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FIRST RECORD OF TRIASSIC RHYNCHOSAURIA (REPTILIA: DIAPSIDA) FROM THE LOWER ZAMBEZI VALLEY, ZIMBABWE

by

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ABSTRACT

True rhynchosaurids are described from Zimbabwe for the first time. The fossils occur as partially associated skeletons and scattered isolates in upward-fining, micaceous fluvial sandstones of the Pebbly Arkose Formation (late Triassic) in the Western Cabora Bassa Basin, Lower Zambezi Valley. On the grounds that the dentary of the Zimbabwean form possesses a row of small, conical lingual teeth in addition to a palisade row of penicillate teeth on the occlusal surface, it is concluded that the taxon present is *Hyperodapedon* sp., and that it is closely related to a rhynchosaurid described from Tanzania. One bone identified as a prosauropod dinosaurian femur was found associated with the Zimbabwean rhynchosaurids. The late Triassic age suggested by the presence of advanced rhynchosaurids is supported by the occurrence of the typical Triassic fossil plant genus *Dicroidium*, and by the general stratigraphy of the beds which contain the fossils (i.e. the fossil-bearing beds are underlain by beds of mid-Triassic age or younger, and are overlain by beds of latest Triassic or early Jurassic age).

INTRODUCTION

In the course of mapping by the second author in the Lower Zambezi Valley, Zimbabwe, over the past five years, fossils have been recovered from a number of new localities in the Dande Communal Lands situated between the southern valley escarpment and the vicinity of the main east-west access road along the valley floor (Figures 1,2; see also Oesterlen 1989: Figure 1). The sedimentary rocks exposed here vary in age from late Palaeozoic to early Mesozoic (Broderick 1984, 1989; Oesterlen, 1989).

One bone-bearing sample from beds mapped as Pebbly Arkose Formation was referred to the third author in 1988, who recognised amongst the material the characteristic tooth-studded maxillary dental plate of a rhynchosaur. Before this, no rhynchosaur material was known from Zimbabwe. Gow and Raath (1977) identified a few tiny jaw fragments recovered from a dinosaur-rich exposure of Forest Sandstone Formation (late Triassic-early Jurassic) in the Chitake River, some 60 km west of the study area, as belonging to "sphenodontid rhynchocephalians". However, modern opinion is that the term Rhynchocephalia should lapse, being too broad to be useful, and that there is "no close relationship between rhynchosaurs and sphenodontids" (Benton, 1985; he classifies sphenodontids as Lepidosauria along with the squamates).

The discoveries reported here therefore represent the first record of Rhynchosauria from Zimbabwe.

Because of the significance of these initial finds it was decided to follow up with a search for more specimens, in an attempt to identify the rhynchosaur taxa concerned and date the deposits. Accordingly, in May 1990 two of us (PMO and MAR) visited the area, which lies between the Manyame and Angwa rivers (Figures 1,2), and collected more rhynchosaurian material from Oesterlen's sites. One locality also yielded an isolated fragment of a dinosaurian femur, loosely associated with one of the rhynchosaur specimens.

PREVIOUS PALAEONTOLOGICAL WORK IN THE MID AND LOWER ZAMBEZI VALLEY

Previous fossil vertebrate finds in the Mid and Lower Zambezi Valley have consisted almost entirely of representatives of two faunas dominated by dinosaurs: an earlier one of terminal Karoo age (from the Forest Sandstone Formation - latest Triassic to early Jurassic), and a later one of Morrison age (late Jurassic) (Bond, 1965; Raath, Smith and Bond, 1970; Raath, 1977; Raath and McIntosh, 1987).

The terminal Karoo fauna is distinctive and ubiquitous, essentially identical or closely comparable faunas being known from southern Africa, Asia, Europe, and North and South America (Tucker and Benton, 1982; Olsen and Galton, 1984). The age of this fauna straddles the Triassic-Jurassic boundary (Olsen and Galton, 1984), and in South Africa, where it is especially well represented, it in turn comprises two readily recognised constituent faunal assemblages,

TABLE 1

Stratigraphy of the Karoo Supergroup and younger rocks in the Cabora Bassa and Mid-Zambezi Basin, Northern Zimbabwe

Era	Period	Group	Formations: Cabora Bassa Basin	Formations: Mid Zambezi Basin	South African Equivalents
Cenozoic	Quaternary Tertiary		Jesse Sands	Jesse Sands	
Mesozoic	Cretaceous		—?— —?— —?— —?— —?—		
	Jurassic		Dande Sandstone	Kadzi Beds Ntumbe Beds Chenje Beds	
	Triassic	Upper Karoo	Forest Sandstone	Batoka Basalt Forest Sandstone	Stormberg Group
			Pebbly Arkose (*rhynchosaur horizon)	Pebbly Arkose	
			Angwa Sandstone	Fine Red Marly Sandstone Ripple Marked Flags Escarpment Grit	
Palaeozoic	Permian Upper	Lower Karoo	Mkanga	Madumabisa Mudstone	Beaufort Group
			—?— —?— —?— —?— —?—		
	Permian Lower		—?— —?— —?— —?— —?— Kondo Pools	Upper Wankie Sandstone Black Shale and Coal Lower Wankie Sandstone	Ecca Group
	Upper Carboniferous			Glacial Beds	Dwyka Formation
Authorities			Oesterlen 1990, 1991	Bond 1967, Broderick 1990	

