. 4. Left maxilla of SMNS 52970. A: lateral; B: medial views.

border to the large antorbital fenestra, and holds a large proportion of the surrounding antorbital fossa.

The ascending process of the maxilla projects posterodorsally at an angle of approximately 45° to the long axis of the element. The lateral edge of this process forms a thickened, rounded, and overhanging ridge that separates the anterior border of the antorbital fossa from the posterior part of the narial fossa. The distal end of the ascending process of the maxilla continues back to contact the lacrimal, with the two elements together forming the dorsal border of the antorbital fenestra and fossa. The anterodorsal edge of the maxillary process articulates intimately with the descending flange of the nasal. At its ventral extent, this contact is a shallow tongue (nasal) in

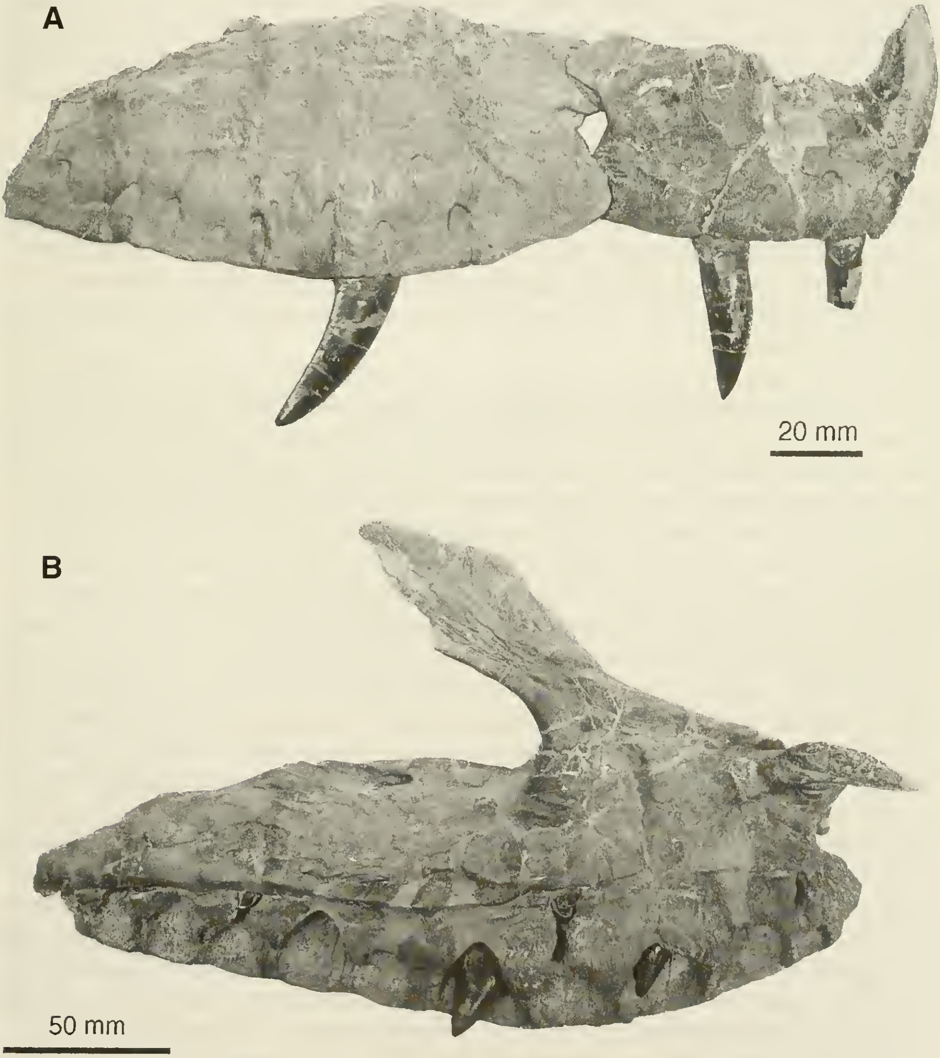

Fig. 5. A: right premaxilla and part of maxilla of SMNS 80260 in lateral view; B: left maxilla of SMNS 52970 in medial view.

groove (maxilla) articulation, and the articular surfaces of each element are gently striated. Further dorsally, the anterodorsal margin of the maxilla is drawn into a narrow, laterally-compressed edge that fits tightly into a correspondingly narrow groove on the nasal. This maxillary edge recedes posteriorly, and the posterodorsal end of the ascending process comes to articulate simply with a depression on the ventrolateral edge of the nasal. The medial surface of this part of the ascending maxillary process bears a striated, triangular depression that articulates with the lateral surface of the tapered anterior end of the lacrimal.

Most of the details of the premaxilla-maxilla articulation have been described above. The notch in the anterior margin of the maxilla represents the anterior terminus of a short groove that has a posterolaterally-anteromedially aligned long axis. Two small foramina lie in this groove just posterior to the notch. The posterior premaxillary process overlaps the maxilla up to the anterior end of the base of its ascending process. Contact is not achieved between this premaxillary process and the ventral flange of the nasal, so that the anterior margin of the maxilla makes a small contribution to the posterior border of the external naris.

Posteriorly, the maxilla articulates with the jugal and prefrontal/lacrimal. A dorsally-open maxillary groove extends from just behind the posterior termination of the antorbital fossa to the posterior edge of the maxilla. This is fairly deep and most of it accepts a significant part of the anteroventral edge of the jugal. The shallower anteromedial limit of the groove (actually present as a distinct slot on the left maxilla of SMNS 80260) receives the ventral tip of the preorbital pillar (perhaps both prefrontal and lacrimal).

There is a long, low step on the medial surface of the maxilla, running immediately above and approximately parallel to the ventral edge of the element (= dental groove of Galton 1985: fig. 3). Located centrally, and close to the edge of this step, is a shallow depression that is interpreted as the area for articulation with the palatine. This depression extends from a point between the fourth and fifth tooth alveolus (in all preserved examples) back to approximately the ninth alveolus. The palatal process of the maxilla is situated far anteriorly – protruding clear of the anterior margin of the main body of the maxilla. It is dorsoventrally compressed, fairly short, and tapered anteriorly. Its dorsal surface is essentially featureless, but the ventral surface is characterized by confluent, depressed anterolateral and medial facets. The medial facet is narrow, tapers anteriorly, and runs for the length of the palatal process. It is hypothesized that the opposite maxillary palatal processes met along the midline, and were underlain by a pair of narrow vomers that articulated with this medial facet and also with each other, along the midline. The anterolateral facet is very shallow, lightly striated, and articulated with the dorsal surface of the premaxillary palatal process. A shallow depression on the medial surface of the anterior part of the maxilla is bounded by the dorsal surface of the palatal process and the thin anterodorsal edge of the part of the maxilla that borders the naris. A deeper hollow is positioned beneath the ventral surface of the base of the maxillary palatal process. An equivalent hollow in *Postosuchus kirkpatricki* was identified by Chatterjee (1985) as a space for the Jacobson's organ, which is absent in at least late embryos and adults of extant archosaurs (Parsons 1970; Døving & Trotier 1998).

A further notable feature on the medial surface of the maxilla is a posteriorly-opening foramen, positioned a short distance behind the ascending process and just below the ventral border of the antorbital fenestra. It occupies a position that represents the approximate location of the centre of radiation of the numerous nutrient foramina seen on the lateral surface, and it is interpreted as transmitting the maxillary nerve and accompanying vessels (e.g. see WITMER 1995, 1997). An equivalent foramen can be seen in many archosaurs, including the rauisuchian *Teratosaurus suevicus* (GALTON 1985: fig. 3A, "infraorbital foramen") and the unnamed Moroccan form (DUTUIT 1979: fig. 1).

Both of the SMNS 52970 maxillae hold eleven tooth alveoli. The number in the smaller SMNS 80260, while approximately the same, is uncertain because of less complete preservation. The septa lying between the alveoli are well defined. Posteriorly they generally form clear interdental plates, similar to those in *Saurosuchus galilei* (SILL 1974), while further anteriorly the distinction between individual plates is less clear (or less well preserved), with a closer resemblance to the maxillae of *Postosuchus kirkpatricki* (CHATTERJEE 1985) and *Teratosaurus suevicus* (GALTON 1985; BENTON 1986), apart perhaps from the possible absence of interseptal foramina in *B. kupferzellensis*.

Certain constructional features of the maxilla of *B. kupferzellensis* are seen in a wide range of early archosaurs (e.g. *Erythrosuchus africanus*, pers. obs.; *Sphenosuchus acutus*, WALKER 1990) suggesting that they are plesiomorphic for at least the archosaur crown-group. These features include the medial neurovascular pit, the shallow facet for the palatine, the groove for an interlocking articulation with the anterior part of the jugal, and the low medial step above and approximately parallel to the ventral margin of the maxilla.

Nasal (Figs. 6, 7)

The morphology of the nasal can be described from the two best-preserved examples, belonging to the left side of SMNS 52970 (Figs. 6A, 7) and the right side of 80260 (Fig. 6B-D). It is a long and slender element with a descending process that articulates with the maxilla. Anteriorly, it possesses a long and laterally-compressed process that forms the internarial bar together with the prenarial ascending process of the premaxilla. Details of the articulation with the premaxilla are not known.

A thickened and rugose ridge extends along most of the dorsolateral edge of the nasal. This ridge is straight to gently curved in lateral view, but the symphyseal medial edge of the nasal is markedly sinusoidal, being at its ventralmost extent just behind a point level with the descending process. The posterior half of the paired nasals therefore exhibits a marked dorsomedial depression bordered by roughened lateral ridges, while the anterior halves, where the ridges converge, form a raised medial convexity. In lateral view, this gives the front of the snout a Roman-nosed appearance (as ROMER 1971a describes for *Luperosuchus fractus*, and BARBERENA 1978 describes for the skull he referred to *Prestosuchus chiniquensis*). The rugose dorsolateral ridges on each nasal, and the central depression on the skull roof that they border, are associated features that closely resemble the condition seen in *Postosuchus kirkpatricki* (LONG & MURRY 1995; pers. obs.). The dorsal surface of the nasals of *Sphenosuchus acutus* (WALKER 1990: 14) and *Dibrothrosuchus elaphros* (WITMER 1997: fig. 24) also bears a posteromedial concavity.

The descending process of the nasal is a fairly short, transversely-expanded, lobelike structure. Its posteroventral surface bears a heavily-striated groove that articulates with the anterodorsal edge of the maxillary ascending process. The lateral edge of the descending nasal process is thickened and it forms a dorsal continuation of the

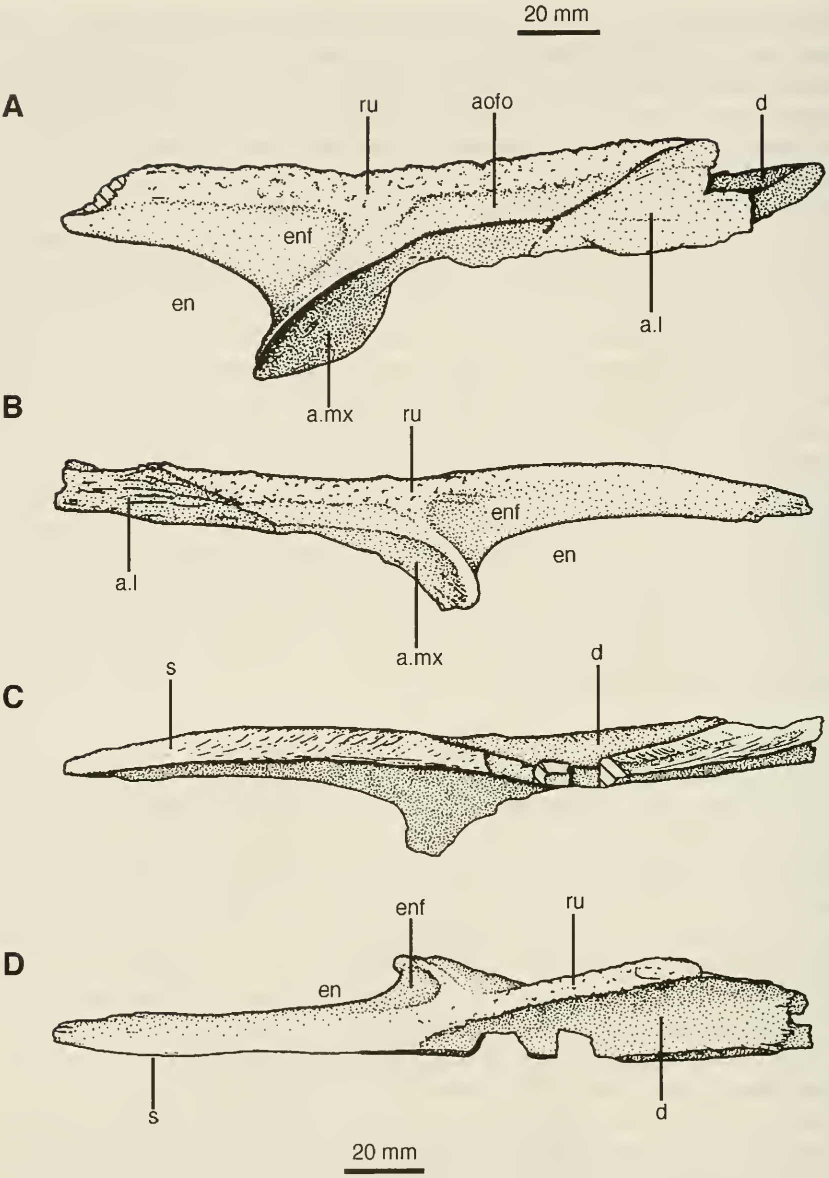

Fig. 6. A: incomplete left nasal of SMNS 52970 in lateral view. B-D: right nasal of SMNS 80260. B: lateral; C: medial; C: dorsal views.

ridge on the ascending maxillary process. This nasal ridge divides a smooth narial fossa, anteriorly, from the dorsal limit of the antorbital fossa, posteriorly. Posterolaterally, the nasal bears a broad facet for the anterodorsal part of the lacrimal, and this is confluent with the posterior part of the facet for the maxillary ascending process. Posteromedially, the ridged and grooved ventral surface of the nasal is underlapped by the frontal. Posterolateral to this, the tapered end of the nasal articulates with a narrow zone along the ventral surface of the frontal-prefrontal commissure.

