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STEREOSPONDYL AMPHIBIANS FROM THE ELLIOT FORMATION OF SOUTH AFRICA

by

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ABSTRACT

This paper documents the first members of the Chigutisauridae (Amphibia, Stereospondyli) from southern Africa and the first post-Triassic stereospondyls from that region. The material, from the Lower and Upper Elliot Formation, was associated with a diverse fauna including early mammals and dinosaurs. Most temnospondyls known to have survived the Triassic are brachyopoids, with large members of the Chigutisauridae present in the Jurassic and Cretaceous of Gondwana, and smaller members of the Brachyopidae in the Jurassic of Eurasia.

KEYWORDS: Jurassic, Chigutisauridae, Gondwana, Elliot Formation, Stereospondyli

INTRODUCTION

Well documented post-Triassic stereospondyl amphibian remains were first described from the Jurassic of Australia (Warren & Hutchinson 1983), to be followed by several reports from Eurasia (Dong 1985; Nessov 1988; Shishkin 1991; Buffetaut *et al.* 1994), and an Early Cretaceous stereospondyl from Australia (Warren *et al.* 1997). All except one (Warren *et al.* 1998) of the described Jurassic and Cretaceous stereospondyls apparently belong to the Brachyopoidea (Brachyopidae and Chigutisauridae) with the Australian taxa, *Siderops kehli* (Warren & Hutchinson 1983) and *Koolasuchus cleelandi* (Warren *et al.* 1997) identified as Chigutisauridae and the Chinese *Sinobrachyops placenticephalus* (Dong 1985), Mongolian *Gobiops desertus* (Shishkin 1991) and Russian *Ferganobatrachus riabinini* (Nessov 1988, Shishkin 1991) as Brachyopidae. Other fragmentary post-Triassic stereospondyl material has been reported from both geographical areas and a full list of these occurrences was presented in Warren *et al.* (1997). The Chigutisauridae is a Gondwanan taxon, appearing first in the earliest Triassic Arcadia Formation of Australia (Warren 1981), with later representatives in the Late Triassic of Argentina (Rusconi 1949, 1951; Marsicano 1999) and India (Sengupta 1995), while the Brachyopidae were cosmopolitan in distribution with a centre of diversity in Australia. Only two post-Triassic Gondwanan stereospondyls have been recorded apart from the Australian specimens. One is a report of brachyopids from the Upper Elliot Formation of South Africa (Kitching & Raath 1984), while the other is a fragmentary mandibular ramus from the Late Triassic or Early Jurassic of Ethiopia, which alone among late surviving stereospondyls appears not to be brachyopoid (Warren *et al.* 1998). In a list of material from the Elliot Formation, Kitching and Raath (1984) included a total of ten amphibian records, those from the Upper Elliot being listed as brachyopids while those from the Lower Elliot were listed as capitosaurids. During a visit to the Bernard Price Institute for Palaeontology in 1998, the senior author examined all of the Elliot Formation stereospondyl material housed in their collections and identified the available specimens (some had been field identifications only and the material was not collected). All of this material was collected by Kitching and Raath during a field trip in 1982, or by Kitching in field trips in the 1970s and 1980s. The present paper is a description of the better preserved specimens. While all the material described is fragmentary, we have attempted to place it taxonomically because of the importance of documenting which higher taxa of stereospondyls survived beyond the Triassic.

AGE OF THE ELLIOT FORMATION

The Elliot Formation of the Karoo Basin of southern Africa is divided into two biostratigraphical units. The lower unit corresponds to the Lower Elliot Formation and was placed in the *Euskelosaurus* Range Zone in the biozonation scheme proposed by Kitching and Raath (1984). This unit is now thought to be a coeval, distal equivalent of the upper part of the Molteno Formation (Cairncross *et al.* 1995; Anderson *et al.* 1998). Based largely on tetrapod data, the Lower Elliot Formation has traditionally been assigned a Late Triassic (Carnian) age (eg. Olsen & Galton 1984; Gauffre 1993; Anderson *et al.* 1998). This is supported by the presence of a characteristically Triassic *Dicroidium* flora associated with the Lower Elliot Formation (Ellenberger 1972). An unconformity, represented by a distinct palaeosol horizon (Kitching & Raath 1984), separates the Lower Elliot Formation from the Middle and Upper Elliot Formation.