an earlier one and an apparently slightly younger successor. The earlier fauna is considered to be of late Triassic (pre-late Norian) age and is characterised by the presence of large euskelosaurid prosauropod dinosaurs and capitosaurid labyrinthodont amphibians. The later assemblage is considered early Jurassic (Liassic) in age and is characterised by abundant remains of the dinosaurs *Massospondylus* (prosauropod), *Syntarsus* (theropod), several taxa of fabrosaurid ornithischians, several taxa of advanced therapsids including abundant remains of the specialised herbivorous cynodont *Tritylodon* (in the northeastern parts of the Orange Free State, South Africa, they are often found concentrated in a well-marked acme zone), several taxa of protosuchid crocodilians, and rare occurrences of early morganucodontid mammals such as *Megazostrodon* and *Erythrotherium* (Kitching and Raath, 1984; Olsen and Galton, 1984). Kitching and Raath (1984) defined two successive biozones in the Elliot Formation of South Africa on the basis of these two faunas - the *Euskelosaurus* Range Zone below, and the *Massospondylus* Range Zone above.

A depauperate version of the Liassic *Massospondylus* Range Zone fauna, so far lacking any ornithischian

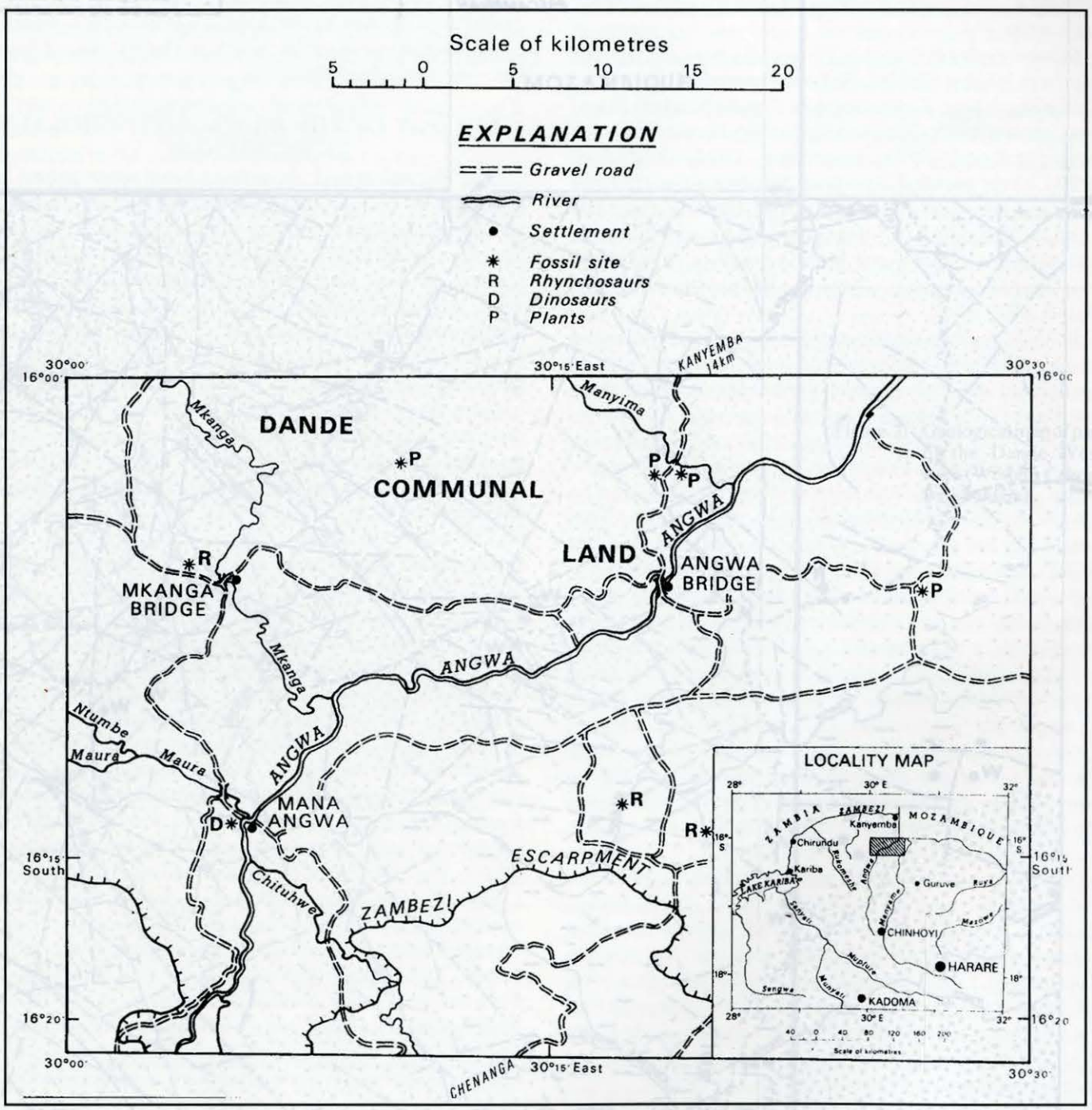

Figure 1: Location of rhynchosaur fossil sites.