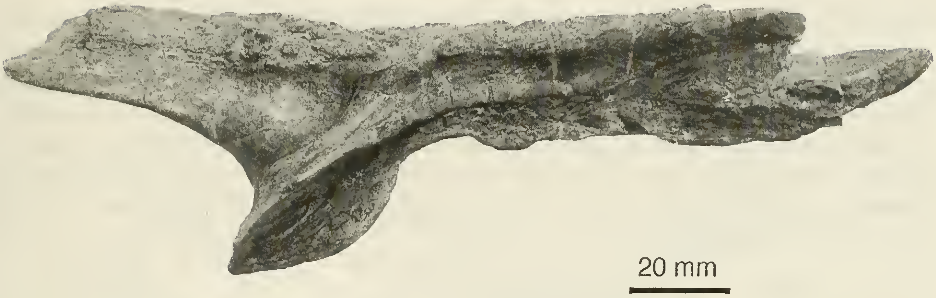

Fig. 7. Incomplete left nasal of SMNS 52970 in lateral view.

Lacrimal (Fig. 8)

Both lacrimals are preserved in the holotype, but they are known only from the crushed remains of the vertical rami. Most of the morphological details of the lacrimal can be described from the right side of SMNS 80260, even though it is incomplete, in two parts, and not entirely distinct from the prefrontal. The element as a whole consists of a broad, inverted L- to V-shaped, thin, laterally-compressed lamella with thickened posterodorsal and lateral ridges. Dorsolaterally, there is a thickened, rugose ridge that extends back from that on the nasal – it continues to define the dorsal border of the antorbital fossa and the lateral border of the depression on the centre of the dorsal surface of the skull roof. The posterodorsal part of the antorbital fossa covers a large area on the gently concave lateral surface of this lamellar part of the lacrimal.

The anterior ramus of the lacrimal bears a longitudinally-striated lateral facet for articulation with the medial surface of the ascending maxillary process. The anterior end of the lacrimal is therefore sandwiched between the nasal medially, and the maxilla laterally. The posterior border of the antorbital fossa is formed by a ridge that ex-

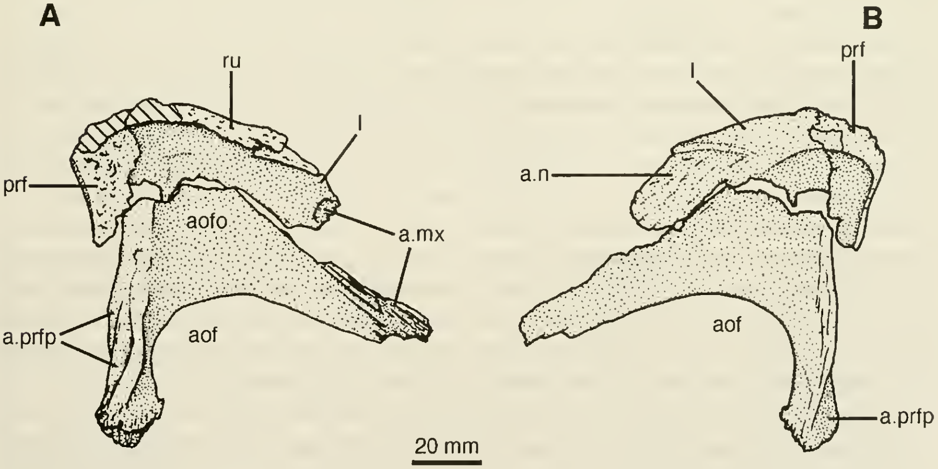

Fig. 8. Right lacrimal and partial prefrontal of SMNS 80260. A: lateral; B: medial views.

tends along the length of the descending ramus of the lacrimal. This ridge bears conspicuous striae aligned with its long axis, and it is interpreted here as being tightly overlapped, posterolaterally, by the descending ramus of the prefrontal with which it formed the preorbital bar. A lacrimal foramen and part of the nasolacrimal canal is perhaps represented by a matrix-filled channel along the interpreted lacrimal-prefrontal suture on the medial surface of the left side of SMNS 80260 (not figured). From the anterior margin of the orbit, this canal travels anteriorly and dorsally into the antorbital cavity.

Prefrontal (Figs. 8, 9)

The dorsal part of the prefrontal is known from the right and left sides of SMNS 80260. In the former example it is tightly sutured to the frontal (it is disarticulated and missing from the right and left frontals of SMNS 52970 respectively), and in the latter a small part is interpreted as being attached to the posterodorsal part of the lacrimal. The prefrontal bears a dorsolateral ridge that continues back from the similar ridge on the nasal and lacrimal. On the dorsal surface of the prefrontal, the posterior end of this ridge curves around medially to define a posterolateral limit to the dorsal depression on the anterior part of the skull roof. The prefrontal contacts the frontal (posteriorly and medially), the nasal (anteromedially) and the lacrimal (anterolaterally). The descending pillar arises from the centre of the ventral surface of the dorsal part of the element (Fig. 9A).

The ventral ramus of the prefrontal of *B. kupferzellensis* is incompletely known, but the form of the lacrimal (Fig. 8) suggests that it would have wrapped around the posterior edge of the ventral ramus of the lacrimal, excluding the latter from the orbit. The prefrontal and lacrimal would have continued ventrally to contact the maxilla (see above) and jugal.

Frontal (Figs. 9, 10)

The thick, short and broad frontal is known from both sides of the holotype, and the left side of SMNS 80260. A deep and transversely narrow dorsal ridge extends along the full length of the medial margin of the frontal. The articulated frontals therefore form a deep symphysis (Fig. 10A) and a pronounced sagittal crest on the dorsal surface of the skull roof. Anteriorly, this crest subdivides longitudinally the posterior end of the depression that extends back from the nasals (Fig. 2). The whole of the dorsal surface of each frontal (Fig. 9C, D) exhibits a distinctive topography, characterized by three main depressions. Firstly, there is the central depression that extends back from the nasals. The posterior margin of this depression is formed by a thickened area that is confluent with the posteromedially-curving ridge on the dorsolateral surface of the prefrontal. A second depression is positioned laterally, bordering the frontal contribution to the dorsal border of the orbit. The final depression on the dorsal surface of the frontal lies posteromedially, positioned between the sagittal crest and the borders to the other two depressions. A small and almost circular concavity lies within the posteromedial part of this depression – deep on the left side of SMNS 52970, but less obvious in the other preserved examples.

The frontal articulates with the postfrontal (posterolaterally), postorbital (posteriorly), and the parietal (posteromedially), with all three of these elements both under- and overlapping the thin rear edge of the frontal in a series of tongue-in-groove joints. The ventral surface of the frontal (Fig. 9A), though mostly featureless,

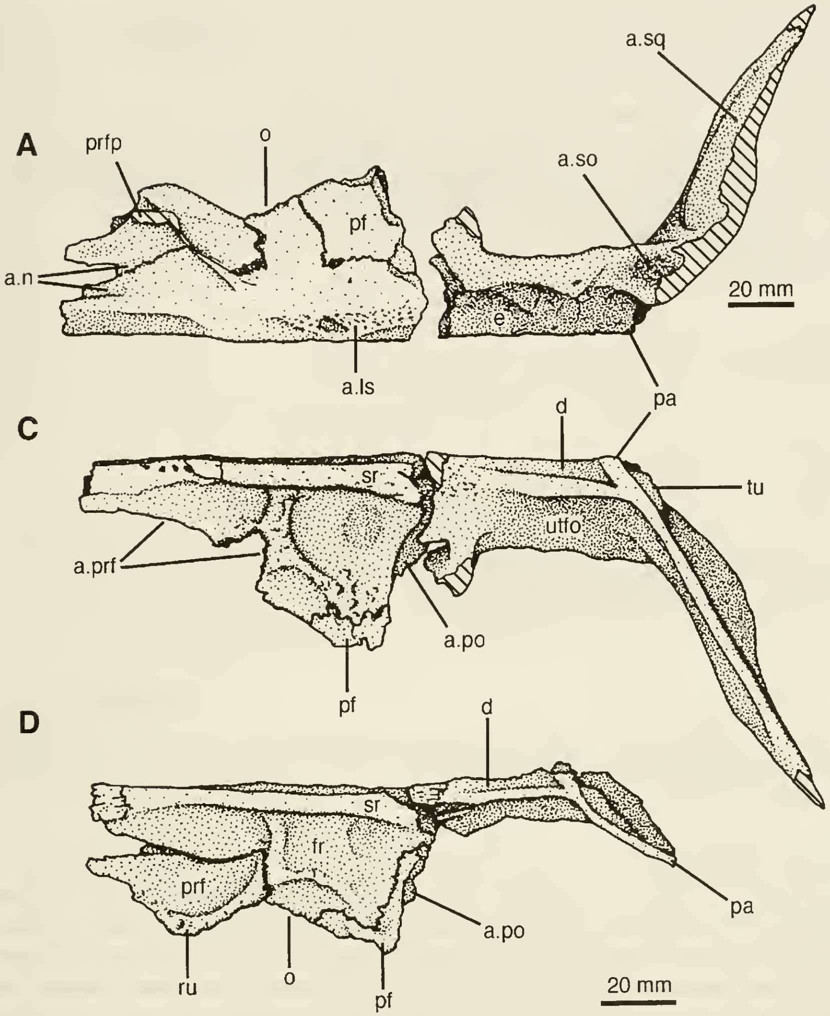

Fig. 9. A: left prefrontal, frontal, and postfrontal of SMNS 80260 in ventral view; B: left parietal of SMNS 52970 in ventral view; C: left frontal, postfrontal, and parietal of SMNS 52970 in dorsal view; D: left prefrontal, frontal, postfrontal, and partial parietal of SMNS 80260 in dorsal view.

bears two long and narrow depressions close to the medial margin. The more posterior depression extends from the posterior edge of the frontal to a point approximately level with the anterior end of the frontal contribution to the orbit. Its surface is roughened, and it is interpreted as an area that articulated with the dorsal edge of what was probably an elongate anterior laterosphenoid process. The anterior depression, separated by a short distance from the posterior one, extends to the anterior limit of the frontal, is smooth, and is interpreted as indicating the position of the olfactory tract.

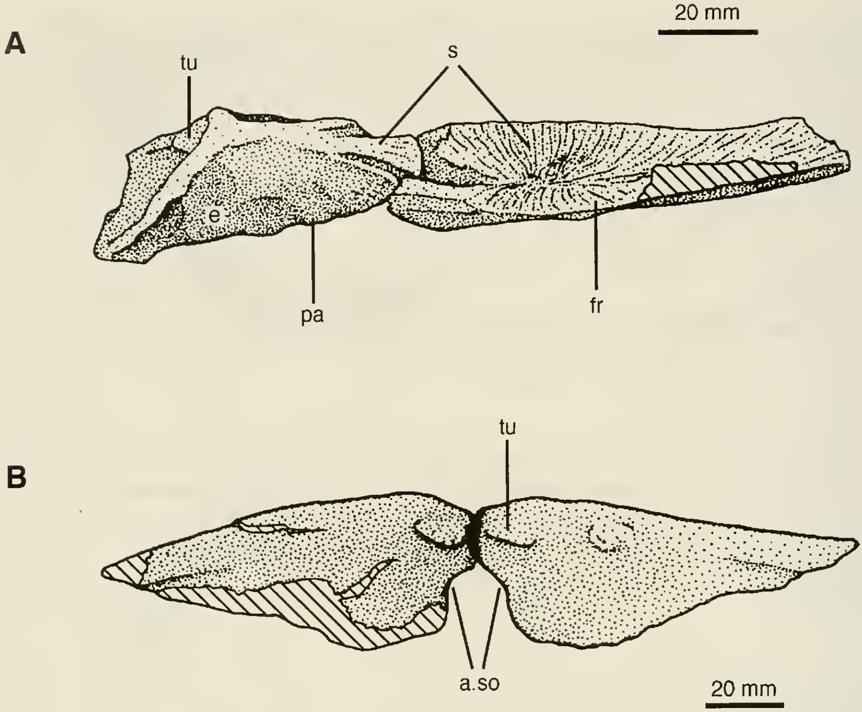

Fig. 10. A: left partial parietal and frontal of SMNS 80260 in medial view; B: left and right parietal of SMNS 52970 in posterior view.

Postfrontal (Fig. 9)

Although postfrontals are absent in some crown-group archosaurs, they are clearly present in *B. kupferzellensis*. Knowledge of the morphology of the prefrontal comes only from incomplete portions preserved in articulation with part of the left side of the skull roofs of SMNS 52970 and 80260. In dorsal view, these fragments are seen only as thin strips, but they can be seen ventrally to underlap the posterolateral corner of the frontals fairly extensively. As well as articulating with the frontal, the postfrontal is also tightly bound, posterolaterally, to the postorbital. There was apparently no contact between postfrontal and parietal.

