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# OLDEST KNOWN STEREOSPONDYLOUS AMPHIBIAN FROM THE EARLY PERMIAN OF NAMIBIA

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ABSTRACT—New temnospondyl material is described on the basis of cranial and postcranial remains from the Gai-As Formation of the Huab Basin, Namibia. An Early Permian age is indicated by U/Pb SHRIMP dating of zircons from fallout tuff beds occurring immediately above the temnospondyl remains. This material represents the oldest known amphibian with stereospondylous vertebrae and has implications for temnospondyl evolution, biogeography and Permo–Triassic Gondwanan basin development models.

## INTRODUCTION

A new fossil discovery from the Early Permian of the Huab Basin in northwest Namibia is the oldest known amphibian with stereospondylous vertebrae. The age is constrained by new U/Pb SHRIMP dating of zircon separates from interbedded fallout tuff beds. Although the fossil material is fragmentary it is of great significance for biogeographic and basin development models. Previously the stratigraphic framework and timing of the host Huab Basin was poorly constrained due to paucity of fossil material. The Huab Basin developed during one of several rifting events between Africa and South America, progressing to an ultimate Early Cretaceous rifting resulting in South Atlantic oceanic onset. Huab basin-fill was identified as a red bed sequence containing the Gai-As Formation (Ledendecker, 1992), separated by a significant hiatus (Stanistreet and Stollhofen, 1999) from an underlying Early Permian sequence. At the top of the underlying stratigraphy is the marine Whitehill Formation (Oelofsen, 1981) and its shallow water counterpart, the Huab Formation. After Whitehill deposition the Huab Basin became more restricted with the rejuvenation of northerly trending marginal rift faults, resulting in the more closely confined lacustrine-mud deposition of the the Gai-As Formation. Fault scarp emergence caused progradation of sand and gravel dominated alluvial fans off the marginal faults into the lake depository to gradationally overlie the muds. Fan-delta deposits are defined as the Doros Formation (Stanistreet and Stollhofen, 1999; Stollhofen et al., 2000), preferentially preserved in hangingwall areas of major northerly trending syn-sedimentary extensional fault systems. Both the Gai-As and Doros Formations are truncated by an unconformity overlain by an Early Cretaceous sequence, incorporating Twyfelfontein Formation, chiefly aeolian sandstones and flood basalts of the Etendeka Group, which heralded the ultimate spreading of the South Atlantic Ocean.

To date very few fossil tetrapod remains have been described from the Huab Basin, which has a basin-fill comprising stacked sequences dating from Carboniferous to Early Cretaceous (Fig. 1). Ledendecker (1992) illustrated some temnospondyl remains from the Tsarabis Formation and Horsthemke et al. (1990) mentioned the presence of coprolites and bone fragments of amphibians in the same depositional unit. Mesosaurid remains are documented from the Whitehill and Huab formations (Oelofsen, 1981; Horsthemke, 1992). Von Huene (1925) described an isolated tooth from the Doros Formation as *Archaeotherium reuningi*, but this specimen has been shown to be part of an amygdale (Hopson and Reif, 1981) derived from overlying basalts. The supposed presence of a dinosaur vertebra within the Gai-As to Doros Formation red beds (Keyser, 1973) also proved to be based on misinterpretations.

A recent collecting trip to a locality about 6 km north of Doros Crater (Fig. 2), displaying good exposures of the Permian of the Karoo Supergroup and Lower Cretaceous Twyfelfontein Formation, yielded several fossils. Calcareous concretions of the upper Huab Formation (Fig. 3) are overlain by a thick lacustrine succession of plane bedded, pink and maroon mudrocks of the Gai-As Formation, which coarsen upward to fine shoreface sandstones of the Doros Formation (Stollhofen et al., 2000). Fossils collected from the lowermost horizons of the Gai-As Formation at a locality north of Doros Crater (20°40.92′S/14°11.65′E) include an abundance of coprolites (some of them up to 30 mm in diameter) containing scales and teeth of paleoniscid fish (Bender, pers. comm.). Higher in the Gai-As Formation (20°40.958′S/14°11.579′E) is an abundance of fossil wood as well as fragmentary remains of paleoniscid fish scales. Within the uppermost Gai-As Formation, close to its transitional contact with the Doros Formation, several determinable amphibian bones were collected (20°40.906′S/14°11.630′E) 14 m below a conspicuous fallout tuff horizon, which provides our age control discussed later.

