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SEDIMENTOLOGY AND TAPHONOMY OF LATE PERMIAN VERTEBRATE FOSSIL LOCALITIES IN SOUTHWESTERN MADAGASCAR.

by

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ABSTRACT

This is the first report of a project that tests the accuracy of the currently accepted palaeoposition of southern Madagascar during the late Permian in juxtaposition to the coast of Tanzania. This is done by comparing the sediments and fossils that accumulated in a series of rift valleys, each around 25 km wide, that formed in this part of Gondwana at the beginning of pull-apart some 250 million years ago. The study reported here on the Madagascan side of the rift system will be followed by a similar study of the Tanzanian portion.

Field data on the sedimentology and vertebrate taphonomy of three separate fossil localities in the Late Permian, Lower Sakamena Formation of southwestern Madagascar are used to reconstruct the subenvironments of the Sakamena axial rift valley lake.

1. *Ranohira*: dominated by microlaminated mudrocks with three horizons of fossil bearing micrite nodules. The fossils are mostly complete articulated skeletons of an ?aquatic procolophonid reptile, *Barasaurus*, which inhabited the offshore epilimnion of a deep, thermally-stratified closed lake.
2. *Zavoloa River*: alternating cross-bedded conglomeratic sandstone and laminated siltstone are interpreted as braided delta deposits entering the linear margin of the lake from the passive side of the half graben. These deposits contain some fully articulated skeletons and numerous winnowed bonebeds of a supposedly semi-aquatic reptile, *Claudiosaurus*, that may be related to sauropterygians.
3. *Mount Eliva*: is dominated by the younginiform reptile, *Hovasaurus*, which occurs as articulated skeletons inside micritic siltstone nodules in the mudrocks of a sub-lacustrine deltaic sequence. Pebble masses in the abdomen of *Hovasaurus* are interpreted as ballast to facilitate swimming. The taphonomic style and sedimentary environment of the host strata confirm this interpretation.

Thermal shock from periodic overturn and poisoning from algal blooms are the most likely causes of mass mortality among the aquatic fauna. Hydrogen sulphide released from anaerobic bacterial decay of soft tissue and girdle cartilage formed reduction halos around the newly buried reptile carcasses. At least 3 "micritization episodes" led to the precipitation of calcium cabonate in the reduction halos forming nodules around the vertebrate fossils. They are interpreted as periods of extended lowstand when thermal stratification could not be maintained and oxygenated waters came into contact with previously anoxic sediments. If such lowstand events were climatically controlled, they may be useful timelines to accurately correlate strata within and between these ancient rift valley lakes in both Madagascar and Tanzania.

KEYWORDS: Madagascar, *Barasaurus, Claudiosaurus, Hovasaurus*.

INTRODUCTION

The concept of continental drift was first proposed by the American F.B.Taylor in 1910 and widely publicised by the German Alfred Wegener in 1915 (Holmes 1965). Until that time the theory was based mainly on the on the congruence of opposing shorelines of the Atlantic. Wegener also demonstrated contiguous mountain ranges, ancient glaciated pavements and palaeobiogeographic similarities and in his opinion the eastern coast of the Americas and the western coast of Africa and Europe matched "as closely as the lines of a torn drawing would correspond if the pieces were placed in juxtaposition". Later, Du Toit (1937) documented the similarity of sediments, fossils, climates and earth movements on each side of the Atlantic. His corroborative evidence was enough to convince the scientific community that the super-continent of Pangaea had formed some 250 million years ago and had slowly fragmented into the present day continental configuration. There followed much research, mainly by geophysicists, into tracking the movements of continental plates through geological time and by the 1960's, plate tectonics was widely accepted as the driving mechanism of continental drift.