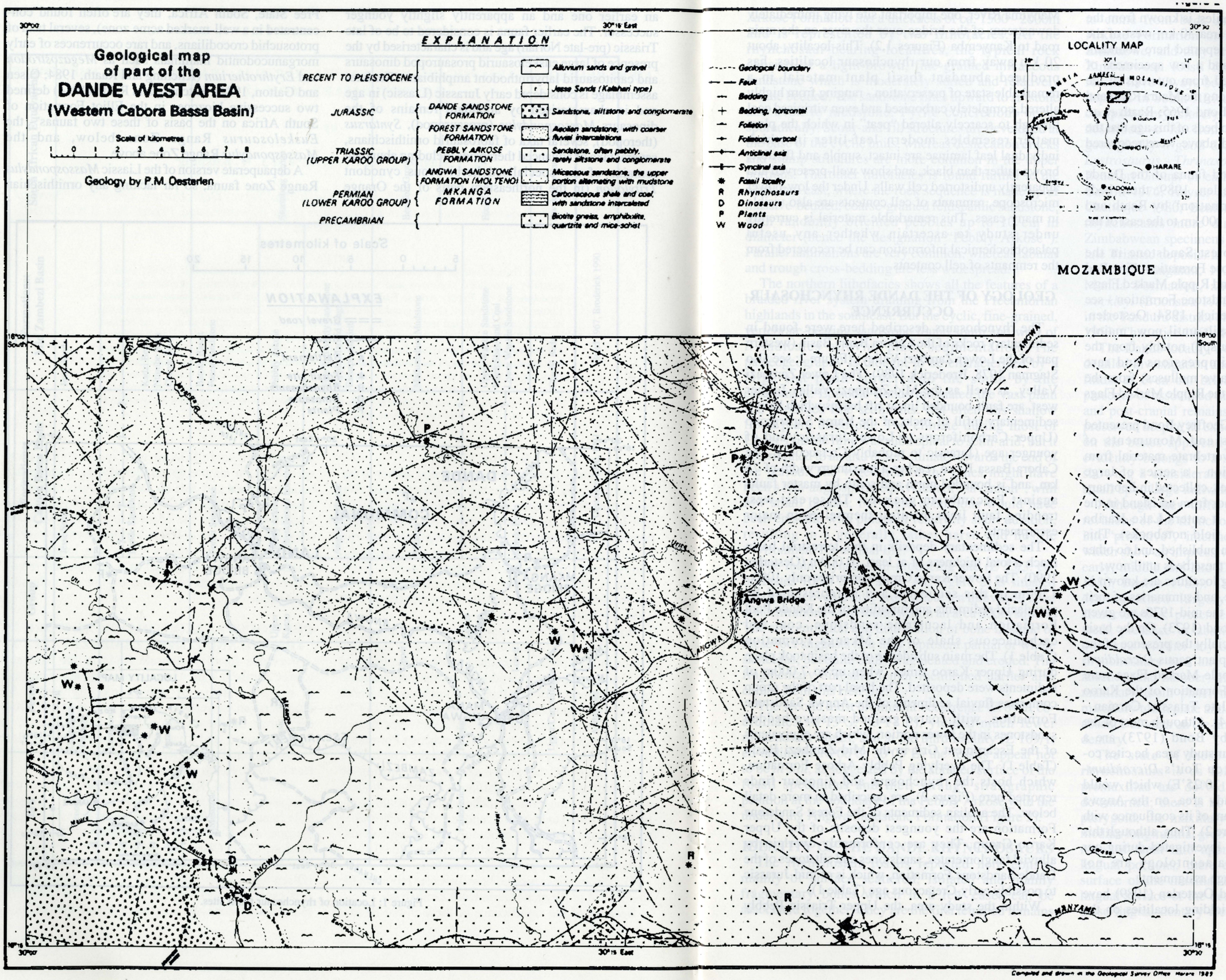

Figure 2: Geological map of part of the Dande West Area (Western Cabora Bassa Basin).

GEOLOGICAL MAP OF PART OF THE DANDE WEST AREA (WESTER CABORA BASSA BASIN)