**Institutional Abbreviations—F**, Geological Survey of Namibia, Windhoek; **BP**, Bernard Price Institute for Palaeontological Research, Johannesburg.

## DESCRIPTION

The material (Figs. 4–6) is identifiable as amphibian and temnospondyl based on a combination of ornamented dermal bone, labyrinthine teeth, and temnospondyl vertebrae. Among temnospondyl amphibians, vertebral structure is of two main morphologies. In rhachitomous vertebrae, which are found in Palaeozoic and some Triassic temnospondyls, the centrum consists of a crescentic intercentrum and paired pleurocentra. Stereospondylous vertebrae arose within later members of the Me-

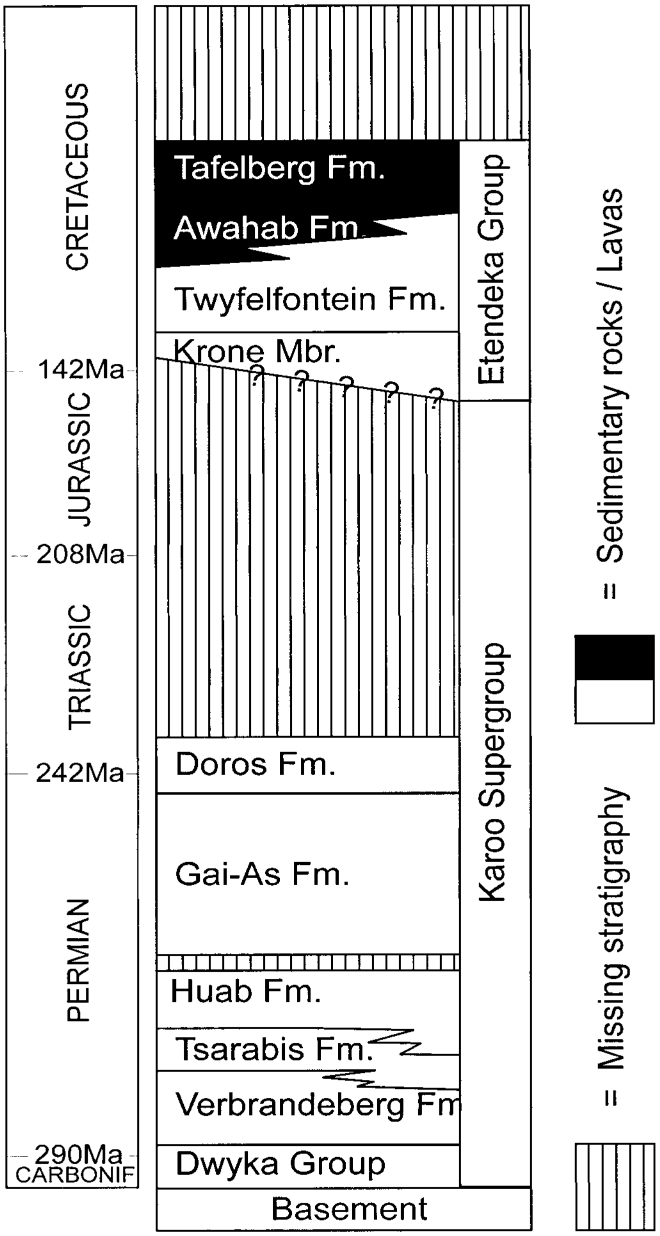

FIGURE 1. Simplified stratigraphic column of Huab basin stratigraphy.

sozoic radiation of temnospondyls (the Stereospondyli) and consist of spool-shaped intercentra and tiny, paired pleurocentra. Such vertebrae have not been described prior to the Middle Triassic.

Most of the amphibian material recovered from the Gai-As Formation is from the vertebral column and consists of 15 or more stereospondylous intercentra, a single partial crescentic intercentrum, neural arches, a pleurocentrum and ribs. Associated fragments of the skull include a well preserved exoccipital condyle, pieces of ornamented dermal bone, and four fragments bearing teeth.