The palaeoposition of Madagascar in relation to the African continent has always been controversial. The major conflict was between palaeomagnetic data, which fitted the north coast of Madagascar alongside the coast of Somalia (Smith 1976), and the geological data which placed the northern margin of Madagascar against Mozambique (Tarling and Kent 1971). Subsequent magnetometer surveys of the seabed have identified a spreading ridge which mirrors the outline of the north coast of Madagascar halfway between

Madagascar and the coast of Somalia (Rabinowitz. *et al* 1983; Coffin 1987; De Wit *et al.*1998). Thus the weight of evidence is firmly in favour of the northerly palaeoposition and the purpose of this study is to report palaeontological and sedimentological details that corroborate this fit. Rayner (1992) began this process by comparing plant fossil assemblages in the Sakoa Formation with those of the Ecca Group of the South African Karoo Basin. This study aims at more precise resolution based on fossil skeletons of aquatic reptiles within the uppermost siltstones of the Lower Sakamena Formation (Late Permian, Tatarian) of southwestern Madagascar. Similar reptile fossils have been recovered in equivalent-aged beds in southern Tanzania and it is the ultimate aim of this project to confirm that these strata were once in continuity.

The Sakamena vertebrate fossils were first discovered in 1906, by Captain Colcanap, a scientist employed by the French army. He first encountered vertebrate-bearing nodules in the lower reaches of the Sakamena River, a northerly flowing tributary of the Onilahy River in southwestern Madagascar. Later he amassed a large collection from a conical hill called Mount Eliva (Figure 1) at the head of the Sakamena valley, some 50 km further south. The discovery and preliminary identification of these fossils was published by Boule in 1908 but it was not until 1925, when Piveteau found more localities in the vicinity of Benenitra and Ranohira, that these occurrences were properly documented (Piveteau 1926). A collection of some 300 specimens is still housed in the Museum National d'Histoire Naturelle in Paris. Since then sporadic but important prospecting, mainly by French survey and exploration geologists, added a few more localities in the area between Ranohira and Benenitra (Tortochaux 1949; Piveteau 1955; Cliquet 1957; and Besairie 1972).

The most common tetrapod fossils in the Paris museum's Sakamena collection are of *Hovasaurus*. These are medium-sized (up to 900mm long, estimated 10kg mass (Currie 1981)) younginiform eosuchian reptiles with long slender digits of variable length, pachyostotic ribs (De Buffrénil and Mazin 1989), strong caudal epiphyses and abdominal quartz pebble masses which are together interpreted as adaptations for an aquatic lifestyle (Currie 1981; Carroll 1981). Another less common younginiform eosuchian, *Thadeosaurus*, is very similar in overall body plan but its limb proportions are considered to be terrestrial (Carroll 1981; Currie and Carroll 1984). It generally, but not always, lacks abdominal stone masses (Carroll 1981). Other minor, but significant elements of the fossil fauna are the supposedly semi-aquatic sauropterygian reptile *Claudiosaurus* (Carroll 1981), the rare gliding diapsid *Coelurosauravus elivensis* (Piveteau 1926), small procolophonid reptiles of the genus *Barasaurus* (Piveteau 1955), fragments of rhinesuchid temnospondyls and one or two palaeoniscoid actinopterygians (*Atherstonia*). Some therapsid fossils of terrestrial origin have been recovered from the Lower Sakamena, including a single dentary of an unknown theriodont (Piveteau 1955), a few dicynodont vertebrae and tusks, and a single skull of *Oudenodon* (Mazin and King 1991).

Piveteau (1955) initially established biostratigraphic correlation with the main Karoo Basin by linking