The Middle and Upper Elliot Formation was placed in the *Massospondylus* Range Zone by Kitching and Raath (1984), along with the lower part of the overlying

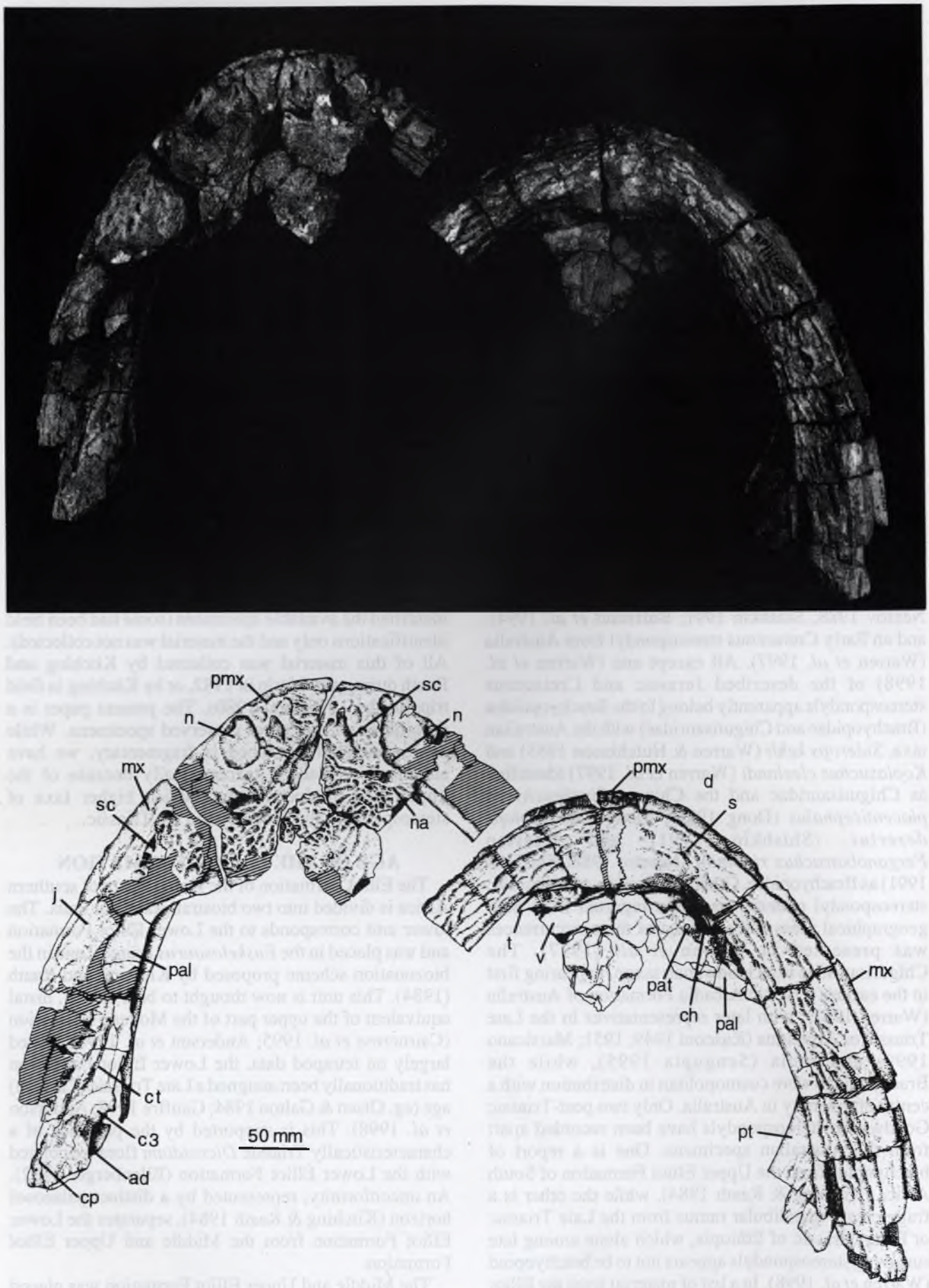


Figure 1. BP/1/5092. Photographs (upper) and drawings (lower) of part of the skull and associated mandible in dorsal (left) and ventral (right) views. Cross hatching indicates broken bone.

Clarens Formation. Based again on tetrapod and floral data (Ellenberger 1972; Olsen & Galton 1984; Anderson *et al.* 1998) the Middle and Upper Elliot Formation has traditionally been assigned an Early Jurassic age. The presence of chigutisaurid temnospondyls in both the Lower and Upper Elliot Formation is not at odds with the presumed ages of both of these faunas, since chigutisaurids occur elsewhere in the Late Triassic of India and Argentina and the Early Jurassic and Cretaceous of Australia (Warren *et al.* 1997).

DIAGNOSES OF HIGHER TAXA

Diagnoses of the Brachyopoidea, Brachyopidae and Chigutisauridae are given below, but in material described in the present paper many of the diagnostic characters were not preserved. It was therefore necessary in most instances to use primitive characters, skull outlines, and differential diagnoses in our taxonomic determinations.