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Figure 2

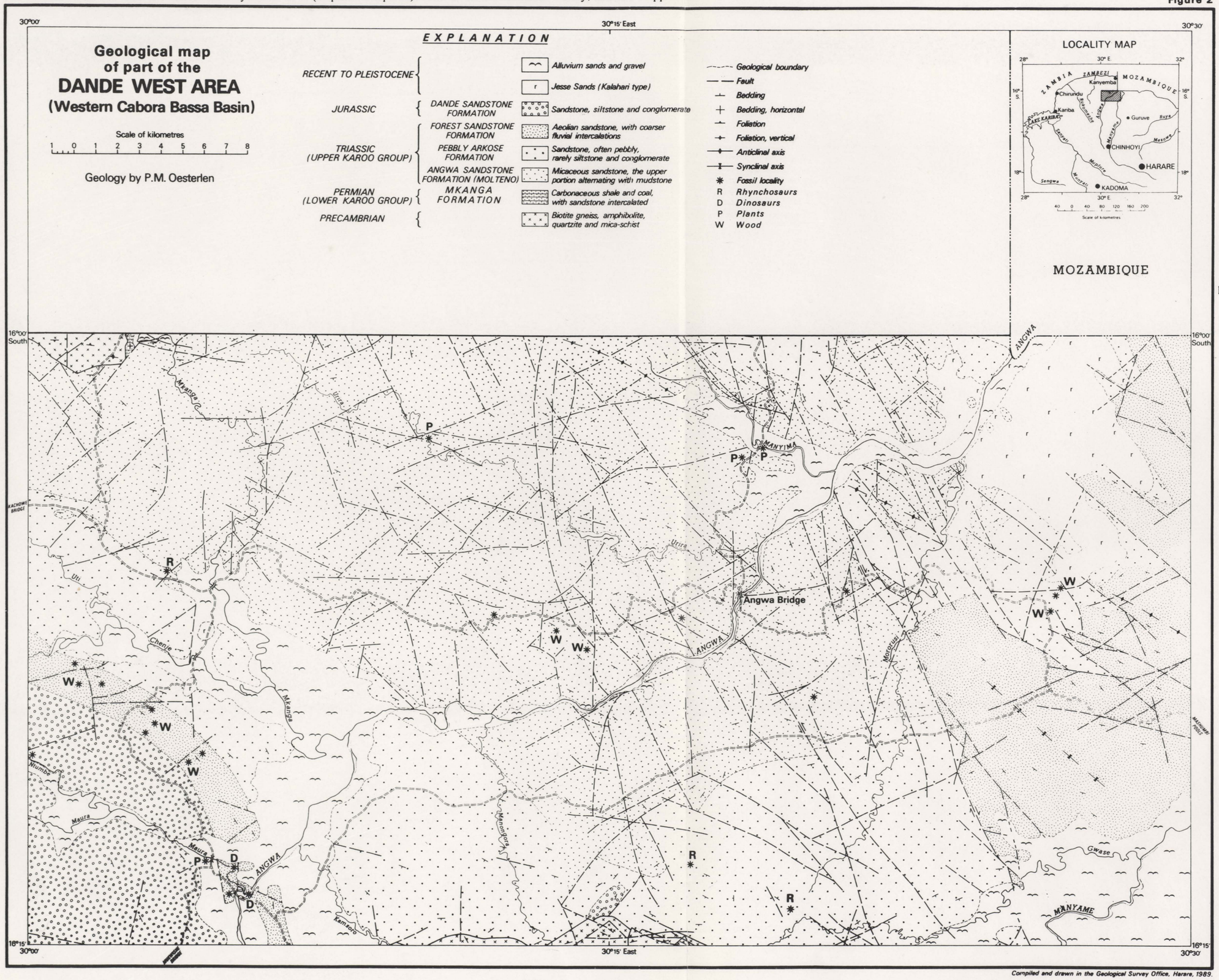

Figure 2: Geological map of part of the Dande West Area (Western Cabora Bassa Basin).

Compiled and drawn in the Geological Survey Office, Harare, 1989.

dinosaurs or mammal-like reptiles, is known from the general vicinity of our study area 30 km west of the rhynchosaur-producing sites reported here abundant remains of *Massospondylus* and a few specimens of *Syntarsus* have been recovered from outcrops of the Forest Sandstone Formation along the Maura River and its tributaries (Figures 1, 2) (Bond 1965; Raath *et al.* 1970; Raath 1977). It was from beds of this age that the sphenodontid jaws mentioned above were recovered from the Chitake River.

The later Jurassic sauropod fauna of the Dande Sandstone Formation (Oesterlen, 1989; these beds were termed the "Kadzi Formation" by Raath and McIntosh, 1987) occurs about 100 km to the east of the study area.

Strata underlying the Forest Sandstone in the Zambezi Valley (Pebbly Arkose Formation, Fine Red Marly Sandstone Formation and Ripple Marked Flags, now known as the Angwa Sandstone Formation - see Table 1; Bond, 1973; Broderick, 1984; Oesterlen, 1989) have yielded few fossils until now, mainly silicified logs (cf. *Dadoxylon* spp) notably from the Pebbly Arkose, and leaf impressions and rare invertebrates (freshwater bivalve molluscs) from the beds beneath, especially from the Ripple Marked Flags (Bond, 1973).

In 1974 the late Professor Geoffrey Bond presented to the National Museums and Monuments of Zimbabwe the only known vertebrate material from the Pebbly Arkose Formation - a series of large dipnoan (lung fish) tooth plates, collected in February of that year by Mr Frank Junor from an island in the Bumi River estuary where it enters Lake Kariba (16°51'S; 28°28'E) (Raath, field notebooks). This record has not previously been published, and no other vertebrates were known from these beds until now.