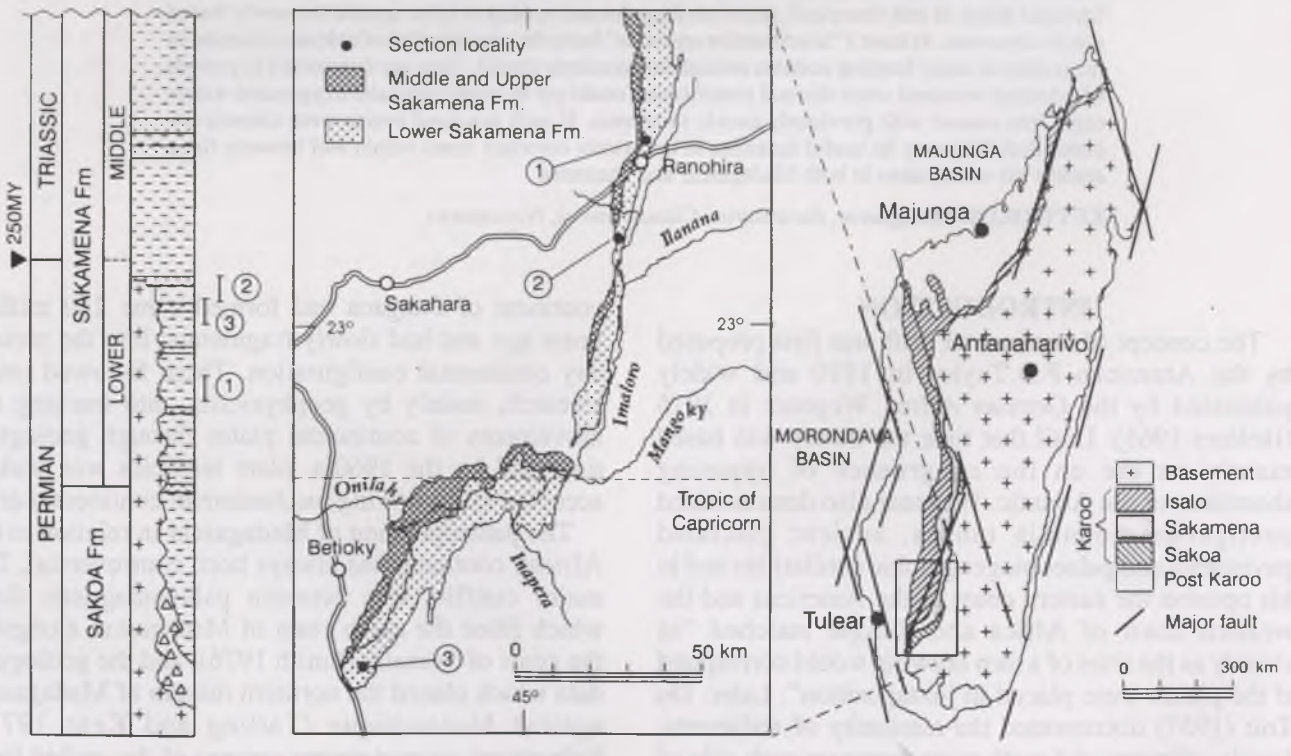


Figure 1 Stratigraphic and geographic location of the 3 Sakamena Formation fossil localities visited in this study. 1=Zavoloa River, 2=Ranohira Cemetery, 3=Mount Eliva.

Barasaurus with *Owenetta* from the former *Cistecephalus* Zone (now *Cistecephalus* Assemblage Zone (Smith and Keyser 1995)). More recently, the Malagasy dicynodont *Oudenodon sakamenensis* has been correlated with the same genus in both *Cistecephalus* and overlying *Dicynodon* Assemblage Zones which are the uppermost Permian (LateTatarian) strata of the Karoo Supergroup (Mazin and King 1991). Currie (1981) compared the Malagasy fauna with the Russian Dzulfian standard stage of the Upper Permian, and recently the similarity of the Sakamena procolophonids with the Russian *Nyctiphruretus* (Arduini 1993) from Russian Zone 111 has reinforced this correlation, giving an absolute age estimate for these strata of 255+/-2Ma.

Having reviewed the Paris Museum collections, Tortochaux's field notes and Germain's private collection, Currie (1981) recognised 4 distinct fossil associations in the Lower Sakamena Formation: 1. Marine invertebrates with no identifiable reptiles; 2. Terrestrial reptiles (*Thadeosaurus, Daedalosaurus, Coelurosauravus*) dominant with the actinopterygian *Atherstonia* well represented; 3. Aquatic reptile *Hovasaurus* abundant, with terrestrial *Acerosodontosaurus* and *Atherstonia* present; 4. Partly aquatic *Claudiosaurus* strongly dominant with terrestrial *Acerodontosaurus*, the glider *Daedelosaurus* and therapsids present. These associations were, however, based on Piveteau's locality data and Currie was unable to accurately confirm their distribution or stratigraphic relationships. Nevertheless, he regarded them as contemporaneous and possibly representing different depositional environments of the fluvio-lacustrine plains.

A fifth fossil association dominated by the procolophonid reptile *Barasaurus* was identified during the course of this investigation in the Ranohira district.