### Vertebral Column

Some of the stereospondylous intercentra are preserved in articulation with their associated neural arches and ribs (Figs. 4, 5). In other instances a series of vertebrae are preserved in articulation and in these a gap is present between adjacent intercentra. There is some variation in size of the intercentra, from a transverse width of 50 mm to approximately 80 mm. Each intercentrum is unusually narrow in lateral view, has a small notochordal perforation positioned slightly dorsal of the midpoint of its anterior and posterior surfaces, and laterally shows a triangular area of finished bone extending from the base to a point near its posterodorsal surface. These intercentra are unlike the anteroposteriorly thickened centra of Metoposauridae and some Brachyopidae, resembling more the thinner, dorsally tapering intercentra that occur towards the anterior part of the vertebral column of more derived members of the Capitosauridae such as *Cyclotosaurus* (Milner et al., 1996). One much smaller, 34 mm diameter, stereospondylous intercentrum has a large notochordal perforation. The single crescentic intercentrum bears a rib facet close to its dorsal edge indicating that its probable position in the vertebral column was immediately presacral rather than caudal. Capitosaurids in which the more anterior intercentra are stereospondylous have crescentic intercentra in a more posterior position in the column. A single probable pleurocentrum was preserved in articulation between a transverse process and an intercentrum. Intercentra which appear stereospondylous through fusion between the intercentrum and the paired pleurocentra were described in the chigutisaurid *Compsocerops* (Sengupta, 1995), and in *Dvinosaurus* (Bystrow, 1938), a member of the Palaeozoic radiation of temnospondyls known as the Dvinosauria (Yates and Warren, 2000).

Each neural arch has well developed pre- and postzygapophyses and short transverse processes. The neural spines are robust, with the top of the spine having an unusually rounded outline in lateral view. No ribs are complete. In cross-section their shape varies from rounded to an elongate ellipse.

### Exoccipital Condyle

This fragment comprises most of the left exoccipital condyle and includes a small part of the parasphenoid. Anteromedially the condyle is unusually thick, indicating the presence of some ossified endocranium. The entire ventral surface of the condyle is scored by anteroposterior grooves, indicating an extensive overlapping suture with the parasphenoid, which must have underplated most of the condyle. Such underplating is found in the Trematosauridae and to a certain extent among the more derived Capitosauridae, but in the Metoposauridae the parasphenoid forms a wedge between the exoccipitals, which have a large exposure on the palate. In trematosaurids the condyles are almost completely underplated by the parasphenoid, which extends in a transverse line across the condyles to suture laterally with the pterygoids. Underplating is rare among the Brachyopidae, but slight underplating is present in one specimen (BP/1/4004 cf. *Batrachosuchus*) and in the Russian *Batrachosuchoides* (Shishkin, 1966). The Namibian condyle differs in that the parasphenoid appears to underplate the condyles medially, but retreats laterally to a presumed more anterolateral suture with the pterygoids. In known rhinesuchids the parasphenoid sutures with the exoccipital laterally, but medially an ossified basioccipital may be present which also sutures with the parasphenoid. Among known dvinosaurians the exocippitals are reduced and are linked by a large basioccipital ossification to form a single occipital condyle. Overall the affinity of the condyle from the Gai-As Formation appears to be with the Trematosauridae or with derived capitosaurids.

### Tooth-bearing Cranial Material

Two of the cranial fragments contain tusks. The larger has a partial tusk beside a semicircular depression which could be either the wall of a choana or anterior palatal vacuity, as found in most Capitosauridae, or the left wall of the left member of