Parietal (Figs. 9, 10)

Both parietals are virtually complete in SMNS 52970, and further examples are known from the heavily crushed occiput SMNS 80261, and incomplete anterior portions from both sides of SMNS 80260. The anterior portions of the paired parietals together form only a narrow central platform between the upper temporal fenestrae. The laterally-expanded anterior limit of each parietal is bifurcated – a medial part overlaps the posterior edge of the frontal, and a lateral part underlaps the frontal and is overlapped by the medial limit of the postorbital.

The parietals form a raised medial area that is continuous with the sagittal crest on the frontals. Anteriorly, this is quite low relative to the level of the surrounding bone, but posteriorly it becomes more strongly defined. The central part of this raised area holds a shallow, unpierced depression. This superficially resembles the pineal fossa seen in some non-crown-group archosaurs (PARRISH 1992; pers. obs.), but differs in being shallower, in shallowing out anteriorly rather than posteriorly, and in not extending onto the frontal.

The occipital (also transverse or posteroventral) process of the parietal is long, slender, triangular, and anterolaterally-posteromedially compressed. It extends at an angle of approximately 120–130° from the midline in SMNS 52970. The posterior surface of each occipital process exhibits a posterior tubercle in its dorsomedial corner, close to where the opposite parietals meet above the supraoccipital. Similar protuberances occur in *Erythrosuchus africanus* (pers. obs.).

The medial edge of the occipital process, below the midline contact with the opposite parietal, bears a concavity that articulates with the dorsolateral area of the supraoccipital (to be described with the braincase). There is a further concavity immediately ventrolateral to this depression that articulates with the dorsomedial edge of the paroccipital process of the braincase. The posttemporal fenestra was, at most, a narrow gap between the ventral edge of the occipital parietal process and the dorsal edge of the paroccipital process. The anterolateral surface of each occipital process carries a large and well-defined, semi-circular depression with a transverse ridge lying within it. This area articulates with the posterodorsal surface of the occipital process of the squamosal, with the two elements closing the posterior border of the upper temporal fenestra.

Postorbital (Fig. 11)

The morphology of the postorbital is known from both elements in SMNS 52970 and the right element of SMNS 80260. The element consists of a thick, horizontally-aligned dorsal region, from which a slender, subvertical ventral process descends. Anteriorly, the dorsal part interlocks with the posterior edge of the frontal, the posterolateral part of the postfrontal, and the anterolateral edge of the parietal. In medial view, the dorsal part of the postorbital is gently sinusoidal, with a shallow anterior depression, and a dorsally-arching process that extends back to meet the squamosal. The posteromedial corner of the dorsal surface of the postorbital bears an oblique, depressed facet that is overlain by the anterior process of the squamosal which also wraps a short distance around the medial/ventromedial edge of this part of the postorbital (see below). The lateral edge of the dorsal part of the postorbital is thickened and rugose, bearing a resemblance to the dorsolateral skull ridge anterior to the orbit. This thickened dorsolateral edge overhangs the descending process of the postorbital and a cavity at the upper end of the lateral temporal fenestra.

The slender ventral process descends from the anterior half of the dorsal part of the postorbital to form the postorbital bar with the ascending process of the jugal. The anterior edge of the ventral process of the postorbital is rather angularly-sinusoidal in lateral view – descending ventrally at first, then anteroventrally, and again ventrally at its distal tip. This gives the postorbital bar the kinked or stepped appearance that has been recorded in several other rauisuchians (e.g. *Saurosuchus galilei*, SILL 1974; *Heptasuchus clarki* DAWLEY *et al.* 1979), and employed occasionally as a phylogenetic character (e.g. BENTON & CLARK 1988; JUUL 1994). The resulting keyhole-shaped orbit might represent a partially bony separation of the orbit into an upper, eye-bearing part and a lower part.

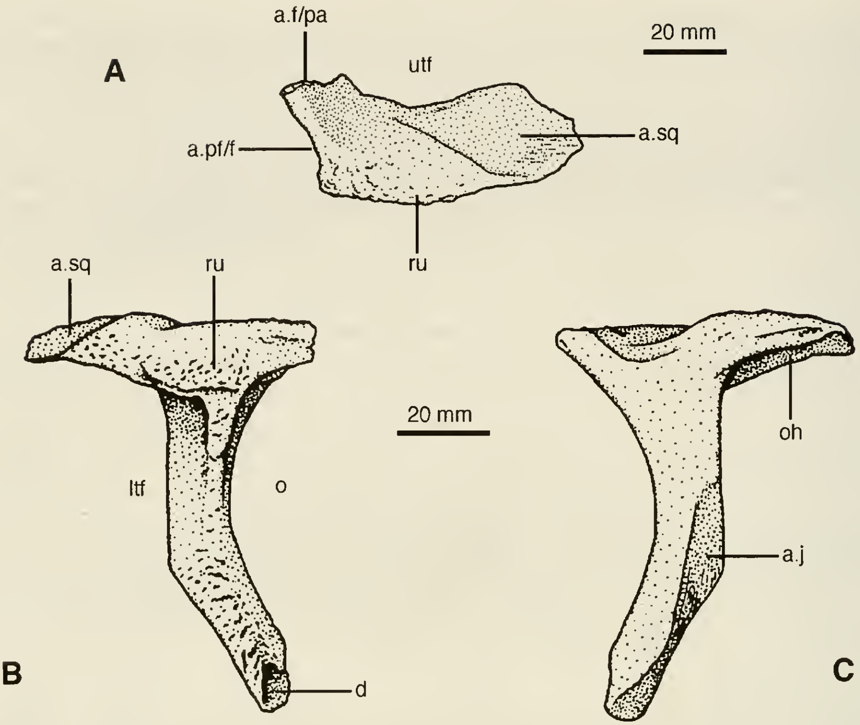

Fig. 11. A: left postorbital of SMNS 52970 in dorsal view (anterior to the left); B: right postorbital of SMNS 80260 in lateral view; C: right postorbital of SMNS 80260 in medial view.

A facet occupies much of the posteromedial edge of the descending process of the postorbital and indicates that contact was maintained with the ascending process of the jugal along almost the entire length of the postorbital bar. A distinctive concavity is positioned on the lateral surface of the ventral tip of the postorbital that has not apparently been recorded in other crurotarsan archosaurs. The lateral edge of the ventral process is lightly rugose.

Squamosal (Fig. 12)

The squamosal is a complex element known from the left and right sides of SMNS 52970, SMNS 80260, and SMNS 80261. The element can be perceived as being composed of four rami that project approximately anteriorly, posteriorly, medially, and ventrally. The anterior ramus forms, in articulation with the posterior process of the postorbital, the bar that divides the lower and upper temporal. Although this bar in *B. kupferzellensis* bears a superficial resemblance to that of crocodylomorphs, in being broader than tall, it differs clearly in that the postorbital is overlapped dorsally by the squamosal, as opposed to the condition in sphenosuchian crocodylomorphs (Sereno & Wild 1992: 446). This articulation in *B. kupferzellensis* is slightly more complex than a simple overlapping contact because a small part of the posteromedial edge of the postorbital is also underlapped by the squamosal, so that it lies in a notch that has a much deeper dorsal than ventral wall. This articulation is construc-

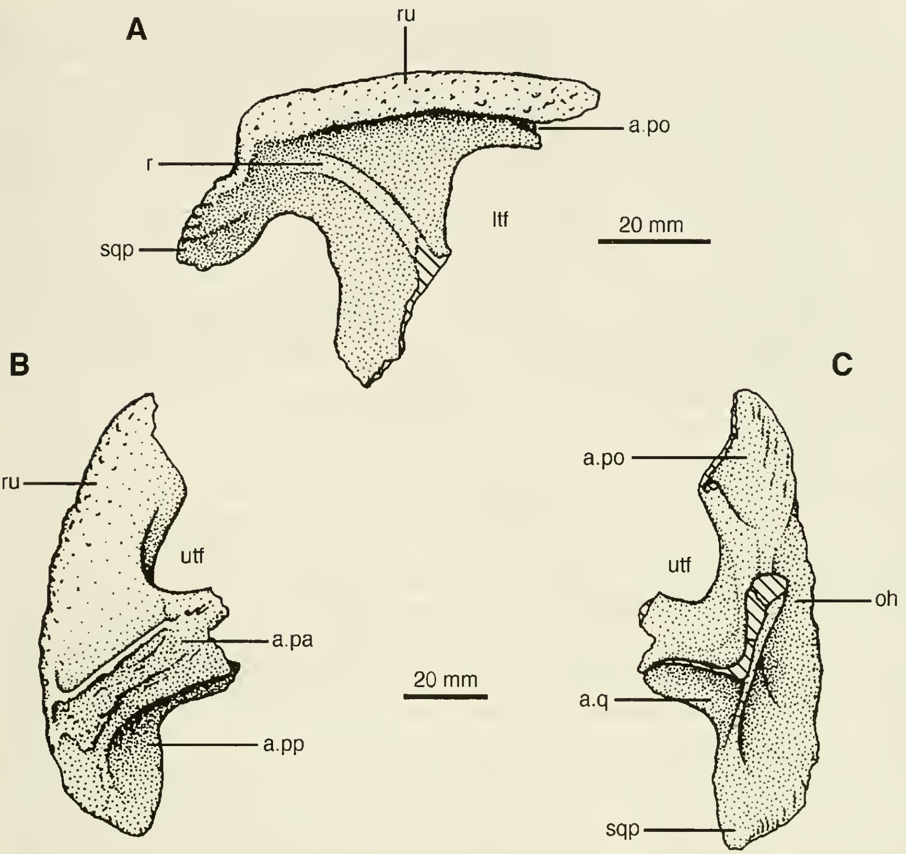

Fig. 12. A: right squamosal of SMNS 80260 in dorsal view; B: left squamosal of SMNS 52970 in lateral view; C: left squamosal of SMNS 52970 in ventral view. Anterior is to the top of the figure in B and C.

tionally similar to that of earlier archosaurs such as proterosuchids and erythrosuchids, in which the postorbital slots into a well-defined lateral squamosal notch (e.g. PARRISH 1992; GOWER & SENNIKOV 1997; pers. obs. of *Erythrosuchus africanus*), but it differs in the presence of an overhanging dorsolateral brow formed by the postorbital-squamosal bar. The anterior tip of the squamosal of *Sphenosuchus acutus* (WALKER 1990: 18) is bifurcated, so the postorbital-squamosal articulation in sphenosuchian crocodylomorphs might also be more complicated than a simple overlap.

As with the postorbital-squamosal bar as a whole, the anterior process of the squamosal is low and broad, and the whole of its lateral edge is thickened and rugose. This edge resembles that of the postorbital, in that it forms a strong overhang, and its ventrolateral surface harbours a concavity at the dorsal end of the lateral temporal fenestra. Similar lateral overhanging of the quadrate head and lateral temporal fenestra by the squamosal is also seen in other suchians including *Postosuchus kirkpatricki*, *Gracilisuchus stipanicicorum*, and crocodylomorphs (e.g. BENTON & CLARK 1988; WALKER 1990; SERENO & WILD 1992).

The posterior ramus of the squamosal forms a short, free-standing projection. Ventromedially, it harbours a smooth concavity that articulates with the head of the quadrate. The descending ramus of the squamosal is incomplete in all preserved examples, so that its ventral extent is currently unknown. Its posterior edge contacted the anterodorsal edge of the quadrate, and its ventral limit would probably have contacted the quadratojugal. This ramus is laterally compressed and is for the most part flat and fairly featureless, except for a distinctive lateral ridge that extends from below the dorsolateral brow of the squamosal, where the anterior and posterior rami merge, to the posterodorsal border of the lateral temporal fenestra. In the skull of UFRGS PVT 0156 referred to *Prestosuchus chiniquensis* by BARBERENA (1978) the squamosal bears a similar ridge that extends onto a small anterior projection that interupts the posterior border of the lower temporal fenestra. The possible presence of a comparable squamosal process in *B. kupferzellensis* can not currently be ascertained because the relevant area is not preserved in any of the SMNS specimens.

The medial ramus of the squamosal is strongly developed and extends a considerable distance medially in contact with the facet on the anterior surface of the occipital process of the parietal. The dorsal edge of the medial ramus bears a strong ridge that is confluent with the thin dorsal edge of the occipital process of the parietal. The area immediately in front of this ridge is broad and dorsoventrally compressed, so that it forms a fossa bordering the posterolateral margin of the upper temporal fenestra. The area behind the ridge forms a subvertical face that bears transverse ridges and depressions for articulation with the anterolateral surface of the paroccipital process. This articulatory surface extends laterally onto the medial edge of the posterior squamosal ramus. A medially-opening foramen is positioned on the occipital surface of the squamosal (not seen in Fig. 12), between the facets for articulation with the occipital process of the parietal and with the paroccipital process of the braincase. This is clearly seen on the squamosals of both SMNS 52970 and 80260, where it is interpreted as perhaps opening into the lateral end of the small posttemporal fenestra.

Jugal (Fig. 13)

The strongly triradiate jugal is known from three incomplete examples – from both sides of SMNS 52970 and the left side of SMNS 80260. The posterior process is the most robust and longest of the three, it tapers to a blunt point, and it has fairly straight dorsal and ventral margins. The medial surface of this ramus bears a striated facet for articulation with the lateral surface of the anterior process of the quadratojugal. In transverse section, the posterior process is medially concave and laterally convex. The lateral surface bears a number of nutrient foramina set within two parallel, longitudinal grooves.

The upturned anterior process of the jugal articulates with the posterodorsal edge of the maxilla and it forms the anteroventral border of the orbit. A horizontal shelf on its lateral surface overlies a longitudinally-striated facet that locks into the slot in the maxilla described above. A depressed area lies between this shelf and the anteroventral border of the orbit. The left jugal of SMNS 80260 (Fig. 13D) shows a small, lightly-striated dorsal area on the medial surface of the anterior jugal process that possibly articulated with the lateral surface of the ventral tip of the preorbital bar (lacrimal/prefrontal). Details of the contacts between elements in this region are not entirely clear.