This is a report on the first phase of a field-based study which is modelled on that of Alex Du Toit (1937), that looks at how closely the sediments and fossils corroborate the structurally and geophysically defined palaeoposition of Madagascar, relative to the African continent, during the latest Permian. It also adds to the pioneer work of Piveteau (1955) and Currie (1981) in providing more details of the palaeo-environmental conditions that existed in this part of central Gondwana at that time. The present study focuses on fossiliferous strata of the Sakamena Group in the southern Morondava Basin of southwestern Madagascar. Future research will concentrate on the contemporaneous and probably laterally continuous strata in the Tanga Basin of southeastern Tanzania.

GEOLOGICAL SETTING

The stratigraphic successions of Karoo-aged basins of western Madagascar are directly related to the tectonics of progressive rifting and subsequent detachment of eastern Gondwana (Figure1). During the Late Carboniferous to Late Permian, extensional block faulting brought about by the closure of the Cape Fold Belt to the south resulted in horst and graben formation along a NS trending belt on the eastern side of southern Gondwana (Jeans and Meerbeke 1995). Two linear grabens formed the Sakamena Basin (Cliquet 1957) which rapidly filled with thick glacial (150m), fluvio-deltaic (700m) and lacustrine (100m) sequences of the synrift Sakoa and lower Sakamena formations. The fluvio-lacustrine sediments of the Lower Sakamena Formation accumulated in the incipient rift as extensional block faulting tilted the basement down to the west (Fabian 1996; Wescott and Diggens 1998). It is these latest Permian reptile-bearing fluvio-lacustrine facies of the Lower Sakamena Formation that are under investigation here. Tectonic activity migrated from east to west and deposition began in the south somewhat earlier than in the north. In the Early Triassic, a period of tectonic quiescence allowed a significant flooding of the Sakamena Basin and deposition of the first basinwide marine sediments, the Middle Sakamena Formation. Renewed block faulting in the basin ensured that terrestrial conditions continued through to the Early Jurassic with the accumulation of the arenaceous Upper Sakamena and Isalo Formations. During the Early Jurassic the previous NE-SW and N-S Karoo structural lineaments were re-activated by the onset of rifting to the north in the Somali Basin. Initially forming restricted lacustrine basins, the rift widened and deepened as eastern Gondwana began to separate from western Gondwana, resulting in a second basinwide marine incursion represented by the Middle Jurassic Dogger limestones. Post-rift subsidence on the passive margin promoted the formation of the Cretaceous Majunga and Morondova Basins.

Thus the overall palaeotopography during deposition of the Lower Sakamena strata in southern Gondwana was of two narrow (+/- 25km wide) fault-bounded grabens trending roughly N-S and separated by an upland interfluve (Fabian 1996). The interfluve continued to separate the basins until the Early Triassic when it was overtopped by the alluvial fan deposits of the basal Isalo Group. To the south the rift valleys were closed by alluvial fans giving way to axial river deltas sourced in the northwardly migrating and rising Cape Fold Mountains (Wescott and Diggens 1998). To the north they opened to a shallow epicontinental sea, as is evidenced by the regional distribution of several marine incursions and two major flooding episodes. Landscapes on the graben floor between these two end 'members' were mainly lowland fluvio-lacustrine, becoming more estuarine northwards and more fluvial southwards (Figure 2). By the Late Permian, the Sakamena Basin was situated at approximately 50° S (Smith, Hurley and Briden 1981) so that climatic conditions in these intra continental rift valleys would have been relatively warm and humid with highly seasonal rainfall, possibly monsoonal (Parrish, Parrish and Ziegler 1986).