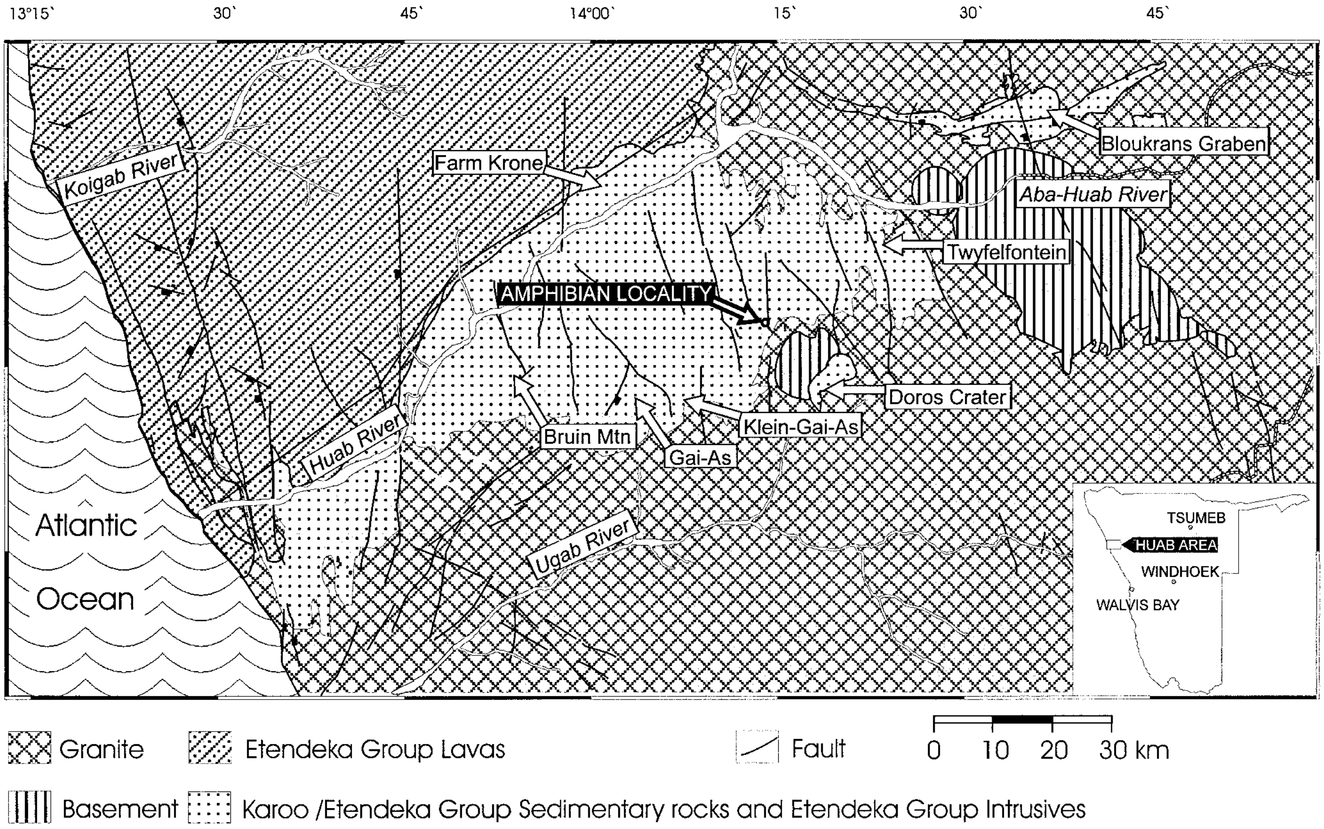

FIGURE 2. Geological map of the Huab and surrounding areas showing the amphibian fossil locality.

a pair of vacuities. The second fragment (Fig. 6) has a smaller tooth preserved beside the tusk and a small part of the wall of a vacuity which may be the choana, in which case the smaller tooth would be a part of the parachoanal tooth row and the tusk a palatine tusk. The tusk is unusual in that it is slightly compressed rather than circular around its base. A third cranial fragment consists of a partial tusk, while a fourth is a piece of maxilla with a series of eight tooth loci in which replacement pits alternate with strongly anteroposteriorly compressed teeth.