Brachyopoidea Broom 1915

Sensory sulci deeply incised between nostrils and orbits; rounded, stalked exoccipital condyles; ascending ramus of the pterygoid arises from the dorsal surface of the pterygoid as a gently concave lamina; dentition present on the middle and posterior coronoids; postglenoid area (PGA) of the mandible slender and elongated; quadrate rami of the pterygoids strongly downturned forming a U-shaped palate; prearticular extending posterior to the glenoid fossa, covering the medial face of the articular on the PGA; absence of the mandibular sensory sulcus on the labial surface of the PGA; quadrate condyles with two parts of subequal size; atlas elongate; absence of an anterior flange on the dorsal process of the clavicle; width of pectoral girdle considerably less than skull width.

Chigutisauridae Rusconi 1949

Strongly horizontally recurved ascending ramus of the pterygoid; presence of a substapedial ridge on the pterygoid; width of interpterygoid pair less than 90% of the length; posterior meckelian foramen bordered by the prearticular and postsplenial exclusively.

Brachyopidae Broom 1915

Ascending ramus of the pterygoid gently concave and posteriorly recurved in vertical section; absence of a column on the ascending ramus of the pterygoid; posttemporal fenestra as wide as deep; maximum width of the interpterygoid vacuity pair greater than 90% of their length; reduced tooth row on palatines and ectopterygoids; absence of otic notch and tabular horns; postglenoid area of the mandible very elongate and slender; lack of a chordatympanic foramen of the mandible; articular below the level of the dentary tooth row; prearticular process of the mandible absent; rod-like dorsal process of the clavicle slopes posteriorly from its base.

LOWER ELLIOT FORMATION MATERIAL

TEMNOSPONDYLI Zittel 1888
STEREOSPONDYLI *sensu* Yates & Warren, in press
BRACHYOPOIDEA Broom 1915
CHIGUTISAURIDAE Rusconi 1949

BP/1/5252

Material

Partial left and right mandibular rami with some attached and some unattached cranial material. The cranial material includes the left lateral portion of the occiput and part of the posterior end of the palate including a probable exoccipital condyle. A large quantity of fragmentary cranial and mandibular material is associated with this specimen.

Locality

Farm Hollywood (Paardeverlies), Lady Grey District, Eastern Cape, South Africa.

Description

Skull. Cranial material preserved carries coarse ornament similar to that in the other Elliot Formation specimens and includes part of the left and right premaxillae and vomers in articulation with the mandible. Incised into the premaxillae are small parts of the margins of the external nostrils. An anterior palatal vacuity is either absent or very small.

A probable exoccipital condyle is present but is unusual in that it appears to be composed of three superimposed bones. The occipital parts of the squamosal and quadratojugal, which form the characteristic brachyopoid squamosal-quadratojugal trough, are preserved. Small marginal teeth on the premaxillae contrast markedly with a large vomerine tusk (20 mm at the base) and enlarged teeth (15 mm) on the transvomerine tooth row. These transvomerine teeth are attached to a raised area of the vomer as they are in *Siderops* and BP/1/5092.

Mandible. In transverse section the anterolateral parts of the mandible are flattened and of similar transverse section to the equivalent areas in BP/1/5092. The two specimens differ in that the mandibular symphysis is shorter anteroposteriorly in BP/1/5252. An anterior coronoid (C1) bone is preserved and is toothless.

Dentition. Those dentary teeth preserved are a little larger than in BP/1/5092 (10-15 mm at the base) and rounded in section. The vomerine tusks are of a similar size to the dentary teeth.

Taxonomic conclusions

This specimen has a parabolic skull outline, dentary teeth larger than the maxillary teeth, and a squamosal-quadratojugal trough, characteristics not present in the Capitosauridae but found in the Brachyopoidea. Within the Brachyopoidea the specimen is most likely to belong

to the Chigutisauridae because it is extremely similar to the other chigutisaurids described in this paper, but distinguishing characteristics were not preserved.

BP/1/4750

Material

A collection of fragmentary cranial and postcranial material, most of which is too weathered for identification.

Locality

Farm Friesland West, Bethlehem District, Free State, South Africa.

Description

Two segments of skull margin with both marginal and inner tooth rows preserved, an exoccipital condyle and a large number of associated fragments were collected. On the cranial fragments the inner tooth row contains larger teeth than the maxillary row, and an ectopterygoid tusk is present, both conditions not characteristic of capitosaurids. The continuous inner tooth row is not found in the Brachyopidae but is present in the Chigutisauridae.

Taxonomic conclusions

The material is most likely to be chigutisaurid.

TEMNOSPONDYLI Zittel 1888
STEREOSPONDYLI *sensu* Yates and Warren, in press

BP/1/4935

Material

A single fragment of lower jaw ramus.

Locality

Farm Mequatling, Clocolan District, Free State, South Africa.

Description

This single fragment of mandibular ramus is of interest for the presence of two small foramina in its lingual surface. It is not determinable beyond Stereospondyli, in which it can be placed through the presence of coarse ornament on the labial surface.