Several fossil plant-bearing localities are known in beds of this age in Zimbabwe, and summaries of their fossil content as known up to the mid-1970s are given in Lacey (1961, 1970) and Bond (1973). On the basis of the contained fossils, especially the presence of the characteristic Triassic fossil plant genus *Dicroidium*, Bond concluded that the Ripple Marked Flags were equivalents of the Molteno Formation of the Karoo Sequence in South Africa (late Triassic: Carnian - Anderson and Anderson, 1984). Although most of the Molteno localities listed by Bond (1973) are a considerable distance from our study area, he cites co-ordinates for one of A. L. du Toit's *Dicroidium*-yielding localities (16°01'S; 30°25'E) which would place it right within our study area, on the Angwa River about 11 km downstream of its confluence with the Manyima River (see Figure 2). Thus, although this locality was not specifically investigated during our visit, the geology and palaeontology are not inconsistent with a Molteno age assignment.

Both Broderick (1984) and Oesterlen (1989) have reported other *Dicroidium*-yielding localities on the Manyima River, one important site lying immediately downstream of the bridge over the river on the main road to Kanyemba (Figures 1,2). This locality, about 20 km away from our rhynchosaur localities, has produced abundant fossil plant material in a remarkable state of preservation - ranging from highly altered, completely carbonised and even vitrinised coal through to scarcely altered "peat" in which the plant matter resembles modern leaf-litter in which individual leaf laminae are intact, supple and flexible, brown rather than black, and show well-preserved and apparently undistorted cell walls. Under the low-power microscope, remnants of cell contents are also visible in many cases. This remarkable material is currently under study to ascertain whether any useful palaeobiochemical information can be recovered from the remnants of cell contents.

GEOLOGY OF THE DANDE RHYNCHOSAUR OCCURRENCE

The rhynchosaurs described here were found in sedimentary rocks of the Cabora Bassa Basin (western part of the Lower Zambezi Valley) (Figure 2; see also Stagman 1978, Broderick 1989). The Lower Zambezi Valley, as well as the Mid-Zambezi Valley further west, are fault-bounded linear rift basins which have a sedimentary infill of rocks of the Karoo Supergroup (Upper Carboniferous to Lower Jurassic) and of younger age (Jurassic to probably Cretaceous). The Cabora Bassa Basin reaches a maximum width of 75 km, and is bounded north and south by master faults against Precambrian gneisses. These east-west trending fault lines manifest themselves in major escarpments.

The sedimentary deposits in this terrestrial basin reach a total thickness of at least 10 000m (Oesterlen 1990). The Lower Karoo Group comprises only 1000 - 1500m of this sequence, and is represented by periglacial sediments and turbidites of the Kondo Pool Formation and lacustrine sandstone, coal and carbonaceous shale of the Mkanga Formation (Table 1). The main subsidence of the basin took place during Upper Karoo times, when up to 7 000m of sediments were deposited. The basal part of the group comprises fluvial sediments of the Angwa Sandstone Formation, with coarse grained massive-bedded sandstones in the lower portion, which are equivalents of the Escarpment Grit in the Mid-Zambezi Basin (Table 1). The overlying Pebbly Arkose Formation, which hosts the rhynchosaur and dinosaur finds reported here (Figure 2), are described in more detail below. The aeolian sediments of the Forest Sandstone Formation are the youngest deposits of the Upper Karoo Group. They are conformably overlain by alluvial fanglomerates, sandstones and siltstones of the Dande Sandstone Formation, which is of mid-Jurassic to possibly early-Cretaceous age (Table 1).

Within the study area, the Upper Triassic Pebbly

Arkose Formation has a thickness of ca. 1500 - 2000m and is represented by two lithofacies. At the rhynchosaur-bearing localities, the typical rock consists of a light-brown, fine-grained micaceous sandstone which is moderately sorted and relatively coarse bedded. The sandstone fines upward to siltstone and even to mudstone. Pyrite concretions occur sporadically. Scour-and-fill structures are developed at the base of the cyclic units, whereas desiccation cracks and slump structures are more common in the upper portions. The other lithofacies is found further to the north and east, where the rock sequence is made up of massive-bedded, coarse-grained feldspathic sandstone, with randomly oriented pebbles up to 10 cm in diameter (hence the designation "Pebbly Arkose"). Parallel laminations are very common, whereas tabular and trough cross-bedding are less widespread.

The northern lithofacies shows all the features of a braided river system draining from the Precambrian highlands in the southeast. But the cyclic, fine-grained, vertebrate-bearing sandstone found south and west of it indicates alluvial plain sedimentation. The palaeogeography is thought to be characterized by a large flat plain bordered to the south by the escarpment. Episodic floods inundated the vast plain and deposited fine sediments. But often this shallow flood plain dried out. The climate during most of Upper Triassic time was subtropical to semi-arid, but it deteriorated to an arid desert climate towards the end of the period. The vegetation of the times might have been a non-angiosperm equivalent of "savannah", with few small bushes; but these conditions would have been episodic with pulses of relatively short duration, resulting in a generally rather harsh and hostile environment for animal life.