A feature common to all of the teeth and tusks of the Namibian specimen is their similar and unusual structure in transverse section (Fig. 6), suggesting that they belong to the same taxon. The parachoanal tooth was ground smooth at its base with carborundum powder, revealing an extremely simple pattern of infolding of the dentine. The dentine folds show no bending and are short, leaving a large central cavity. This is a pattern seen before only among the Rhytidosteidae, Plagiosauridae, and *Dvinosaurus* (Warren and Davey, 1992), but now known to be present also in the Rhinesuchidae. Teeth of other temnospondyl taxa differ in basal section in that the infoldings of dentine develop tight meanders, their complexity increasing with the size of the tooth and with proximity to the tooth base. Although other teeth of the Namibian specimen are broken above the base, their structure appears to be uniformly simple. A second unusual feature of their tooth histology is that dark dentine is present. This poorly understood phenomenon is found only among tetrapods and is common if not universal among anthracosaurs, but also appears among temnospondyls in *Eryops* and *Mastodonsaurus.* Dark dentine has not been found in any of the Rhinesuchidae.

## TAXONOMIC CONCLUSIONS

The material comes from a similar-sized, large temnospondyl and, as the components were found together, it is assumed that the fragments belong to the same individual. Among temnospondyl amphibians it probably belongs to the Stereospondyli, the temnospondyl clade which originated during the Late Permian and to which most Mesozoic temnospondyls belong (Yates and Warren, 2000). However, none of the previously described Permian members of the Stereospondyli have stereospondylous vertebrae, which were hitherto unknown before the Middle Triassic. A member of the predominantly Laurasian Dvinosauria has recently been found in the Early Triassic of South Africa (Warren, 1999), but its vertebrae are not stereospondylous. The structure of the stereospondylous intercentra suggests that the specimen is a derived capitosaurid from the Middle or Late Triassic, a conclusion supported by the structure of the exoccipital condyle. Similarly shaped intercentra have not been reported from the Permian or Early Triassic, although an intercentrum fused to pleurocentra has been described in *Dvinosaurus* from the Late Permian of Russia. In the teeth the simple infolding of the dentine is close to that of the Late Permian Rhinesuchidae, and to *Dvinosaurus,* but unlike that of the Capitosauridae which are complexly folded. Dark dentine has not been found in rhinesuchids. It is possible that the material belongs to a derived member of the Rhinesuchidae with stereospondylous intercentra, or to a previously undescribed clade of temnospondyls. In any case the stereospondylous intercentra of the Namibian specimen must have developed in parallel to those of Middle-Late Triassic stereospondyls.