Taxonomic conclusions

Stereospondyli indet.

UPPER ELLIOT FORMATION MATERIAL

TEMNOSPONDYLI Zittel 1888
STEREOSPONDYLI *sensu* Yates & Warren, in press
BRACHYOPOIDEA Broom 1915
CHIGUTISAURIDAE Rusconi 1949

BP/1/5092

cf. *Siderops* sp. Warren & Hutchinson 1983

Material

A partial skull and attached mandibular rami. Preserved are the anterior half of a left mandibular ramus and the anterior quarter of a right ramus, with the skull margins attached to them. The skull includes part of the left orbit, both external nostrils, and part of the maxilla on both sides. Although the margins of the palate are obscured by the attached mandible, some detail of the palate adjacent to the interpterygoid vacuities is preserved and includes the tusk pairs from vomers, palatines and ectopterygoids.

Locality

Farm Vastrap, Ladybrand District, Free State, South Africa. The specimen came from a playa lake deposit which also yielded almost complete lungfish remains and an abundance of conchostracans.

Description

Skull roof (Figures 1, 2). Preserved is the most anterior part of the skull roof, with a complete left naris and the inner margin of the right naris, the left hand margin of the maxilla and part of the jugal including some lateral orbital margin, and the palate underlying these marginal parts of the skull. The reticulate ornament is relatively fine, especially on the nasal bones, but the remnants of the sensory canal system are broad and deeply impressed. An almost circular left naris is placed far laterally on the skull roof and is farther from the right naris than is typical of chigutisaurids. Most sutures cannot be discerned.

Palate (Figures 1, 2). While much of the palate preserved is obscured by the attached mandible, some of its structure is visible. No trace of an anterior palatal fenestra is evident, but posterior to its expected position



Figure 2. Outline of a chigutisaurid skull with those parts of the skull roof preserved in BP/1/5092 indicated in black.

one transvomerine tooth and a replacement pit are preserved. The left choana is sub-circular and flanked by paired vomerine and palatine tusks, with a few smaller parachoanal teeth on the medial border. A few large palatine and ectopterygoid teeth are present, as is a replacement pit for the ectopterygoid tusk. An isolated portion of the right ectopterygoid, palatine and attached maxilla retains a palatine tusk and replacement pit, an enlarged tooth on the ectopterygoid which might be a tusk, other ectopterygoid teeth and smaller maxillary teeth. Of interest is the presence of a suture running almost parallel to the margin of the interpterygoid vacuity. This must be a suture between a posterior process of the palatine and the ectopterygoid and indicates that the ectopterygoid may be excluded from the margin of the interpterygoid vacuity by a suture between the palatine and the pterygoid. Although almost the entire lateral margin of the right interpterygoid vacuity is preserved, no sutures are determinable. A portion of the left palatine ramus of the pterygoid remains, from which the position of the body of the pterygoid, and hence the approximate size of the skull, could be estimated.

Palatal dentition. All well-preserved teeth of both the skull and mandible are strongly keeled as in the Australian chigutisaurids *Siderops kehli* and *Koolasuchus cleelandi*, and slightly curved lingually towards the tip. In contrast to the situation in *Siderops*, none are serrated. The larger teeth of the mandible are markedly larger (20 mm by 10 mm at the base) than the largest teeth on the maxilla (9 mm by 4 mm). The dentary tusk is 20 mm in diameter while the vomerine tusks are rounded and an estimated 15 mm in diameter. Marginal teeth on the premaxillae and maxillae are of fairly uniform small size with a slight decrease towards the posterior end of the maxilla. Transvomerine and parachoanal teeth are a little larger than the maxillary teeth. Where teeth can be seen in transverse section near the base, labyrinthine infolds having secondary folds (Warren & Davey 1992) are present, with greater complexity in the larger teeth.

Mandible. The mandible is preserved in part, from the symphysis to the level of the adductor fossa, just below the coronoid process. It is markedly flattened dorso-ventrally and is a little anteroposteriorly expanded in the region of the symphysis. Few sutures are discernible. The anterodorsal margin of the adductor fossa is preserved and appears similar to the area in *Koolasuchus*. Just anterior and dorsal to the fossa, a row of coronoid teeth is carried by a ridge on coronoid three.

Mandibular dentition. In common with most brachyopoids, the marginal teeth of the mandible are smaller anterior to the symphyseal area, but increase in size for most of the length of the dentary to decrease in size again near the end of the dentary tooth row. An irregular row of smaller teeth is present on the posterior coronoid (C3), but the presence or absence of dentition on coronoids one and two cannot be determined. Although the area of the symphyseal tusks is obscured by the attached skull roof, one can be seen in transverse section in a break close to the symphysis. Posterior to the tusk a small pit may indicate the presence of a postsymphyseal row of teeth such as was present in *Siderops* and *Pelorocephalus* (Marsicano 1999) but not *Koolasuchus* (Warren *et al.* 1997) or *Compsocerops* (Sengupta 1995).