The main rhynchosaur-producing site (Z 53/3, co-ordinates 16°14'S; 30°20'E; see Figure 2) is situated on a grass-covered hilly area, where ten individual bone concentrations were found within an area 200m square. The concentration and distribution of bone in some of these loci suggests that they represent partial or whole skeletons, but quite badly fragmented and eroded. The fragmentary dinosaur femur mentioned earlier also comes from this rich site.

The second most prominent occurrence (Z 64/1, co-ordinates 16°13'S; 30°17'E), yielded much fewer rhynchosaur bones, and at the third locality (Z 109/1, co-ordinates 16°06'S; 30°03'E) the fossils appear not to be *in situ*, as suggested by the abraded surface of the fossil specimens and their strange stratigraphic position at the boundary of the Pebbly Arkose with the underlying Angwa Sandstone Formation (Figure 2).

IDENTITY OF THE DANDE RHYNCHOSAURS

The rhynchosaur fossils reported here consist mainly of surface scattered, isolated and mainly fragmentary bones which in a few cases can be associated together. They are the first tetrapod remains to come from beds assigned to either the Pebbly Arkose Formation or Molteno-equivalent beds in Zimbabwe, and they bring a new perspective to the Zimbabwean fossil fauna. Hitherto, Zimbabwean fossils have always been compared with fossils from deposits in South Africa, with which they seemed to compare very closely. But the only rhynchosaurs described so far from South African deposits are geologically a good deal older, from as low as the *Lystrosaurus - Thrinaxodon* Assemblage Zone in the Beaufort Group, of early Triassic age (Malan 1963; Carroll 1976; Keyser and Smith 1978; SACS 1980; Chatterjee 1980; Benton 1985). On the other hand, rhynchosaurs more directly comparable with the Zimbabwean specimens are known from middle- and late Triassic deposits in Tanzania - *Stenaulorhynchus stockleyi* Haughton, 1932 from the middle Triassic Manda Formation, and the large *Supradapedon stockleyi* (Boonstra 1953) from late Triassic deposits in the Tunduru district of southern Tanzania (Boonstra 1953; Chatterjee 1969, 1980; Benton 1983).

The Dande locality would undoubtedly repay more detailed investigation and controlled excavation of the finds, as even our brief reconnaissance proved the presence of associated material, including both cranial and post-cranial remains, some of it reasonably well preserved despite its exposure, and many of the breaks on the bones apparently fresh. What we recovered evidently belongs to a single taxon of rhynchosaur, showing a considerable size-range from relatively small up to large individuals.

Although they differ in matters of detail, recent revisions of the rhynchosaurs agree in dividing them into "primitive", "intermediate" and "advanced" forms which show an impressive correlation with deposits of early, middle and late Triassic age (Chatterjee 1969, 1980; Benton 1983). These "clusters" of forms are distinguished largely on the basis of dental characteristics: presence or absence of premaxillary teeth; presence or absence of palatal teeth (Benton questions whether any of the middle or late Triassic rhynchosaurs had any palatal teeth); presence or absence (and number) of longitudinal grooves on the maxillary tooth plate; number of toothrows on the maxillary tooth plate and on the mandible; presence or absence of teeth on the lingual surface of the maxilla or dentary.

The state of these characters in the Dande rhynchosaurs is as follows (Figures 3,4,5): the premaxillae are devoid of teeth and are strongly downturned; there is no sign of palatal teeth on the pterygoid; the maxillary dental battery has a single median longitudinal groove which divides the multiple rows of teeth into approximately equal labial and lingual portions; there are no teeth on the lingual surface of the maxilla, but teeth are present on the lingual surface of the dentary. It is not clear whether these lingual dentary teeth are arranged in a distinct