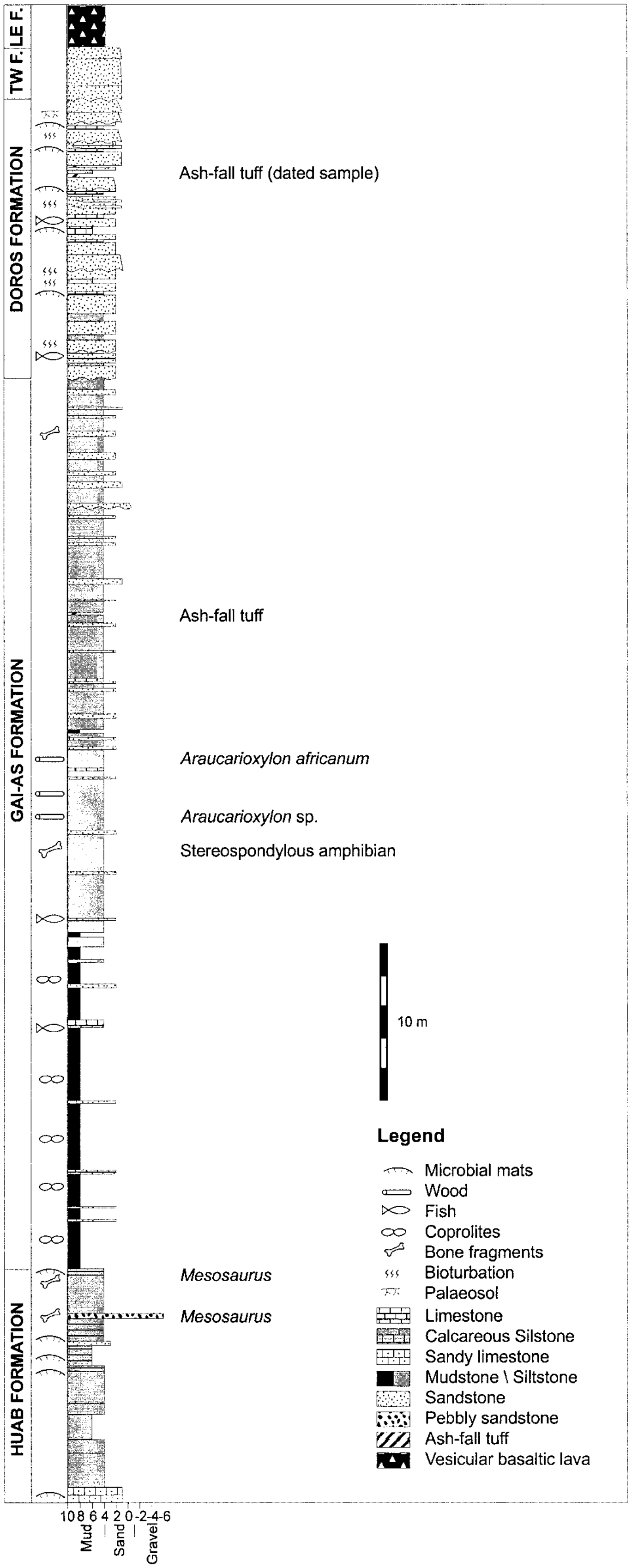

FIGURE 3. Stratigraphic column through the Huab, Gai-As and Doros formations within the eastern Huab area, showing the lithology and position of the amphibian find.

## PALEOENVIRONMENTAL SETTING

The fauna described from the Gai-As Formation so far comprises freshwater bivalves, fish remains and the temnospondyl described in this paper. The Gai-As Formation muds appear to have been deposited in a permanent lake (Stollhofen et al., 2000), which may have been occasionally stressed by higher salinity and alkalinity, promoting the formation of marginal algal mats now preserved as stromatolitic limestones, some of which have been dolomitised (Horsthemke, 1992). Stollhofen et al. (2000) describe how the lake system was confined by faulting, and how fan-deltas debouched into the lake from the marginal faults to develop the gravel and sand facies which prograde over the Gai-As lacustrine offshore and shoreface muds. The fault controlled fan-deltas and occasionally stressed permanent lake are reminiscent of characteristics described from modern intracontinental rift lakes of East Africa by Crossley (1984) and Vondra and Burggraf (1978).

## CHRONOSTRATIGRAPHIC CONSTRAINTS

The Huab Formation paraconformably underlies the Gai-As and Doros Formations and contains fossils of *Mesosaurus*, considered to be of Early Permian age (Oelofsen, 1981). Recent U/Pb SHRIMP dating of zircons from two of several fallout tuff beds in the Gai-As Formation 14 m above the stereospondyl find gave weighted mean values of 272±1.8 Ma and 265±2.5 Ma (Wanke, in prep.), both equivalent to late Early Permian (cf. Ross et al., 1994; Haq and Eysinga, 1998). In addition, the Gai-As Formation contains fossils of the bivalve *Leinzia similis* which is characteristic of the *Terraia altissima* biozone of the Brazilian Rio do Rasto Formation, considered to be of Late Permian age (Rohn, 1994; Stollhofen et al., 2000). Fossil wood from the Gai-As Formation suggests a Permian to Jurassic age (Bamford, 2000). In addition, the Doros and Gai-As formations at the locality Brandberg (Fig. 2) sit disconformably beneath arkosic sandstones and gravels correlatable with the Middle Omingonde Formation as defined by Holzförster et al. (1999). The latter formation is biostratigraphically equivalent to the *Cynognathus* Assemblage Zone, currently dated as late Early to Middle Triassic (Rubidge et al., 1995).

## CONCLUSIONS

The fact that the remains of a stereospondylous amphibian have now been recognised in rocks which have been dated as Early Permian considerably pushes back the age range of amphibians with such vertebrae. It also suggests that such vertebrae must be used with caution as indicators of a Middle–Late Triassic age. This has implications for our understanding of the biogeographic distribution of stereospondylous amphibians and is of significance for future modelling of Permo–Triassic Gondwanan basin developments and rifting that preceded and led to the opening of the southern South Atlantic.