Taxonomic conclusions

Most characters used in the diagnosis of Brachyopoidea above are not determinable. However, this specimen is clearly a member of the Brachyopoidea through its short, broad and parabolic skull with rounded nares placed close to the anterior margin of the skull. The orbits are situated close to the nares and the sensory canal system is deeply-impressed in this area. Within the Brachyopoidea the specimen belongs to the Chigutisauridae, rather than the Brachyopidae, through the presence of a continuous tooth row between the tusks on the vomers, palatines and ectopterygoids. Its placement within the Chigutisauridae is more tenuous and we place it as cf. *Siderops* sp. until more complete material is available. Its assignment to *Siderops* is based on the presence of teeth on the posterior coronoid. These are absent in other members of the Chigutisauridae. In Figure 2 we have restored the posterior parts of the skull after *Siderops* and using the palatine ramus of the pterygoid as a guide to the position of the occiput. Unless the proportions of BP/1/5092 were quite different from those of *Siderops*, this should be fairly accurate. The resultant skull has orbits placed further posteriorly and nostrils more widely separated than in *Siderops*.

BP/1/5111

Material

Weathered large fragments of skull with attached mandible, weathered neural arches in articulation with centra, a fragment of interclavicle and detached partial ribs.

Locality

Broken Slopes, an annex of the farm Vastrap, Ladybrand District, Free State, South Africa.

Description

Skull. A part of the quadratojugal, occipital part of the squamosal, quadrate and pterygoid are preserved in articulation with the posterior part of the left mandibular ramus. Also present is a part of the basis cranii with parts of the exoccipital, pterygoid and parasphenoid. The quadratojugal is present at the posterolateral margin of the skull but is broken posteriorly so that the presence or absence of the chigutisaurid postquadratojugal process cannot be determined. On the left of the occipital surface parts of the quadratojugal and squamosal bones forming the squamosal-quadratojugal trough are preserved but are

positioned a little anterior to the ventral part of the quadrate with the attached quadrate ramus of the pterygoid. The quadrate may have overlain part of the squamosal-quadratojugal trough.

Mandible (Figures 3, 4). The posterior part of the left ramus is preserved in articulation with the skull, as well as a second section of the left ramus from just anterior to it. The posterior end of the mandible behind the articulation (the postglenoid area) is broken off but in section shows the subcircular cross section characteristic of brachyopoids. A suture running anteroposteriorly along the lingual surface separates the prearticular (above) from the angular (below). In brachyopids the angular is barely exposed on the lingual surface of the mandible whereas in the chigutisaurids *Compsocerops cosgriffi* (Sengupta 1995) and all three species of *Pelorocephalus* (Marsicano 1999) a large angular exposure is present. Australian post-Triassic chigutisaurids were restored with a low angular exposure on the lingual side of the mandible but neither *Siderops kehli* nor *Koolasuchus cleelandi* were well preserved in that area, so in reality the suture could have been higher. A chordatympanic foramen, which is usually found in chigutisaurids but not brachyopids, is present on the lingual side of the ramus below the glenoid fossa. The ornamented angular extends along the ventral surface of both sections of ramus and continues beneath the postglenoid area. While most of the labial surface of the more posterior block is obscured by the quadratojugal, a little of the surangular is present below the glenoid fossa, and on the anterior block the surangular sutures with the posterior margin of the dentary. No teeth are preserved in BP/1/5111.