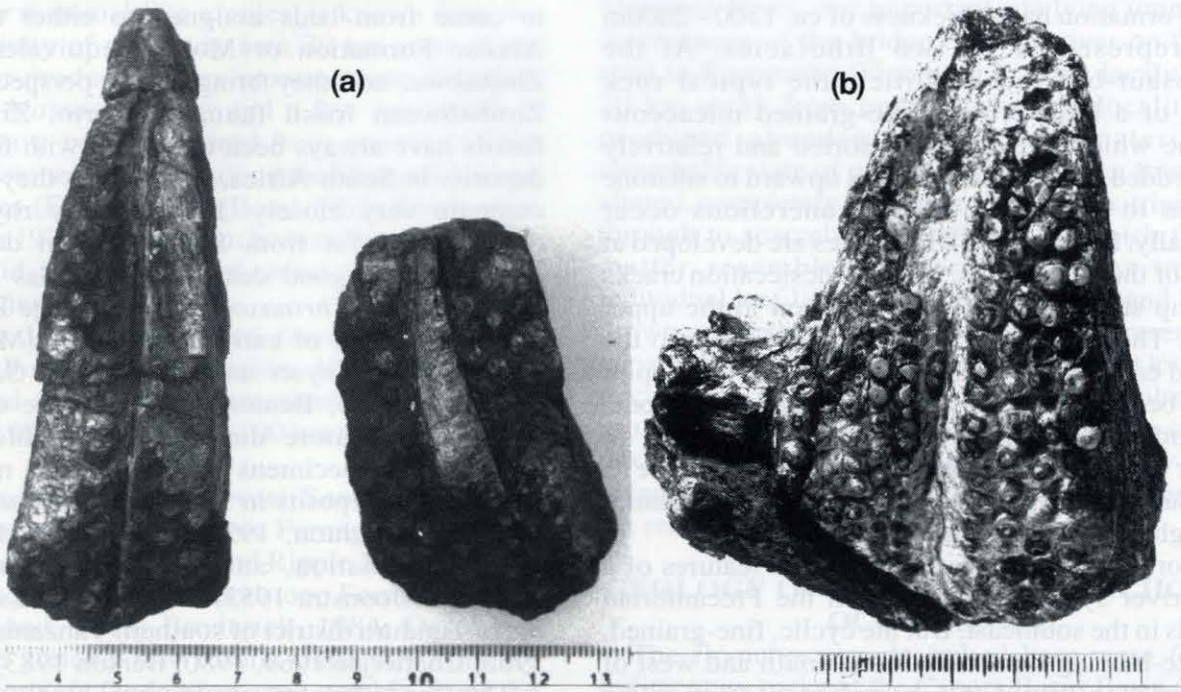

Figure 3:
(a) Occlusal view of (l-r) right and left maxillary dental plates of rhynchosaur specimen from site Z 53/3 (1), Lower Zambezi Valley, Zimbabwe (? adult specimen). These tooth plates were associated with more cranial and postcranial remains (see also Figure 6);
(b) Occlusal view of left maxillary dental plate of *"Supradapedon" (? = Hyperodapedon) stockleyi* (Boonstra, 1953), from the Late Triassic of Tanzania (SAM 11704: courtesy South African Museum, Cape Town; photo C. Booth).
Smaller scale divisions = mm.

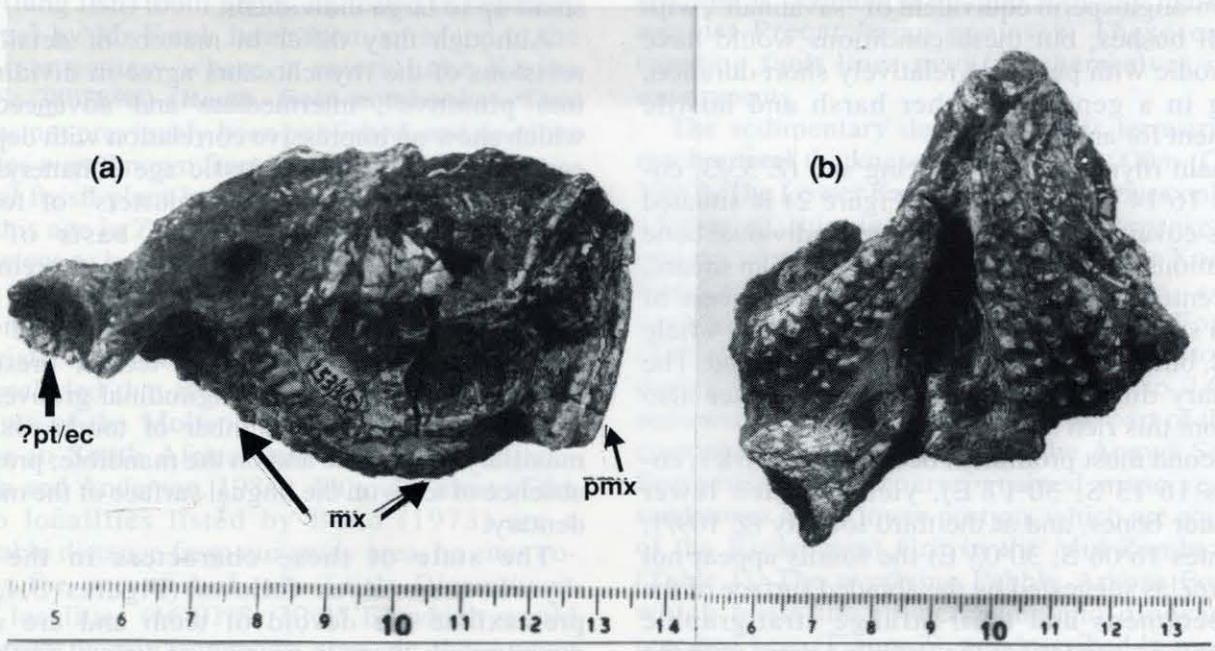

Figure 4:
Portion of snout of a smaller individual from site Z 53/3 (5):
(a) right lateral view. The down-curved premaxillae (pmx) are visible along the right side of the specimen; the curved maxillary dental plate (mx) defines the lower edge; the cup-shaped bone protruding to the left is part of the palatal complex, probably the pterygoid/ectopterygoid (?pt/ec); the dorsal parts of the specimen are eroded away.
(b) palatal view of the same specimen.
Smaller scale divisions = mm.