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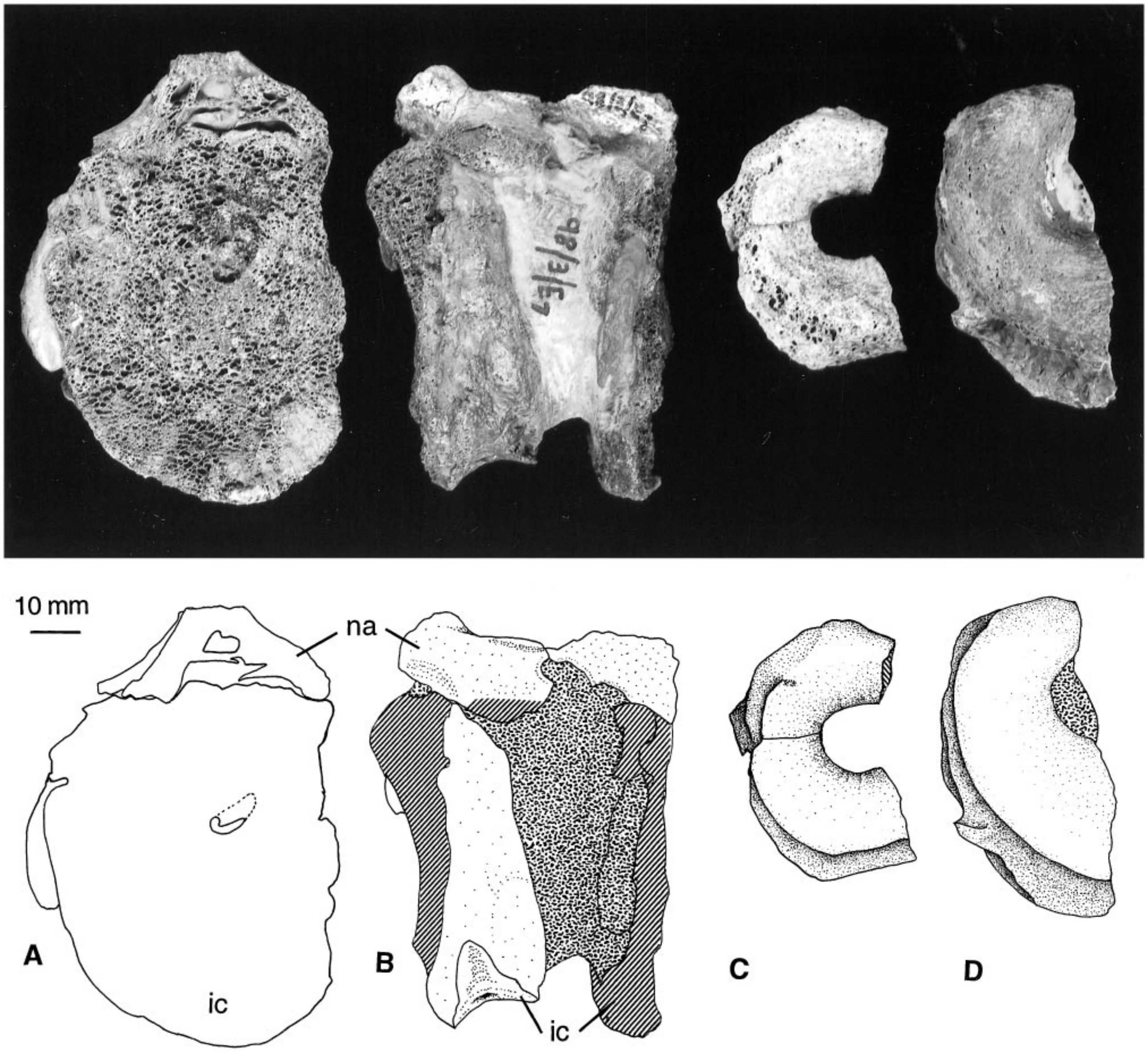

FIGURE 4. Stereospondylous intercentra (F 311) from the Gai-As Formation; upper, photographs; lower, drawings. **A**, **B**, two intercentra with attached neural arches in **A**, anterior and **B**, right lateral views; **C**, posterior view of isolated smaller stereospondylous intercentrum; **D**, posterior views of crescentic intercentrum. In the lateral views cross hatching indicates weathered or broken bone, while coquille shading indicates matrix. The bone in **A** is all weathered. **Abbreviations**: **na**, neural arch; **ic**, intercentrum.