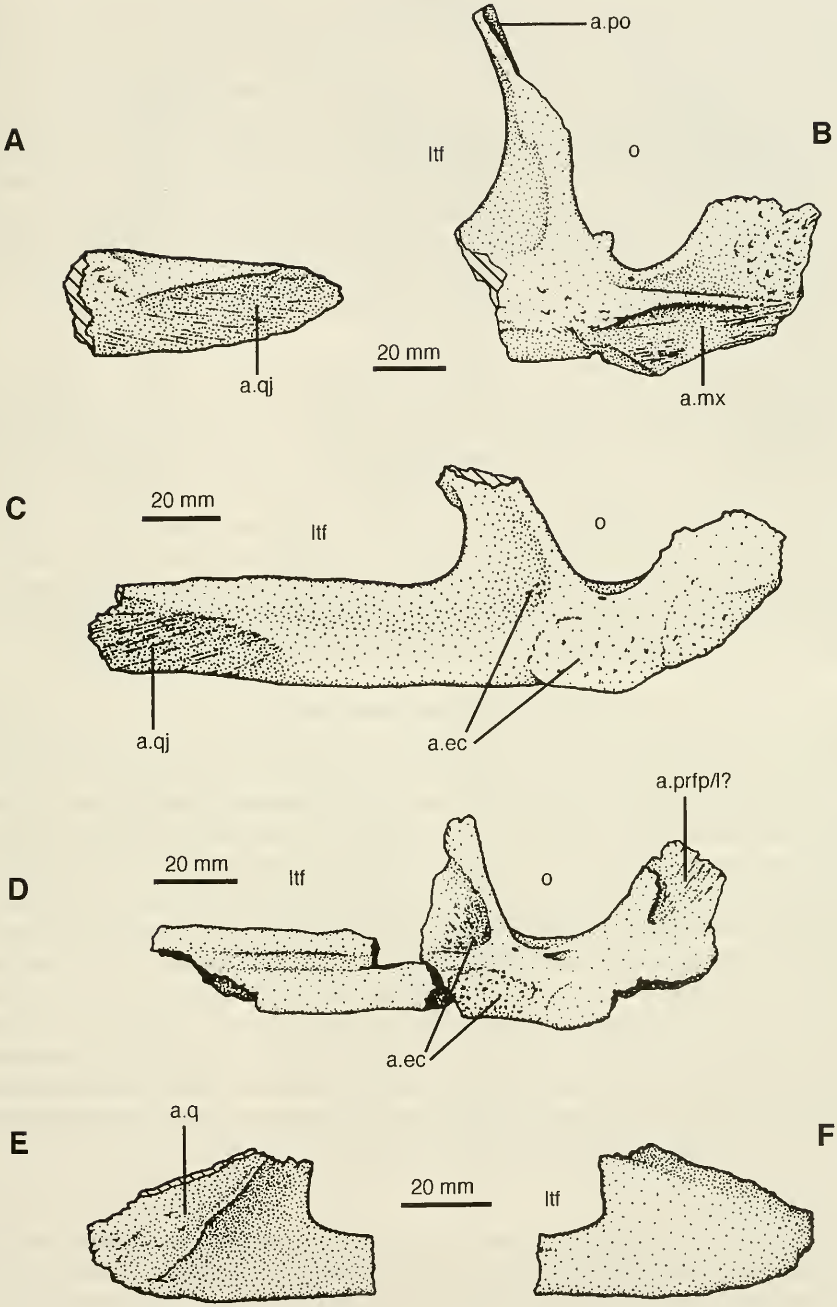

Fig. 13. A: medial view of posterior end of right jugal of SMNS 52970; B: lateral view of anterior end of right jugal of SMNS 52970; C: left jugal of SMNS 52970 in medial view; D: left squamosal of SMNS 80260 in medial view; E: left quadratojugal of SMNS 80260 in medial view; F: same in lateral view.

The whole length of the anterior surface of the ascending process of the jugal bears a facet for articulation with the ventral process of the postorbital. The jugal process is narrow dorsally and it fits into a concave facet on the posterior edge of the ventral process of the postorbital. Further ventrally, the ascending process of the jugal is expanded transversely, and its concave anterior surface accepts the whole transverse width of the ventral tip of the postorbital. Medially, where the ascending and anterior processes of the jugal merge, two lightly pitted surfaces are interpreted as facets for the ectopterygoid. The larger of these areas lies along the ventral edge of the jugal, and it extends forwards to a point directly below the ventral limit of the orbit. The second facet lies a short distance above and behind this, just behind the thickened anterior edge of the base of the ascending process.

Quadratojugal (Figs. 13E, F, 17)

The quadratojugal is known only from the equally incomplete left examples of SMNS 52970 and SMNS 80260. Both examples preserve the angled part of the quadratojugal that forms the posteroventral corner of the lateral temporal fenestra. Although the anterior ramus of the quadratojugal is incomplete, knowledge of its extent comes from the medial surface of the posterior process of the jugal, by which it was overlapped laterally. The medial edge of the ascending quadratojugal ramus articulated with the lateral edge of the quadrate, and must have formed the lateral border to the quadrate foramen, but its dorsal extent and the nature of its probable articulation with the ventral process of the squamosal are currently unknown.

5.3. Palatal complex

Vomer

While no vomers have been identified among the preserved material, their presence in life can be deduced from the form of the preserved parts of other anterior palatal elements. The premaxillary and maxillary palatal processes meet along the midline, but make a short and anteriorly restricted contribution to the palate as a whole. There is a long gap between the posterior edge of the maxillary palatal process and the articulatory surface for the palatine on the medial wall of the maxilla, this gap representing the lateral border of the choana. The presence of well-defined, anteriorly-tapering facets on the ventral surface of the maxillary palatal processes, and the preserved form and position of the palatine, together suggest that the vomers were long, narrow elements that met along the midline and separated the anteromedial edges of the two choanae. The available evidence therefore indicates that the ventral view of the anterior part of the palate in *B. kupferzellensis* resembled that restored for *Saurosuchus galilei* by SILL (1974: fig. 4).

Palatine (Fig. 14A, B)

The palatine of *B. kupferzellensis* is known from the almost complete left and right examples of SMNS 80260. It is an approximately oval-shaped element and, for the most part, is flat and plate-like. Much of its lateral edge forms an expanded facet for articulation with a shallow depression on the medial surface of the maxilla. Contrary to the situation in e.g. *Sphenosuchus acutus* (WALKER 1990), the palatine of *B. kupferzellensis* is not strongly waisted between the facet for articulation with the maxilla and the main body of the element – so that the region between the choana and suborbital fenestra is long relative to the length of the palatine. The anterior and

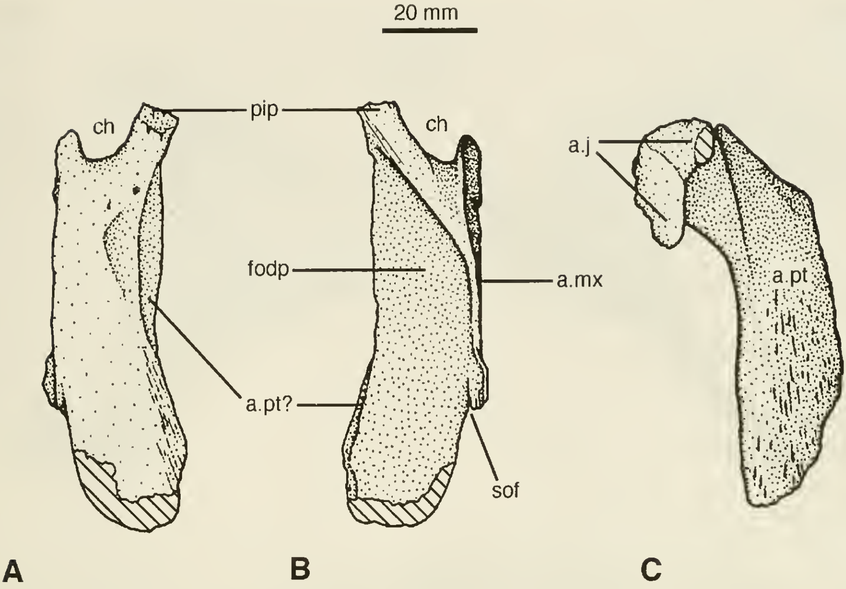

Fig. 14. A-B: right palatine of SMNS 80260. A: ventral; B: dorsal views. C: left ectopterygoid of SMNS 80260 in dorsal view. Anterior is to the top of the figure.

posterior limits of the facet for articulation with the maxilla mark the posterolateral edge of the choana, and the anterolateral edge of the suborbital fenestra, respectively. The medial border of the choana is formed by a thickened anterior process of the palatine, the pila postchoanalis of WITMER (1997). This process is incomplete in both examples. The dorsal surface of the palatine posterior to the pila postchoanalis bears an extensive fossa for attachment of the dorsal pterygoideus muscle (see WITMER 1997). The ventral surface is generally flat, except for a very shallow, triangular, anteromedial depression. The posterior edge of the palatine is unknown, but the thin medial edge would have probably articulated with the anterolateral edge of the pterygoid.

Pterygoid (Fig. 15)

No complete pterygoid is known, but the following description is based on extensive fragments from at least two of the smaller Kupferzell individuals – from both sides of SMNS 80260 and the right side of SMNS 80344. The element is strongly triradiate and generally similar in overall form to the pterygoid morphology of a wide range of basal archosaurs.

Much of the lateral edge of the thin posteroventral ramus bears a cleft in its lateral edge for the ectopterygoid. The quadrate ramus of the pterygoid is strongly expanded. The anterior ramus is long, with a thickened dorsal edge, proximomedially. Anteriorly, this anterior ramus has a broad, obtusely-angled, V-shaped cross-section. At the anterior-most known part of the pterygoid, the vertically-aligned dorsal limb of this V is reduced in height and grooved dorsally. The function of this dorsal groove is unclear, but it is possible that it served as an attachment point for the interorbital/internasal septum or that, in part, the posterior end of the vomer interlocked

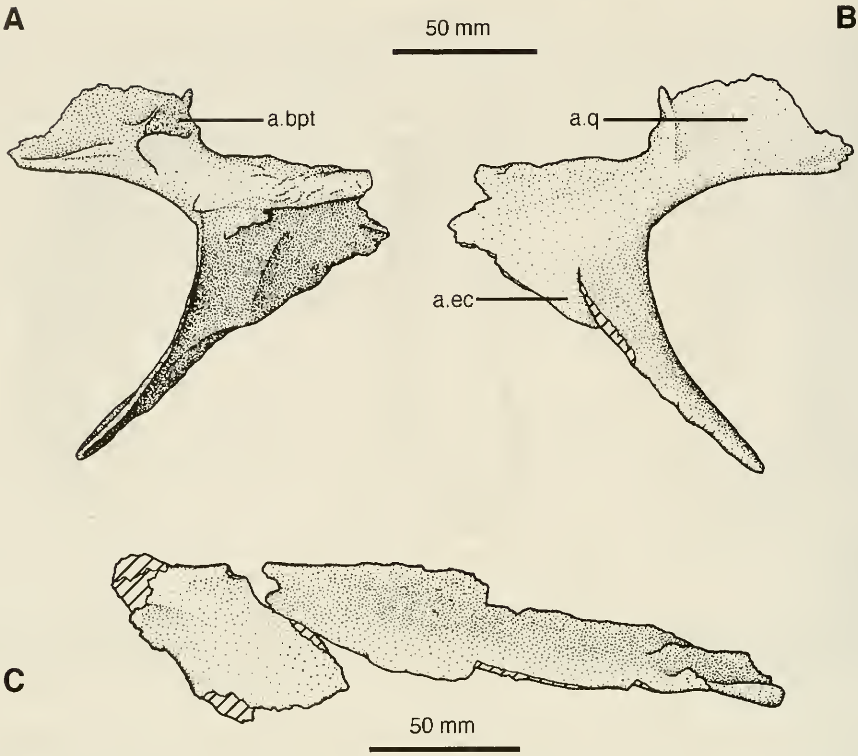

Fig. 15. A-B: posterior portion of left pterygoid of SMNS 80260. A: medial; B: lateral views. C: anterior ramus of right pterygoid of SMNS 80344 in lateral view.

with it. The preserved anterior fragments of this process from the left and right of SMNS 80260 fit together via a simple low ridge (left side) in shallow groove (right side) joint, indicating that these elements both belong to the same individual and that an interpterygoid vacuity was absent at least anteriorly. The ventrolaterally-projecting limb of the V-shaped cross-section must have articulated with the medial edge of the palatine, but this area is not preserved in any example.

The basal articulation is similar to that of many basal archosaurs, in consisting of a simple facet on the medial wall of the base of the quadrate ramus, and an opposing medial projection that hooks around onto the medial surface of the basipterygoid process of the basiparasphenoid.