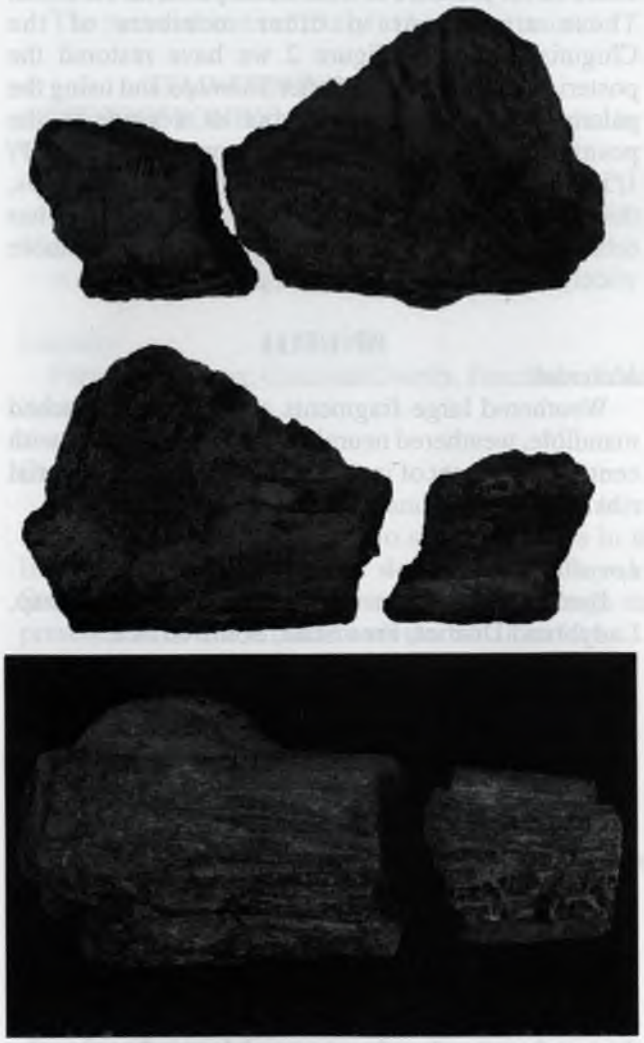


Figure 3. BP/1/5111. Photographs of the posterior part of the left mandibular ramus. Orientation as in Figure 4.

Vertebrae (Figure 5). A total of six neural arches and seven intercentra are preserved in three blocks. The neural arches are extremely abraded but appear to have been robust with stout transverse processes. Among the Chigutisauridae the intercentra are unusual in that they are notochordal, that is, the bone has grown around the sides and dorsal surface of the notochord, leaving a pit. They differ from other notochordal (stereospondylous) intercentra in that they are not circular in anterior or posterior view but are dorsoventrally flattened. In lateral view they have the same wedge-shaped outline as in other chigutisaurid intercentra. While notochordal centra are not normally associated with chigutisaurids and were not present in the Jurassic chigutisaurid *Siderops kehli* (Warren & Hutchinson 1983), notochordal as well as rhachitomous centra were found in the same deposits as the Cretaceous chigutisaurid *Koolasuchus cleelandi* (Warren *et al.* 1997). Sengupta (1995) described a 'pseudostereospondylous' centrum, in which the pleurocentra had fused to the crescentic intercentrum, associated with the Indian chigutisaurid *Compsocerops cosgriffi*, but this fusion is not the case in BP/1/5111.

Ribs. The five rib heads preserved are of varying size and all but one are from the pectoral region.

Interclavicle. The part of the interclavicle remaining is extremely weathered but preserves a small part of the articular area for the left clavicle.

Taxonomic conclusions

The presence of a squamosal-quadratojugal trough is characteristic of the Brachyopoidea. Morphologically, the posterior end of the left mandibular ramus resembles that of brachyopoids in that the postglenoid area is small and rounded in cross section, the angular extends a long way posteriorly on the ventral surface of the mandible, and the prearticular covers the posterodorsal face of the lingual surface so that the articular is not exposed lingually. The presence of a chordatympanic foramen in BP/1/ 5111 indicates that it is chigutisaurid rather than brachyopid.

BP/1/5406

Material

Fragments of skull and attached mandible, intercentrum, neural arch and a section of femoral shaft.