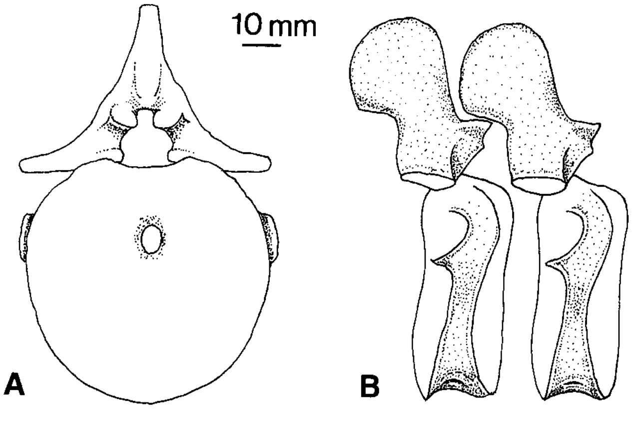

FIGURE 5. Composite reconstruction of adjacent stereospondylous vertebra from the Gai-As Formation. **A**, anterior view; **B**, right lateral view.

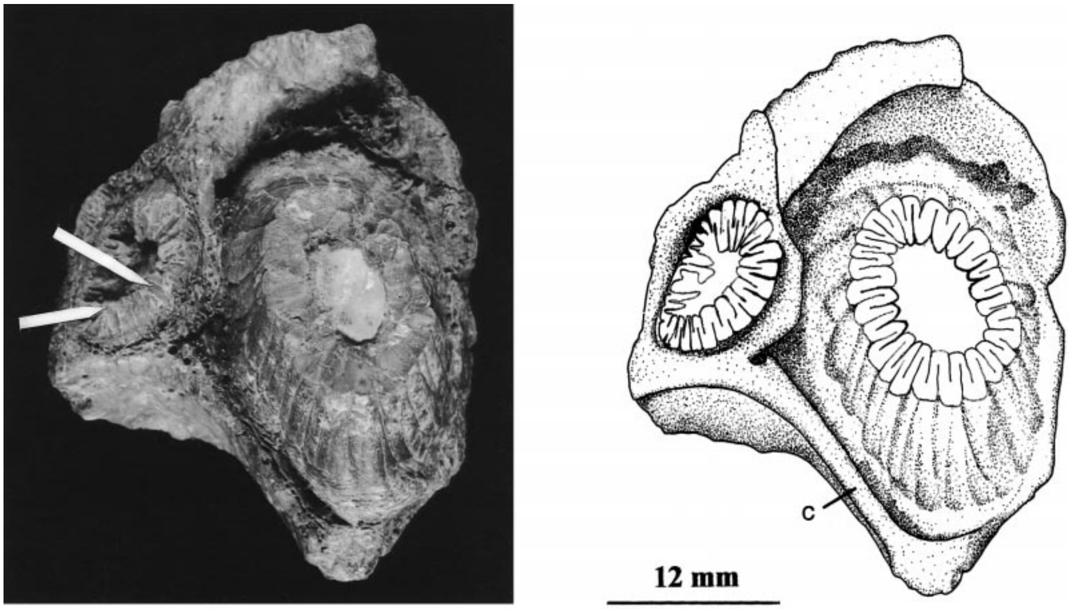

FIGURE 6. Photograph, left and drawing, right of part of? palatine bone (F 311) showing part of the choana and two teeth. The large tooth is assumed to be a palatine tusk and the smaller a component of the palatine tooth row. Note the simple dentine infolding within the teeth. The smaller tooth is sectioned near its base and more clearly shows the petal-like nature of the dark dentine indicated by arrows on the photograph. **Abbreviation**: **c**, border of choana.

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