Quadrate (Figs. 16, 17)

The morphology of the quadrate is known well from the essentially complete left and right examples of both SMNS 52970 and 80260. A rounded dorsal head fits into the smooth concavity on the ventral surface of the squamosal. A strong posterior ridge extends along the main axis of the quadrate. Lateral to this lies a thin, narrow wing that contacts the posterior edge of the descending ramus of the squamosal. The lateral edge of the quadrate is punctuated, about halfway down, by the medial half of a large quadrate foramen. Below this, the posterolateral edge of the quadrate bears a well defined facet for articulation with the medial edge of the quadratojugal. The

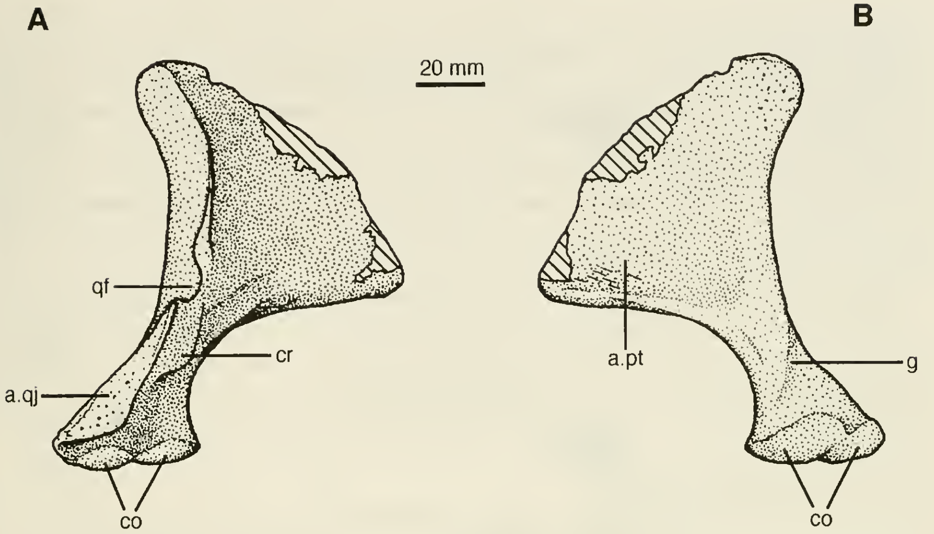

Fig. 16. Right quadrate of SMNS 80260. A: lateral; B: medial views.

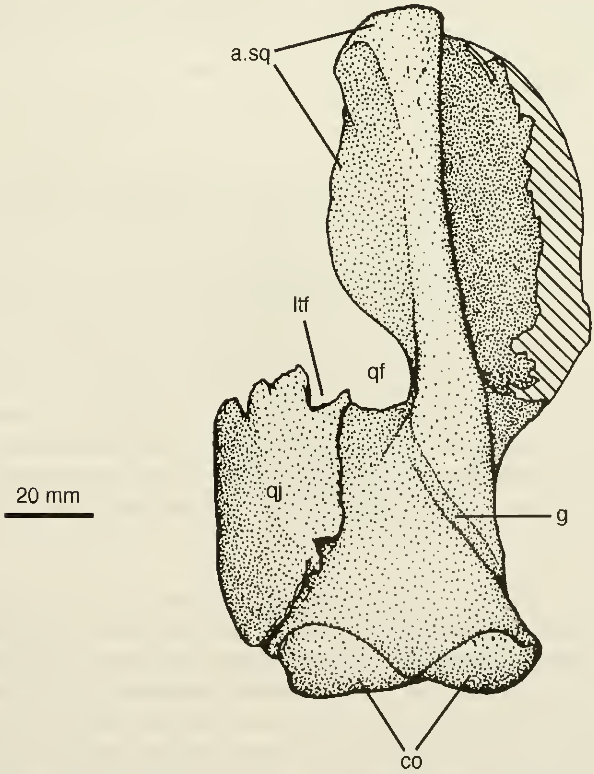

Fig. 17. Left quadrate and quadratojugal of SMNS 52970 in posterior view.

condyle for articulation with the mandible is formed entirely by the quadrate, and it projects clear, ventrally, of the quadratojugal. A posteroventral notch partially separates the condyle into two parts. A shallow but well-defined groove, preserved in all examples, is seen on the posterior surface of the distal end of the quadrate, extending from near the medial border of the quadrate foramen to just above the posterolateral edge of the condyle. In its position and course it resembles the lower part of the faint impression (fainter than the well-defined groove in *B. kupferzellensis*) on the posterior surface of the quadrate of *Sphenosuchus acutus* that was interpreted by WALKER (1990: 30, fig. 29f) as the attachment point of the tympanum.

The main feature of note on the anterior surface of the quadrate is the presence of a well-defined ridge that runs from the posteroventral end of the pterygoid ramus to just above the lateral half of the condyle. This is perhaps homologous with "crest B" described for Recent crocodilians by IORDANSKY (1964), and the similar ridge documented for *Sphenosuchus acutus* by WALKER (1990: 28).

Ectopterygoid (Fig. 14C)

The ectopterygoid of *B. kupferzellensis* is known from the nearly complete left-sided examples of SMNS 52970 and 80260. It is comparable in form with that of suchian archosaurs including *Postosuchus kirkpatricki* (CHATTERJEE 1985), *Ornithosuchus longidens* (WALKER 1964), and *Sphenosuchus acutus* (WALKER 1990), in having a small 'head' articulating with the jugal, and a long posterior process that has an extensive contact with the ventolateral edge of the pterygoid. The head is divided into two distinct facets separated by a groove. An equivalent of the possibly pneumatic cavity within the head of the ectopterygoid of *Sphenosuchus acutus* is absent in *B. kupferzellensis*.

Epipterygoid

The form of this element in *B. kupferzellensis* is currently unknown.

5.4. Mandible

Reconstructions of the mandible are presented in Fig. 18. The overall proportions of this reconstruction are fairly accurate, but uncertainty exists about sutural contacts. For the lateral view, this is chiefly in the central region – particularly the form of the posterior part of the dentary (see description below). The reconstruction of the medial surface is necessarily more speculative. The chief uncertainties here are the form of the coronoid, the anterior extent of the splenial, and the form and position of the contacts among the prearticular, splenial, and coronoid.

Dentary (Figs. 19, 21)

Although both dentaries of the holotype are known, the left dentary of SMNS 80260 is the best preserved example. In lateral view, the anterior end of the dentary is mildly expanded dorsoventrally, although this is less pronounced in the larger material. The lateral surface is liberally covered with nutrient foramina, most of which are conspicuously distributed in two approximately parallel longitudinal rows. Much of the medial surface of the dentary was covered by the splenial. The symphyseal region is restricted to a small and only very weakly differentiated anterior zone. The posterior part of the dentary is interpreted as possessing three tapering process-

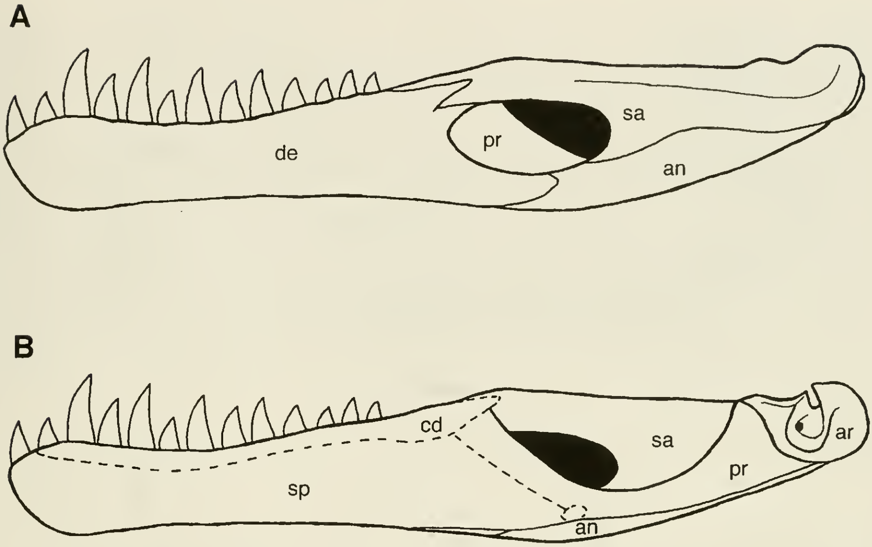

Fig. 18. Reconstructions (see text, section 5.4) of the mandible of *Batrachotomus kupferzellensis*. A: lateral; B: medial views. The text should be consulted for morphological data on individual elements, and it is recommended that this figure is not used as a primary source of phylogenetic data.

es, such as are seen in some of the earliest archosaurs (e.g. *Erythrosuchus africanus*, pers. obs.). This part of the dentary of *B. kupferzellensis* is not preserved in any of the known specimens, but evidence for the presence of three processes comes indirectly from anterolateral (Fig. 20A) and anteromedial (Fig. 20B) facets on the surangular and an anterolateral facet on the angular (Fig. 23A). The preserved dentaries indicate the presence of 11 or 12 mandibular teeth. As with the situation in the upper jaw, interdental plates would seem to be present, but how much they merged together into a single lingual lamella is not entirely clear.

Splenial (Fig. 19C)

The simple, plate-like splenial is best known from the right side of SMNS 80260, with some incomplete, currently unnumbered fragments possibly representing small parts of additional examples. The splenial forms most of the medial wall of the meckelian canal by covering much of the medial surface of the dentary. A narrow dorsal groove perhaps articulated with an elongate, slender coronoid (see below).

Coronoid

The form of the coronoid is unclear. There is apparently no direct evidence, and interpretation from the form of other lower jaw elements is inconclusive. It is possible that a long slender coronoid (as found in archosaur taxa including erythrosuchids, pers. obs., *Sphenosuchus acutus* and some mesosuchian crocodyliforms, WALKER 1990, and perhaps *Chanaresuchus bonapartei*, ROMER 1971b) could have been present, lying alongside the base of the interdental plates of the dentary and perhaps articulating with the narrow dorsal groove on the splenial. However, re-

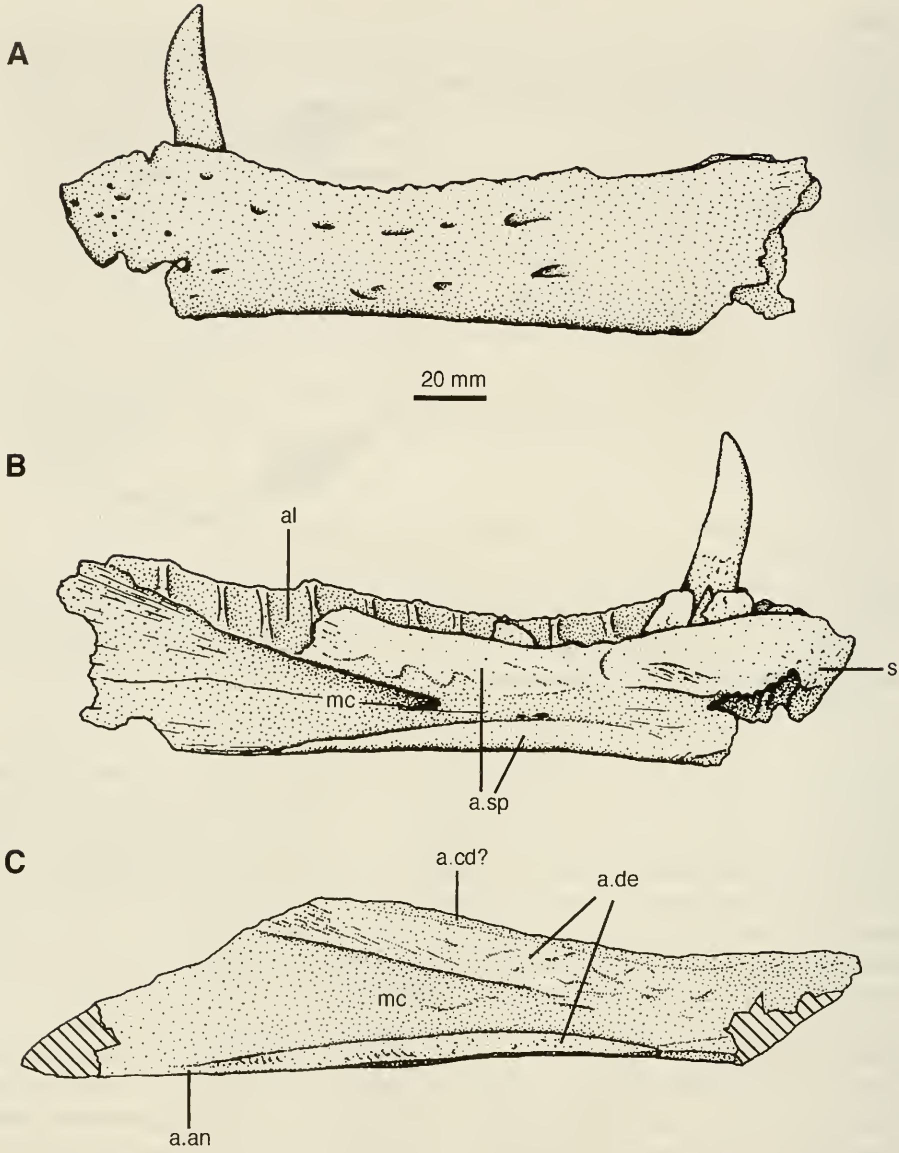

Fig. 19. A-B: left dentary of SMNS 80260. A: lateral; B: medial views. C: right splenial of SMNS 80260 in lateral view.

duced coronoids similar to those seen in extant crocodilians (e.g. IORDANSKY 1973) cannot be ruled out completely. Current specimen conservation (pers. obs. of TTU material) prevents confirmation that the coronoid in *Postosuchus kirkpatricki* was a foreshortened, crescentic element (CHATTERJEE 1985: fig. 8), rather than elongate and slender.