Figure 5: Dentary of small specimen from site Z 53/3 (5):
(a) labial view, with occlusal palisade of penicillate teeth arrowed (the gap in the row is an artifact due to breakage);
(b) buccal view, with two small conical labial teeth arrowed (t).
Smaller scale divisions = mm.

row or are scattered, as only two teeth are preserved in one section of jaw recovered so far (Figure 5b). The main row of occlusal dentary teeth along the apex of the labial margin are deep-rooted, narrow, penicillate teeth which are tightly packed in the "palisade row" typical of advanced rhynchosaurs.

In terms of Benton's (1983) analysis, this character state places the Dande rhynchosaurs unquestionably within the sub-family Hyperodapedontinae of the family Rhynchosauridae. This sub-family is typical of the late Triassic (Chatterjee 1980; Benton 1983). Within that sub-family Benton (1983) includes the genera *Hyperodapedon*, *Paradapedon*, *Scaphonyx*, *'Supradapedon'* and forms as yet undescribed from the Dockum Group of Texas, USA (Benton 1987). He regards *'Supradapedon'* from Tanzania as possibly a large *Scaphonyx* or *Hyperodapedon* (Benton 1983: p. 712), and having examined the specimen itself (Figure 3b) in the South African Museum, we agree. Benton goes on to suggest that the relationship between *Hyperodapedon*, *Paradapedon* and *Scaphonyx* is so close that they might well be congeneric, although as he points out the lack of lingual teeth on the dentary of *Scaphonyx* might prove to be a valid character separating it from the others.

On these grounds, therefore, it seems safe to refer the Dande rhynchosaur to a species in the *Hyperodapedon* / *Paradapedon* group; since *Hyperodapedon* Huxley 1859 has priority over *Paradapedon* von Huene 1938, the Dande form is provisionally referred to *Hyperodapedon*. On the tentative and imprecise grounds that the longitudinal groove on the maxillary tooth plate divides the tooth rows into roughly equal labial and lingual portions, as is seen in the Indian form *H. huxleyi* (=*Paradapedon huxleyi*), the Dande form is provisionally referred to *Hyperodapedon* sp., cf. *H. huxleyi* Lydekker 1881.

However, it should also be noted that according to Benton's view, *Hyperodapedon* might well prove to be monotypic, with Huxley's original species (*H. gordoni* from the Lossiemouth Formation of Scotland) the only valid species, and the Dande specimens would therefore be referable to *Hyperodapedon gordoni* Huxley 1859.

AGE OF THE DANDE RHYNCHOSAURS

Part of the interest in rhynchosaurs lies in their apparent usefulness for dating sedimentary deposits (Benton 1983; Chatterjee 1969, 1980). The assignment of the Dande rhynchosaurs to the Hyperodapedontinae identifies them as belonging to a group characteristic of and apparently confined to the late Triassic. This accords well with the age indicated by the plant fossils from the area (*Dicroidium*), and is further supported by the discovery of the fragment of dinosaurian femur from the same site as rhynchosaur specimen Z 53/3. On the basis of fourth trochanter morphology, this femur seems to belong to a prosauropod (Figure 6).

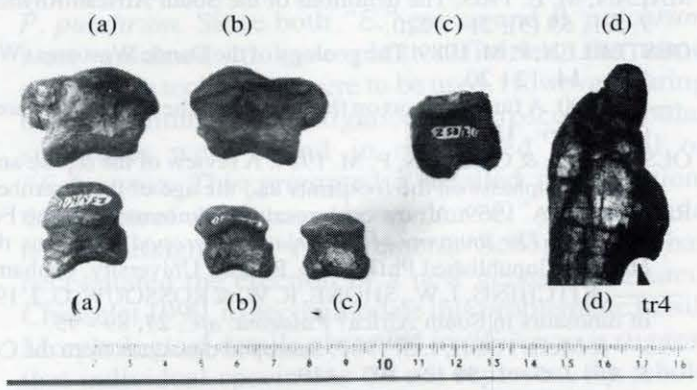

Figure 6:
(a,b) Metatarsals of specimen from site Z 53/3 (1);
(c) Centrum of ?caudal vertebra (Z 53/3 (1));
(d) Fragment of femur of ?prosauropod dinosaur (fourth trochanter arrowed "tr4"), from site Z 53/3 (7);
(e-g) Phalanges (Z 53/3 (1)).
Smaller scale divisions = mm.

Prosauropods are characteristic of the Triassic-Jurassic transition – especially the Elliot Formation in South Africa and its equivalents worldwide and they are not known from beds older than the late Triassic (Carnian) (see discussion on age of dinosaur-bearing deposits in Olsen and Galton, 1984).

Recently, tridactyl bipedal dinosaur tracks have been recorded in Molteno-age (late Triassic) *Dicroidium*-bearing beds in the northeastern Cape of South Africa (Raath, Kitching, Shone and Rossouw, 1990), proving the presence of dinosaurs (although not necessarily of prosauropods) in beds of this age.

Thus the three separate palaeontological indicators - plants, dinosaurs and rhynchosaurs - all converge in indicating a Late Triassic age for the Dande deposits, which is in accord with age deductions based on general stratigraphy.

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