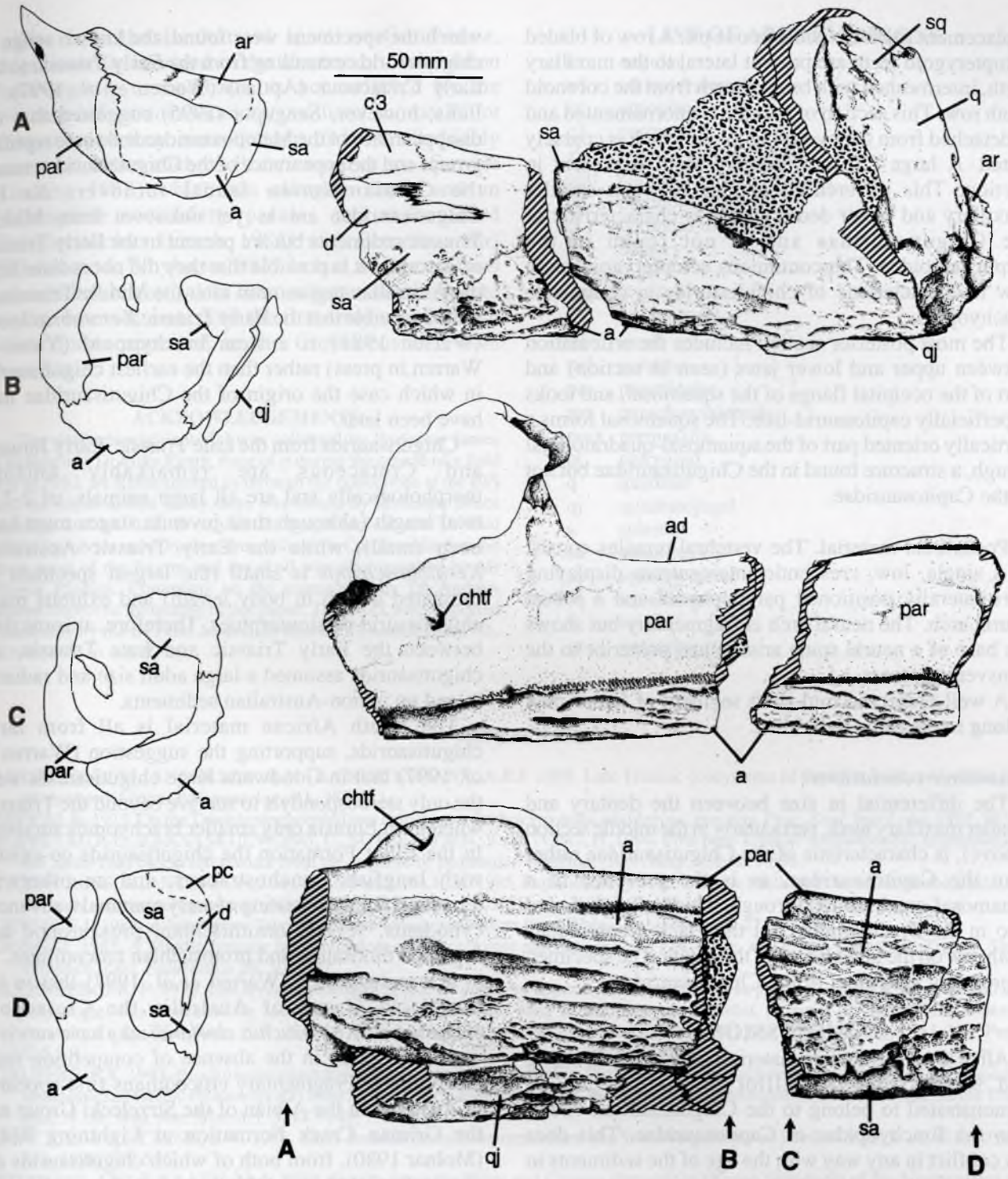


Figure 4. BP/1/5111. Drawings of posterior part of the left mandibular ramus and attached quadratojugal and quadrate, in labial (upper), lingual (middle) and ventral (lower) views. In the labial view anterior is to the left while in lingual and ventral views anterior is to the right. Transverse sections on the left are from the positions indicated (A-D) in the lower drawing, but each is drawn as if looking from behind the jaw. Cross-hatching represents broken bone while coquille hatching represents matrix.

Locality

Farm Vastrap, Ladybrand District, Free State, South Africa.

Description

Skull and mandible. Three pieces containing portions of the left mandibular ramus and cranium are from the region of the choana, towards the posterior end of the maxilla, and the posterior end of the skull. The more anterior piece has a row of four maxillary teeth with pitted ornament above them, a section of a large ?palatine tusk, and dentary teeth in section. The dentary teeth (25 mm in height) are slightly larger than the maxillary teeth (an estimated 22 mm).

The middle section has a maxillary row of ten tooth loci containing eight small (11 mm) teeth. In section a

replacement tooth is visible in one pit. A row of bladed ectopterygoid teeth are present lateral to the maxillary teeth, intermeshed with broken teeth from the coronoid tooth row. This section of maxilla is unornamented and is detached from the overlying jugal, which is coarsely pitted. A large (20 mm) dentary tooth is present in section. This differential in size between smaller maxillary and larger dentary teeth is characteristic of the Chigutisauridae and is not found in the Capitosauroidea. The continuous ectopterygoid tooth row is characteristic of chigutisaurids in contrast to brachyopids.

The most posterior section includes the articulation between upper and lower jaws (seen in section) and part of the occipital flange of the squamosal, and looks superficially capitosaurid-like. The squamosal forms a vertically oriented part of the squamosal-quadratojugal trough, a structure found in the Chigutisauridae but not in the Capitosauridae.

Postcranial material. The vertebral remains consist of a single, low, crescentic intercentrum displaying dorsolaterally positioned parapophyses and a robust neural arch. The neural arch is fragmentary but shows the base of a neural spine arising just posterior to the transverse process.

A well preserved mid-shaft segment of femur may belong to the same individual.

Taxonomic conclusions

The differential in size between the dentary and smaller maxillary teeth, particularly in the middle section (above), is characteristic of the Chigutisauridae rather than the Capitosauridae, as is the presence of a squamosal-quadratojugal trough. This trough is found also in the Brachyopidae but they lack a continuous tooth row on the inner bones of the palate. The specimen is probably a member of the Chigutisauridae.