Surangular (Figs. 20, 21B)

The surangular is known from both the left and right sides of SMNS 52970 and SMNS 80260. Its basic construction is one widespread among 'thecodontians' – it is long, composed of a dorsal ridge plus a posteroventral plate, and it forms much of the border of the lateral mandibular fenestra. The posteroventral plate bears a lateral depression that articulated with the medial surface of the posterior part of the angular. The gently flexed dorsal ridge carries an anterolateral notch (Fig. 20A) for the reception of a tapering posterodorsal process of the dentary (by comparison with e.g. *Erythrosuchus africanus*, pers. obs.). The medial surface of the anterior part of the surangular (Fig. 20B) also resembles that of *Erythrosuchus africanus* (pers. obs.) in that it bears a depression that is interpreted as receiving the tapered end of a central dentary process that lay medial to the surangular. This second articulatory depression lies immediately under the overhang formed by the thickened dorsal ridge. The right surangular of SMNS 52970 (Fig. 20B) bears two additional, smaller notches in front of that just described. It is possible that at least one of these articulated with the posterior end of the coronoid.

The surangular foramen lies beneath the lateral underhang of the ridge at a point just anterior to the mandibular cotyle. The medial opening of this foramen lies at the base of a strong anteromedial plate, against the posterior surface of which the articular abuts. A low medial ridge extends anteromedially from the base of this plate. Laterally, the surangular contributes a small outer part of the cotyle for articulation with the quadrate, while further posteriorly it makes only a small contribution to the retroarticular portion of the mandible.

Articular (Figs. 20, 21B)

The firm articulation between the articular and the surangular is preserved in all known examples from Kupferzell. The medial surface of the articular, best preserved on the right example from SMNS 80260 (Fig. 20C), exhibits some distinctive features. A transverse, trough-like depression lies between the posterior border of the cotyle and a slightly hooked ascending process. The ascending process is laterally compressed and its dorsal surface was apparently not finished with a firm layer of compacta bone. The main bulk of the retroarticular region of the articular, posterolateral to this vertical process, has a simple, slightly concave upper surface. The transverse trough-like depression extends medially beyond the edge of the vertical process and onto the dorsal surface of a free-standing, tongue-like, dorsoventrally-compressed medial process of the articular. A large foramen pierces this medial process – it can be seen passing between two broken surfaces of the medial tongue of the right articular of SMNS 52970 in Fig. 20B. This very closely resembles the condition in *Postosuchus kirkpatricki* (Chatterjee 1985: fig. 8, 9b; pers. obs.), *Rauisuchus tiradentes* (Huene 1942: pl. 25, fig. 3b; pers. obs.), *Tikisuchus romeri* (pers. obs.), and *Fasolasuchus tenax* (Bonaparte 1981, fig. 6), although the process in the latter may not be pierced by a foramen. A tongue-like medial process is also seen in an undescribed right articular of *Stagonosuchus nyassicus* (pers. obs. of GPIT specimen), but the probably equivalent piercing foramen is in a more lateral position. Chatterjee (1985: 411) interpreted the foramen in *Postosuchus kirkpatricki* as transmitting the chorda tympani branch of the facial nerve, and this is followed here. An alternative to the hypothesis that the foramen piercing the medial process in *B. kupferzellensis* is for the chorda tympani, is that it is instead a pneumatic feature, perhaps indicating

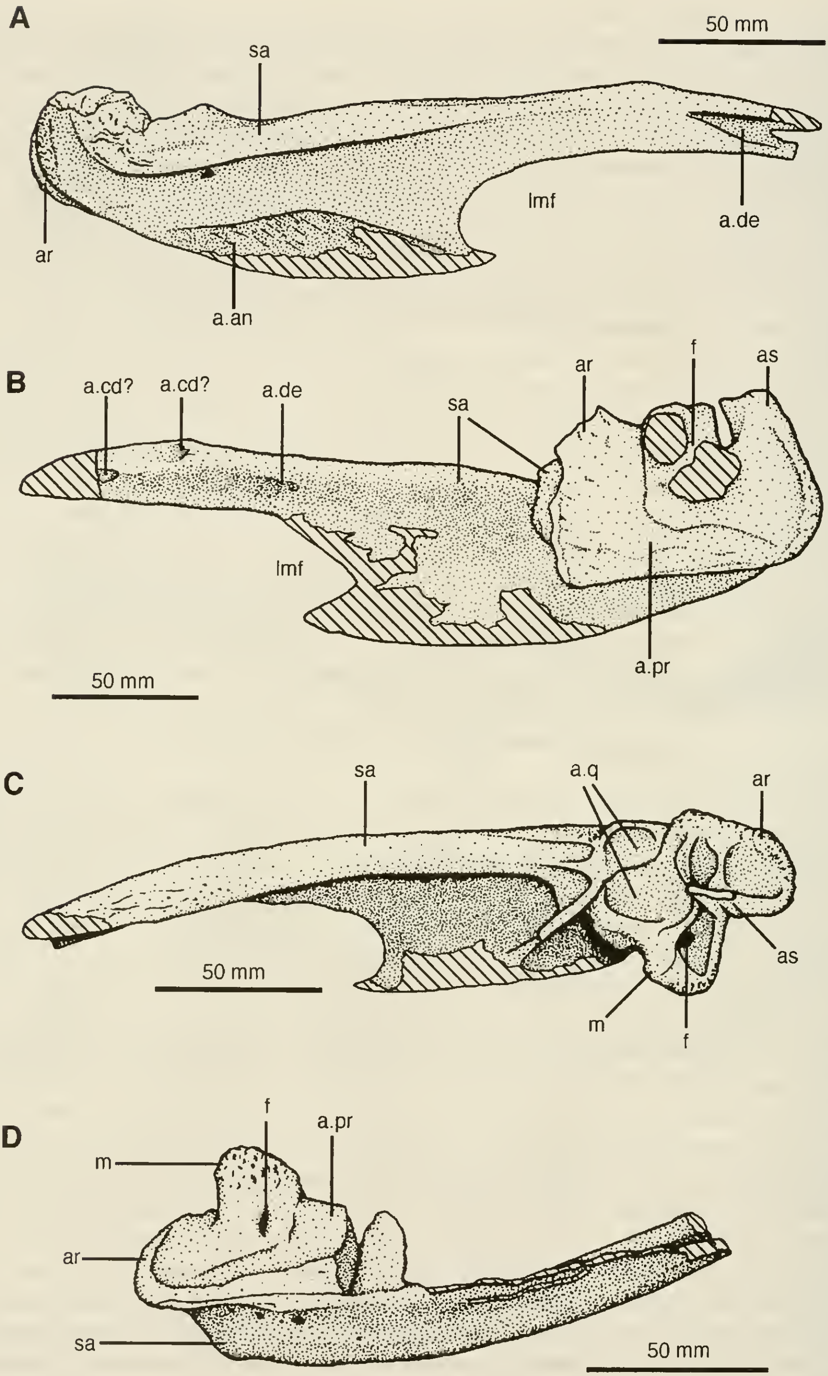

Fig. 20. Surangular and articular. A: lateral view of right ramus of SMNS 80260; B: medial view of right ramus of SMNS 52970; C: dorsomedial view of right ramus of SMNS 80260; D: ventral view of left ramus of SMNS 80260.

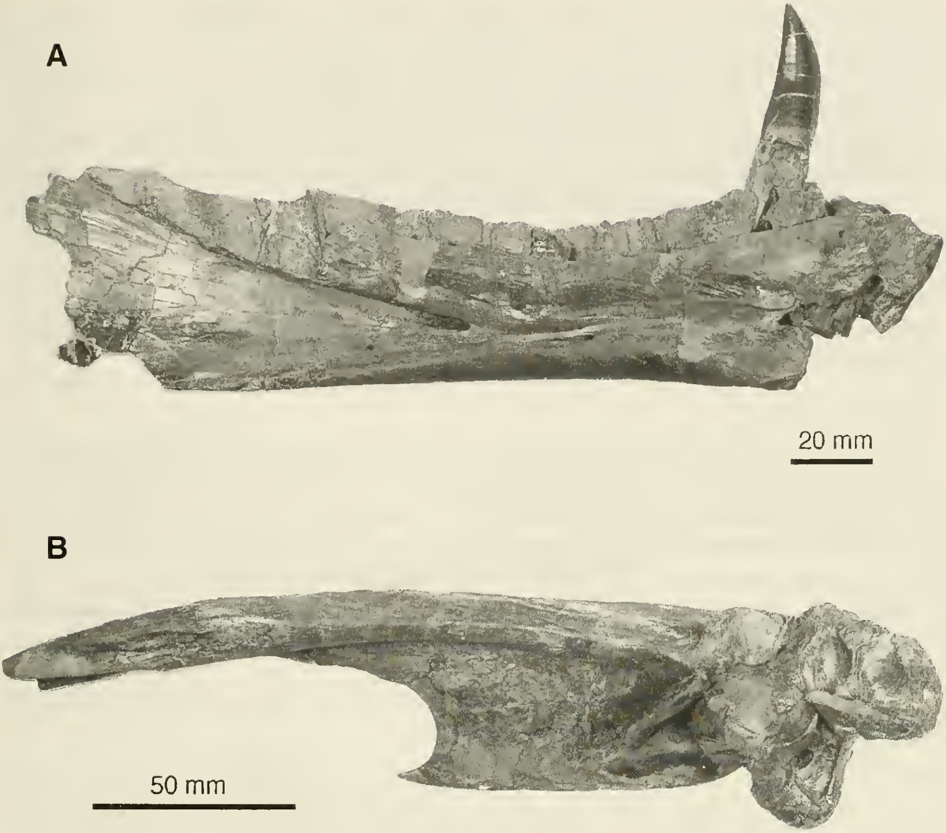

Fig. 21. A: left dentary of SMNS 80260 in medial view; B: right surangular and articular of SMNS 80260 in dorsomedial view.

the position of the siphonium (= the articular diverticulum of the tympanic cavity). Among crurotarsan archosaurs, such a feature has only been previously recorded among crocodylomorphs (e.g. Iordansky 1973, Walker 1990, Wu & Chatterjee 1993), where a foramen aërum opens into a pneumatic cavity. There are two points that weigh against a pneumatic interpretation for the foramen in *B. kupferzellensis*: (1) the foramen passes directly through the medial articular process rather than opening into a blind, potentially pneumatic cavity, and (2) an alternative path for the chorda tympani nerve cannot be positively identified in the preserved examples (see Witmer 1990: 367 for cautioning against confusing interpretations of the paths of the articular diverticulum and chorda tympani). Perhaps weighing against the chorda tympani interpretation favoured here is the large size of the foramen and its far medial position in comparison with other extinct and extant reptiles, inlcuding Recent crocodilians.

A vertical process, trough-like depression, and articular medial process pierced by a foramen (presumably for the chorda tympani) is also found among parasuchians e.g. *Nicrosaurus kapffi* (pers. obs. of BMNH 38036 and 42744), although the medial process is less prominent and more ventrally-projecting than in *B. kupferzellensis*.

In the early archosaur *Erythrosuchus africanus* (pers. obs. of BMNH R3592), there is a fairly robust medial projection, but the interpreted route of the chorda tympani nerve bypasses this. Some confusion might be introduced in the discussion of these medial and ascending processes of the retroarticular region of the articular through use of an indiscriminate terminology. For example, the medially-directed "retroarticular process" in *Stagonolepis* discussed by WU & CHATTERJEE (1993: 84) is actually a medially-positioned, dorsally-projecting process (WALKER 1961: fig 6) resembling (and possibly homologous with) the ascending process described in *B. kupferzellensis* above. The term "retroarticular process" is sufficient in the discussion of extant crocodilians – where the whole retroarticular region forms a relatively simple, single posterior process (IORDANSKY 1973) – but more precision is required where there are multiple distinct projections.

Prearticular (Fig. 22)

The prearticular is known from two incomplete examples (both lacking the anterior end), from the left side of SMNS 52970 and the right side of SMNS 80260, and it closely resembles that of e.g. *Postosuchus kirkpatricki* (CHATTERJEE 1985: fig. 9d). Its expanded posterior end articulates with the posteromedial surface of the articular. The posterior edge is similarly incomplete in both preserved examples. The strongly curved dorsal surface forms the lower margin of the adductor fossa. In transverse-section it is C-shaped, with a well-defined lateral groove for Meckel's car-

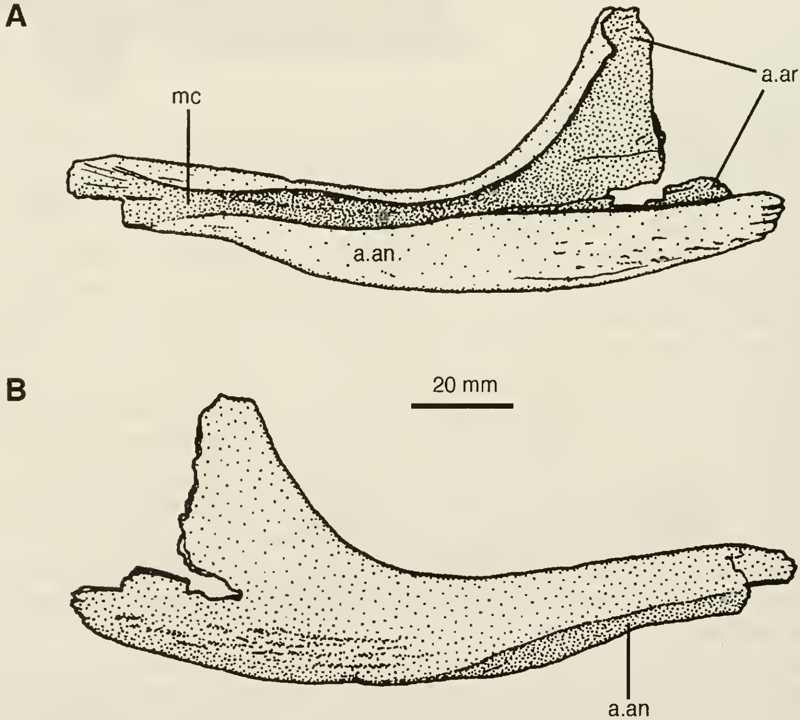

Fig. 22. Left prearticular of SMNS 80260. A: lateral; B: medial views.