DISCUSSION

All of the determinable material collected by Kitching and Raath from the Elliot Formation can be demonstrated to belong to the Chigutisauridae rather than the Brachyopidae or Capitosauridae. This does not conflict in any way with the age of the sediments in which the specimens were found, the known range of chigutisaurids extending from the Early Triassic to the Early Cretaceous (Aptian) (Warren *et al.* 1997). In India, however, Sengupta (1995) suggested that the disappearance of the Metoposauridae and some reptilian groups and the appearance of the Chigutisauridae marks the Carnian-Norian faunal turnover. As the Chigutisauridae are as yet unknown from Middle Triassic sediments but are present in the Early Triassic of Australia it is possible that they did not radiate from the Australian region until after the Middle Triassic. It is also possible that the Early Triassic *Keratobrachyops* (Warren 1981) is a stem brachyopoid (Yates & Warren,in press) rather than the earliest chigutisaurid, in which case the origin of the Chigutisauridae may have been later.

Chigutisaurids from the Late Triassic, Early Jurassic and Cretaceous are remarkably uniform morphologically and are all large animals, of 2-3 m total length (although their juvenile stages must have been small), while the Early Triassic Australian *Keratobrachyops* is small (the largest specimen an estimated 40 cm in body length) and exhibits many chigutisaurid plesiomorphies. Therefore, at some time between the Early Triassic and Late Triassic, the chigutisaurids assumed a large adult size and radiated to end up in non-Australian sediments.

The South African material is all from large chigutisaurids, supporting the suggestion (Warren *et al.* 1997) that in Gondwana large chigutisaurids were the only stereospondyls to survive beyond the Triassic, whereas in Eurasia only smaller brachyopids survived. In the Elliot Formation the chigutisaurids co-existed with lungfish, conchostracans, and an otherwise terrestrial fauna consisting of early mammals, advanced cynodonts, several ornithischian, prosauropod and theropod dinosaurs, and protosuchian crocodilians.

It was suggested (Warren *et al.* 1997) that in the Strzelecki Group of Australia the Cretaceous chigutisaurid *Koolasuchus cleelandi* may have survived until the Aptian in the absence of competition from crocodilians. Fragmentary crocodilians first appeared in Australia in the Albian of the Strzelecki Group and the Griman Creek Formation at Lightning Ridge (Molnar 1980), from both of which chigutisaurids are absent. It might be said that no potential crocodile rich strata are present in Australia prior to the Aptian. Nevertheless at least some strata with tetrapods are known in the Early and Middle Jurassic of Australia although they are not abundant. For instance, in the Early Jurassic Evergreen Formation, the chigutisaurid *Siderops* was associated with freshwater plesiosaurs (Thulborn & Warren 1980), while the Middle Jurassic Injune Creek Beds of southern Queensland have yielded remains of the sauropod *Rhoetosaurus brownei* (Longman 1926). In addition, Middle Jurassic theropod dinosaurs and a plesiosaur are known from the Colalura Sandstone of Western Australia (Long & Molnar 1998).

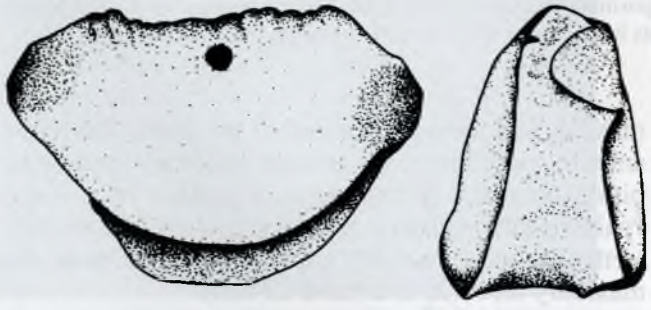


Figure 5. BP/1/5111. Intercentrum in posterior (left) and left lateral views (right).

The hypothesis that, at least in Gondwana, chigutisaurids survived in the absence of competition from aquatic crocodilians, is not nullified by the presence of protosuchian crocodilians in the Elliot Formation as they were thought to be small, highly terrestrial forms such as *Pedeticosaurus* sp. (Gow & Kitching 1988) which has elongate limbs and an incomplete secondary palate, and the related *Terrestrisuchus* (Crush 1984) and *Lesothosuchus* (Whetstone & Whybrow 1983). In fact, all crocodilians were either terrestrial or semi-aquatic but linked to marine environments until the first semi-aquatic fresh water forms appeared in the Cretaceous of North America.

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LIST OF ABBREVIATIONS

a	angular
ad	adductor fossal
ar	articular
c3	coronoid 3
ch	medial wall of choana
chtf	chordatympanic foramen
cp	coronoid process
ct	coronoid tooth row
d	dentary
j	jugal
mx	maxilla
n	external naris
na	nasal
pal	palatine
par	prearticular
pat	parachoanal teeth
pmx	premaxilla
pt	pterygoid
q	quadrate
qj	quadratojugal
s	splenial
sa	surangular
sc	sensory canal
sq	squamosal
v	vomer
vt	vomerine tusk

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