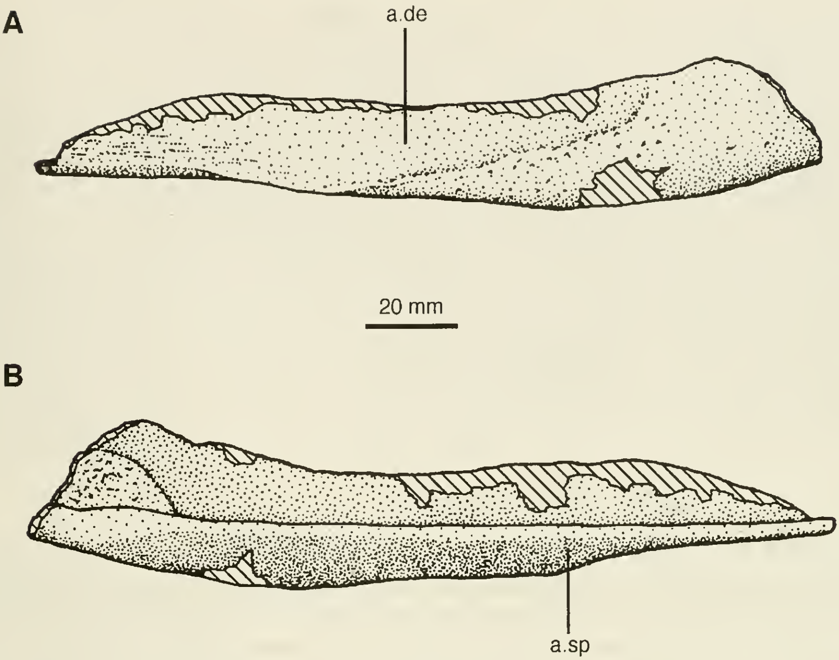

Fig. 23. Left angular of SMNS 80260. A: lateral; B: medial views.

tilage. The lower limb of the 'C' is broadened ventrally into an articulatory surface for the surangular and, further anteriorly, the angular. As preserved, there is no indication of the position or form of an inframeckelian foramen.

Angular (Fig. 23)

The angular is known from only a single, incomplete, and uncertainly identified example from the left side of SMNS 80260. As interpreted, only the slender, tapering anterior part is preserved. This bears a lateral depression for articulation with the lower part of the posterior end of the dentary. If this interpretation is correct, then the lower posterior process of the dentary probably extended back along the lower border of the lateral mandibular fenestra for a considerable distance. The proposed angular is L-shaped in transverse section and it possesses a medial surface for contact with the prearticular/splenial. The outline of the missing posterolateral surface can be deduced from the shape of the facet on the lateral surface of the surangular (Fig. 20A).

5.5. Dentition

The available material indicates that the premaxillae held four teeth each, the maxillae eleven, and the dentary eleven or twelve. The teeth are typical of carnivorous archosaurs in that they are laterally compressed, recurved, serrated along both edges, and have long roots that are held in clearly defined sockets. Most of the teeth are known from tens of isolated examples. The few that remain articulated with the jaw hint at a possible pattern of variation. Those associated with premaxillae are slender,

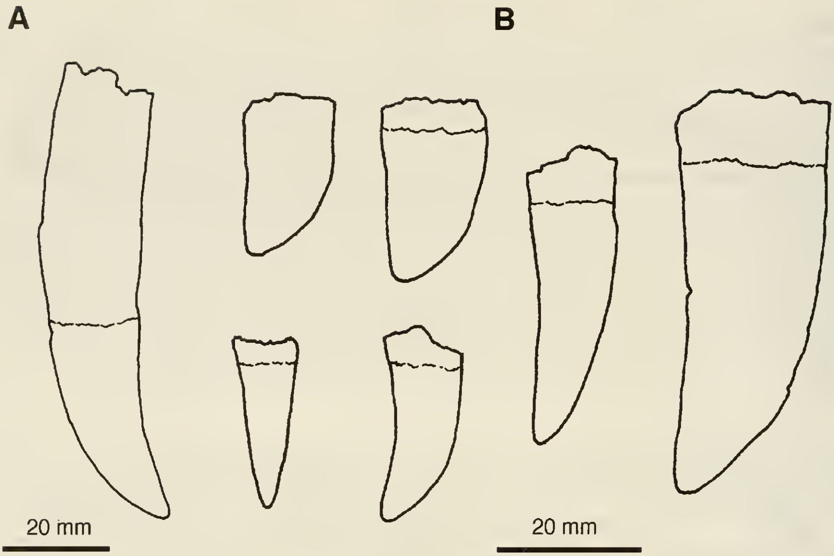

Fig. 24. Isolated teeth. A: SMNS 52970; B-F: six isolated specimens (SMNS unnumbered) from the 1977 excavation of the Kupferzell-Bauersbach locality.

those from the anterior part of the maxilla have a straight posterior edge and a strongly convex anterior edge (in lingual view), while those from the posterior part of the maxilla are similar, but more strongly convex anteriorly, and have shorter crowns.

Tens of isolated teeth from the 1977 Kupferzell excavation can be referred with confidence to *B. kupferzellensis* (on the basis of similar overall size and morphology, and the apparent absence of other archosaur taxa in the Kupferzell deposits) and these provide further evidence of variation in tooth morphology (a sample is outlined in Fig. 24), although it is not known which elements they were dislodged from. A full study of variation in serration denticle morphology and density among this material has not been undertaken. Some of the teeth, seen in lateral view, appear to have slightly expanded crown bases (Fig. 3, 19A), although compression during preservation means this is not absolutely certain in many cases. Teeth in which the base of the crowns are expanded, bulbous, or "lanceolate" (Colbert 1952), are found among certain sphenosuchian and crocodyliform crocodylomorphs (e.g. Parrish 1991, Sereno & Wild 1992). Tooth replacement appears to have occurred alternately in *B. kupferzellensis*, with the left and right upper tooth rows of SMNS 80260 clearly out of step with each other. The mode of replacement can be seen in some instances. The replacing tooth arises lingual to the mature one, and develops within a pit in the latter (Fig. 3B, 4B).

6. Discussion

6.1. Intraspecific variation

A detailed qualitative or quantitative analysis of osteological variation in *B. kupferzellensis* is not yet possible because of the limited number and incomplete preservation of known specimens. However, the two best-preserved skulls are of different sizes (estimated total lengths of approximately 400 and 500 mm) and they allow some hypotheses about ontogenetic variation to be formulated. The dorsolateral ridge along the edge of the nasal, lacrimal, postorbital, and squamosal is more rugose and pronounced in the larger material, and the ridges and depressions on the dorsal surface of the skull roof also appear to be more strongly defined. The jugal facets for articulation with the ectopterygoid are more clearly defined and have a more pitted surface in the smaller material. The anterior end of the dentary is more noticeably expanded (dorsoventrally) in the smaller material.

6.2. Soft tissues of the antorbital region

Witmer's (1995, 1997) recent studies of the evolution of the bony and soft tissues of the antorbital cavity of crown-group archosaurs have paved the way for an accurate consideration of soft-tissue presence and form in individual fossil archosaur taxa. Given the excellent preservation of the Kupferzell material, the generally rather incomplete preservation of other rauisuchians, and previous ignorance of the importance of pneumaticity, it seems worthwhile to consider here osteological evidence for the form of soft tissues in the antorbital region of the cranium of *Batrachotomus kupferzellensis*. This will be done with reference to osteological correlates of several soft-tissue structures found in the antorbital region of extant archosaurs: paranasal air sinuses; nasolacrimal duct; nasal gland; dorsal part of the pterygoideus muscle; maxillary nerve and accompanying vessels (Witmer 1995, 1997).

B. kupferzellensis has well-developed internal and external antorbital fenestrae, with the antorbital fossae extending onto the lateral surfaces of the maxillae, nasals, lacrimals, and jugals. There is no evidence that any of these elements were invaded by accessory pneumatic cavities. The course of the nasolacrimal duct is interpreted as being indicated by a matrix-filled channel within the lacrimal-prefrontal suture of the medial surface of the left side of SMNS 80260. From the anterior margin of the orbit, this channel passes anterodorsally into the antorbital cavity, but the position of its anterior opening is unclear. Osteological correlates of the nasal gland of archosaurs are less obvious (Witmer 1997: 11), but evidence for the presence and position of this soft-tissue structure in *B. kupferzellensis* is perhaps indicated by the narrow recess on the ventral surface of the nasals, lateral to the midline thickening at the symphysis (Fig. 6C). The large dorsal fossa on the palatine (Fig. 14B) can be interpreted confidently as a site of attachment for the dorsal part of the pterygoideus muscle. This fossa belongs clearly to the "second type" described for crurotarsan archosaurs by Witmer (1997: 16). Finally, the foramen on the medial surface of the maxilla (Fig. 4B) probably transmitted the maxillary nerve and associated vessels.

The form and relative position of osteological correlates in the antorbital region of *B. kupferzellensis* are entirely consistent with Witmer's (1995, 1997) hypotheses of the identity and arrangement of these soft-tissues in extinct crown-group archosaurs. The soft tissues associated with the opening between the premaxilla and maxilla of *B. kupferzellensis* and other rauisuchians is unclear (see Gower in review), but studies such as those by Witmer on the antorbital cavity suggest that this problem is solvable.

6.3. Cranial and mandibular kinesis

The preservation of the Kupferzell cranial material of *B. kupferzellensis* as disarticulated elements provides the opportunity to consider the possibility of cranial kinesis. Among extant archosaurs, the crania of living crocodilians are akinetic, while extensive kinesis is widespread among birds (e.g. Zusi 1993), where commonly streptostyly (pivoting of the quadrate about its articulation with the squamosal) is combined with the elevation and depression of the upper jaw about a craniofacial hinge (= prokinesis). Among living diapsids, cranial kinesis is widespread among lizards and snakes. For example, in lizards (see e.g. Arnold 1998 and references therein) streptostyly is often combined with a hinge-like frontal-parietal articulation (mesokinesis), a mobile braincase-parietal articulation (metakinesis), a mobile palate, and the absence of a bar closing the ventral border of the lower temporal fenestra.

Considerations of cranial kinesis among extinct suchian archosaurs have been rare, but Walker (1972, 1974, 1990) has discussed the possibility of kinesis in the skull of the crocodylomorph *Sphenosuchus acutus*. Walker proposed that there was a degree of streptostyly and an associated lifting and lowering of a snout segment about pivots between the nasals and frontals and maxillae and jugals. This movement was postulated to have occurred chiefly in the juvenile skull (not yet known for *S. acutus*) because moveable articulations occur between e.g. the quadrate and squamosal in the adult skull, but the realization of this kinetic potential is suppressed by the morphology of other articulations. It is clear that extensive kinesis was not possible in adult skulls of *Batrachotomus kupferzellensis*. There is no hinge between frontals and nasals, the bar forming the ventral border of the lower temporal fenestra is complete, and the probable presence of an elongate laterosphenoid would have precluded a significant braincase-parietal pivot. Satisfactory assessment of possibly more restricted cranial kinesis in *B. kupferzellensis* is difficult for several reasons. Unlike Walker's study of *S. acutus*, there is no complete single skull of *B. kupferzellensis* currently available and, while preservation is generally very good, information has been lost around the edges of several of the preserved elements – edges that would have increased the information that could be obtained on the details of articulations between elements. There is also ignorance about the soft tissues that were associated with inter-element articulations, and soft tissues are known to play an important part in dictating the amount and type of movement observed in crania of living diapsids (e.g. Arnold 1998). Palaeontologists might be tempted to over-interpret the significance of apparently loose articulations between elements in the absence of soft tissue data – even apparently mobile joints in the kinetic skulls of living diapsids are often not involved in cranial kinesis (e.g. Bühler *et al.* 1988).

The dorsal part of the dermatocranium of *B. kupferzellensis* forms what was probably a rigid structure. There is direct evidence that the frontal, prefrontal, and postfrontal were all firmly articulated. In neither SMNS 52970 nor 80260 has the frontal-parietal or frontal-nasal articulation survived intact, but it is clear that only a very minor amount of rocking or sliding, at most, may have been possible between these elements. As in *S. acutus* (Walker 1990), the head of the quadrate and associated squamosal concavity are smooth. This articulation potentially allowed some streptostyly, although a similar configuration is seen in basal archosaurs in which quadrate movement seems unlikely (e.g. pers. obs. of *Erythrosuchus africanus*). Possible impingements on this potential streptostyly in *B. kupferzellensis* are difficult to assess. The ventral limit of the squamosal and dorsal limit of the quadratojugal, together forming the posterior border of the lower temporal fenestra, are incomplete in all known specimens, but protraction of the quadrate would probably have been restricted or prevented by (even the little of what is known of) the ventral process of the squamosal. Very slight retraction or perhaps even some medial movement may have been possible. There is no indication that a small amount of sliding between quadrate and pterygoid was not possible and, while the anterior part of the palate is unknown, the articulation between ectopterygoid and jugal may also have permitted a small degree of pivoting. The quadrate-quadratojugal articulation does not give the appearance of being mobile because there are irregular ridges and grooves on the surface of both elements. This means that retraction of the quadrate (if it occurred) would have had to have been accompanied by sliding between quadratojugal and jugal (unlikely, but possible based on known morphology of these elements, although the quadratojugal-squamosal articulation is not yet known) or between jugal and maxilla + preorbital bar (even less likely).

The remaining region of the skull in which movement might have occurred is at the front of the snout. The loose articulation between premaxilla and maxilla may have allowed a restricted amount of rocking to occur in a sagittal plane, approximately around a point defined by the position of the premaxilla-maxilla opening (if the unknown premaxilla-nasal articulation permitted this). The morphology of the palatal processes of these two elements suggests that a small amount of associated sliding might have been possible. The presence of a moveable articulation between premaxilla and maxilla is supposed to be diagnostic for at least some subset of rauisuchians (e.g. BENTON 1986; BENTON & CLARK 1988; LONG & MURRY 1995), although the nature of the premaxilla-maxilla articulation has not yet been documented in sufficient detail for most taxa. Knowledge of the mandibular morphology of *B. kupferzellensis* is far from complete, particularly in the region where the anterior and posterior elements would have articulated, but there is no evidence for a significantly flexible intramandibular joint. The apparently restricted and simple symphysis would have perhaps allowed each ramus to move in a partially independently manner.

In conclusion, it would seem that significant cranial kinesis in *B. kupferzellensis* was absent, but that there may have been a restricted amount of probably passive movement of some elements, most notably some sagittal pivoting of the premaxillae. Streptostyly where the quadrate pivoted backwards about its articulation with the squamosal, in association with sliding between the quadratojugal (attached to the quadrate) and the jugal, seems unlikely and can be ruled out if future discoveries show the palatal or quadratojugal-squamosal articulations to be immobile. The possible function of these potential movements is not discussed here. As WALKER (1990) has proposed for *S. acutus*, potential movement between elements in the absence of significant cranial kinesis as a whole might be explained by a decrease in cranial kinesis through ontogeny, and this hypothesis can be tested when juveniles are discovered. To date, there is no evidence that extensive (particularly powered) cranial kinesis evolved within non-ornithodiran crown-group archosaurs.

6.4. Phylogeny

A satisfactory consideration of the precise phylogenetic position of *Batrachotomus kupferzellensis* is not yet possible. There is no stable framework for rauisuchian systematics (see introduction; Gower in review), detailed comparisons are often limited by the less perfect preservation of many of the other known rauisuchian taxa, and the braincase and postcranial material of *B. kupferzellensis* has yet to be described. Incomplete knowledge of the distribution of morphological features seen in rauisuchians, combined with the lack of a robust phylogeny, means that even where shared features are identified, it is not yet known whether many of these are plesio- or apomorphies. The focus in the following discussion is on cranial characters present in *B. kupferzellensis* that can be hypothesized to be derived for subsets of suchian archosaurs.

Some derived cranial characters are present in *B. kupferzellensis*, some other rauisuchians, and basal (i.e. at least sphenosuchian) crocodylomorphs. These include the overhanging lateral edge of the squamosal and postorbital at the dorsal end of the lateral temporal fenestra and – in association with this – a low, broad postorbital-squamosal bar. The overhanging of the squamosal was once thought to be diagnostic for crocodylomorphs (e.g. Bonaparte 1982; Benton & Clark 1988), but has been recognized recently to have a broader distribution (Parrish 1993). The less prominent lateral squamosal ridge in some basal phytosaurs (e.g. Long & Murry 1995) is possibly a homologous feature (Hungerbühler 1998, pers. comm.). Among their list of sphenosuchian synapomorphies, Sereno & Wild (1992) included some other features of the squamosal that are also seen in *B. kupferzellensis*, namely the 'arcuate' shape of the squamosal in dorsal view, and the development of a posterolateral rim bordering the upper temporal fossa. Also common to basal crocodylomorphs and at least some rauisuchians is the topography on the dorsal surface of the skull roof, namely a central depression on the nasals, a sagittal ridge on the frontals, and extensive fossae bordering the upper temporal fenestrae. An anterior extension of the upper temporal fossae has been interpreted as a dinosaurian synapomorphy that evolved independently in basal crocodylomorphs (Novas 1996: 730). The exact distribution of these cranial features and their phylogenetic informativeness is not yet clear but, taken at face value, they provide evidence for a clade of Crocodylomorpha + some rauisuchians. Recent improvement in the documentation of sphenosuchian osteology and multiple analyses of crocodylomorph phylogeny (e.g. Walker 1990; Sereno & Wild 1992; Wu & Chatterjee 1993) has advanced knowledge of the origins of the distinctive morphology seen in extant crocodilians, but a wider picture is obscured by the confusion surrounding the relationships of crocodylomorphs to other crurotarsan archosaurs, and the less than detailed existing documentations of the osteology of many of these taxa. The well-preserved Kupferzell material of *B. kupferzellensis* will be important not only in the resolution of rauisuchian ingroup relationships, but also in clarifying morphological evolution of crocodilian-line archosaurs – a neglected topic in comparison with the evolution of bird-line archosaurs, the other major clade in the archosaur crown-group.

A further set of cranial characters appears to be shared by a restricted group composed of *B. kupferzellensis* and various other rauisuchians. For example, a tongue-like medial process of the articular, a kinked postorbital bar, and a 'Roman nose' formed by an anteriorly-arched nasal. The lateral ridge on the descending process of the squamosal (Fig. 12) is an apparently derived feature shared (pers. obs.) with specimen UFRGS PVT 0156 referred to *Prestosuchus chiniquensis* by BARBERENA (1978). At least two further derived characters appear to be restricted (based on current documentations of rauisuchian morphology) to *B. kupferzellensis* and *Postosuchus kirkpatricki* (CHATTERJEE 1985; LONG & MURRY 1995; pers. obs.) – an extensive rugose ridge along the dorsolateral edge of the skull roof, and an articulation between premaxilla and maxilla that interlocks (as described above) around a premaxilla-maxilla opening. Again, these features might be found to have a wider distribution once better material and documentations for other rauisuchians become available. Confirmation that these two taxa belonged to a clade within (even a possibly non-monophyletic) Rauisuchia would be interesting. The Ladinian *B. kupferzellensis* is one of the older known rauisuchians while *P. kirkpatricki* is from Mid-Carnian to Norian rocks. Two cranial features in *B. kupferzellensis* represent potential autapomorphies within Rauisuchia – a naris larger than the antorbital fenestra (also occurs within Aetosauria), and a distinctive depression on the ventral end of the lateral surface of the postorbital (Fig. 11).

In addition to the unsatisfactory knowledge of rauisuchian morphology and relationships, further analytical challenges in the accurate estimation of suchian phylogeny lie in understanding the derived cranial morphology of one of the proximal outgroups (phytosaurs) and one of the major ingroups (aetosaurs) of uncertain affinity, and the disputed relationships of the Ornithosuchidae (GOWER & WILKINSON 1996). Future numerical analyses of suchian and especially rauisuchian phylogeny will also need to tackle the important issues of character and taxon selection and missing data.

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9. Appendix I – current hypodigm of *Batrachotomus kupferzellensis*

Specimens from the 1977 Kupferzell excavation.

Cranial material has been catalogued under four separate numbers, because it represents a minimum of four individuals. The postcranial material represents a minimum of five individuals (indicated by the presence of five right ilia). Both the cranial and postcranial material falls into two clearly separable size classes. In only one instance has cranial and postcranial material been assigned to the same catalogue number (SMNS 52970), because it represents all of the larger size class material, and it was retrieved from a localized area within the deposit (R. Wild, pers. comm.).

9.1. Holotype

SMNS 52970

Disarticulated, but associated cranial and postcranial material from (probably) a single large individual (estimated skull length approximately 500 mm). No other archosaur material of this size was recovered from the 1977 Kupferzell excavation.

Right (Parrish 1993: fig. 8) and left premaxillae, right (Galton 1985: fig. 1B, C; Parrish 1993: fig. 8) and left (Wild 1979: photograph on p. 49) maxillae, nasals, frontals (+ partial postfrontals), parietals, squamosals, postorbitals, jugals, quadrates, dentaries, surangulars, articulars, right lacrimal, right prefrontal, left quadratojugal, left ectopterygoid, left prearticular. Five isolated teeth (Wild 1978a: 190, 1981: fig. 9). Three dorsal, a single sacral, and three caudal vertebrae. Single dorsal osteoderm. Right ilium (Galton 1985: fig. 1A). Right (proximal fragment only) and left femora, left tibia, left fibula.

9.2. Referred specimens

SMNS 80260

Disarticulated, but associated cranial material from a single individual smaller than the holotype (estimated skull length approximately 400 mm). While the cranial material of this size class recovered from the 1977 Kupferzell excavation represents a minimum of three individuals, and the postcranial material of a matching size a minimum of four individuals, almost all of the smaller cranial material has been catalogued under a single number. There is direct evidence that a substantial part of it must derive from a single individual. For example, exact articulations link the left parietal – left frontal + postfrontal – left nasal – right nasal (+ right lacrimal) – right maxilla, and other contacts at least do not rule out the possibility that they represent a single individual. Less confidence can be had in assigning the SMNS 80260 mandibular and palatal elements to the same individual, where identifying natural articulations is often not possible.

Both premaxillae, maxillae (left figured by Wild 1980b: fig. 7, Hagdorn & Simon 1985: fig. 62), nasals, lacrimals, left frontal (+ partial postfrontal), right postorbital, left jugal, prefrontals, parietals (anterior fragments only), squamosals, palatines, left ectopterygoid, pterygoids, quadrates (right figured by Wild 1978a: photograph p.191), braincase (lacking laterosphenoid and basiparasphenoid rostrum), left dentary, splenials, surangulars, articulars, left angular.

SMNS 80261

Heavily crushed occiput. This specimen shows a different preservation to all of the other 1977 Kupferzell rauisuchian material, in being articulated, heavily crushed, and with poorer surface preservation. It represents a similar-sized individual to SMNS 80260 and SMNS 80344. Its preservation suggests that it derives from a (minimum) third individual represented by cranial material, and this is confirmed by the presence of homologous pieces of pterygoid in SMNS 80260 and SMNS 80344.

SMNS 80344

Incomplete right pterygoid, catalogued separately because it cannot belong to the same individual as the right pterygoid referred to SMNS 80260 or 80261, despite being of a similar size.

SMNS 80268, left ilium and left and right ischia.
SMNS 80269, left and right ilia and pubes.
SMNS 80270, left and right ilia, pubes, and proximal ends of ischia.
SMNS 80271, left and right scapulae and coracoids (Parrish 1993: fig. 5c).
SMNS 80272, left and right ilia.
SMNS 80273, right ilium.
SMNS 80274, incomplete left and right scapulae.
SMNS 80275, right humerus, radius, and ulna.
SMNS 80276, right humerus (Wild 1978: photograph p.192).
SMNS 80277, fibula.
SMNS 80278, left femur (Wild 1978: photograph p.192).
SMNS 80279, left pubis.
SMNS 80280, articulated left and right ischia.
SMNS 80281, proximal end of right scapula.
SMNS 80282, distal end of right pubis.
SMNS 80283 – 80343 inclusive, vertebrae. All but two of these 61 catalogue numbers represents a single, disarticulated vertebra or significant vertebral fragment. Two of these numbers (SMNS 80310 and 80339) each represent two associated vertebrae. These mostly disassociated finds represent a minimum of two individuals (demonstrated by two axis elements – SMNS 80322, 80323). Establishing associations between individual vertebrae is generally not possible – partly because all of these specimens belong to individuals of approximately the same size (and preserved ilia of an approximately matching size indicate that at least four individuals could be represented).

The SMNS collections house additional, currently uncatalogued Kupferzell material that probably (e.g. isolated osteoderms, ribs, girdle fragments, haemal arches, tens of isolated teeth) or possibly (unidentified cranial and postcranial fragments) belong to *B. kupferzellensis*. Isolated and fragmentary SMNS archosaur material from other localities in the Lettenkeuper may also represent rauisuchians, but are here considered to be too poorly known to be diagnostic. More extensive material referrable to *Batrachotomus* has also been recovered from Lettenkeuper deposits at Vellberg-Eschenau, some 19 km southwest of the Kupferzell locality (W. Kugler, pers. comm.; R. Wild, pers. comm.).

10. Appendix II – abbreviations used in figures

a.	surface/facet for articulation with...
al	tooth alveolus
an	angular
aof	antorbital fenestra
aofo	antorbital fossa
ar	articular
as	ascending process of retroarticular region
bpt	basipterygoid process of the basisphenoid
cd	coronoid

ch	choana
co	condyle
cr	crest
d	depression
de	dentary
e	endocranial cavity
ec	ectopterygoid
en	external naris
enf	fossa bordering en
fodp	fossa for attachment of dorsal part of pterygoideus muscle
f	foramen
fr	frontal
g	groove
j	jugal
l	lacrimal
lmf	lateral mandibular fenestra
ls	laterosphenoid
ltf	lower temporal fenestra
m	medial, tongue-like process of retroarticular region
mc	meckelian canal
mx	maxilla
mxp	palatal process of maxilla
n	nasal
no	notch
o	orbit
oh	overhang of postorbital-squamosal bar at dorsal end of ltf
pa	parietal
pal	palatine
pf	postfrontal
pip	pila postchoanalis
pmx	premaxilla
po	postorbital
pp	paroccipital process of opisthotic
pr	prearticular
prf	prefrontal
prfp	prefrontal pillar/descending process
pt	pterygoid
q	quadrate
qf	quadrate foramen
qj	quadratojugal
r	ridge
rt	replacement tooth
ru	rugose ridge along dorsolateral edge of skull
s	midline symphyseal surface
sa	surangular
so	supraoccipital
sof	suborbital fenestra
sp	splenial
sq	squamosal
sqp	posterior process of squamosal
sr	sagittal ridge
tu	tubercle
utf	upper temporal fenestra
utfo	fossa bordering utf
v	vomer
?	uncertain identification

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