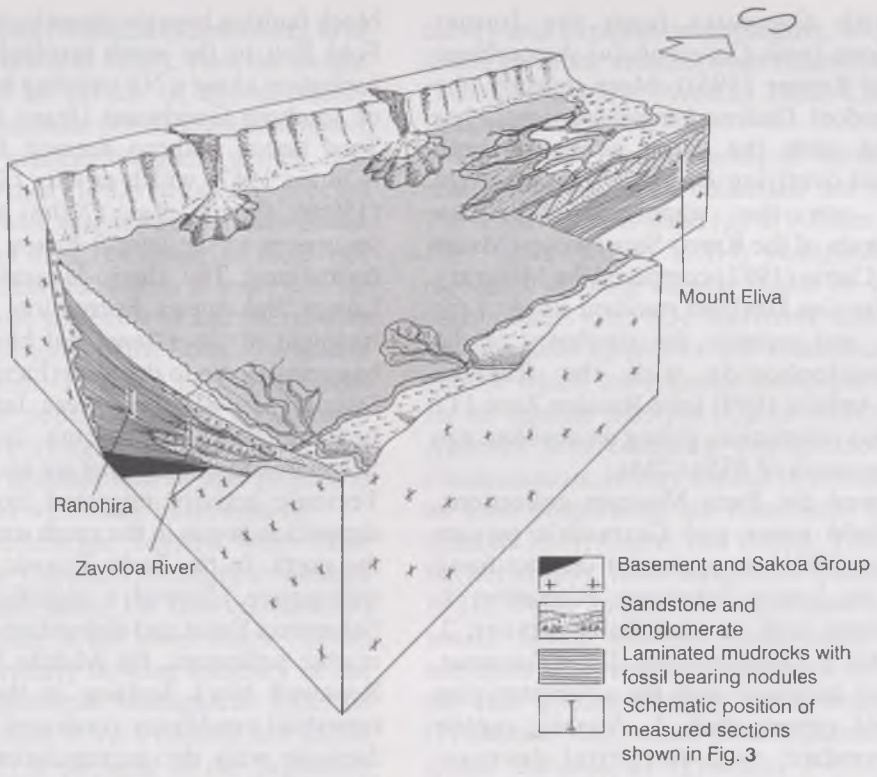


Figure 2. Sedimentary environments of the Sakamena rift valley lake during the Latest Permian, showing interpreted sub-environments of the 3 fossil localities studied.

SEDIMENTOLOGY AND TAPHONOMY OF SAKAMENA FOSSIL LOCALITIES

Two field visits of 3 weeks each were made to the Ranohira, Leoposa and Mt Eliva localities (see Figure 1) in 1994 and 1996. These trips were made possible within a collaborative research project, the 'Gondwana Project', involving research geologists and students from Rand Afrikaans University, University of Cape Town and University of Antananarivo.

At each locality care was taken to locate *in situ* nodules and accurately plot their occurrence on a sedimentological log of the outcrop, which was measured with a graduated staff to an accuracy of 5cm. Each fossil-bearing nodule was split and taphonomically assessed on site, recording the taxon, degree of disarticulation, orientation and attitude of the skeleton, type of bone mineralization and associated plant material. A total of 48 specimens have been accessioned by the South African Museum (SAMPK8263-8297 & 8569-8581) and an equivalent number reside in the palaeontology store of the University of Antananarivo.

Findings indicate that the fossil-rich strata of the Lower Sakamena accumulated in both nearshore and offshore facies of linear rift-valley lakes (Figure 2). Both facies were episodically affected by floodwater discharge, creating turbulent bottom currents which transported coarse-grained sand and gravel into an otherwise mud-dominated environment. Each facies contains a distinctive faunal and taphonomic signature that has significance for palaeoecological interpretations.

Ranohira Cemetery [S22°32'51.4" E45°25'25.2"]

Sedimentology

This *Barasaurus*-rich locality lies some 500m north of the edge of the village of Ranohira in southwestern Madagascar (Figure 1). The outcrops are formed by the incision of the Menamety River and its tributaries into the virtually flat-lying uppermost Lower Sakamena strata, exposing a maximum stratigraphic thickness of approximately 25m. (Figure 3). The succession is composed of drab greenish-grey (Munsell colour code 5Y4/2) siltstone with minor interbedded lenses of horizontally laminated fine-grained sandstone. Towards the top of the outcrop the sandstone beds become coarser textured, thicker and more laterally extensive with conglomeratic lags at the base and structured throughout with trough cross-bedding. It is onto this sandstone cliff that the villagers have constructed numerous white painted tombs from baked clay.

The siltstones at the base of the outcrop are microlaminated with 3-5mm thick lighter coloured bands separated by much thinner, <1mm-thick dark grey (5Y3/1) intermittent laminae. The lighter laminae are clean siltstone, the dark, paper-thin laminae are highly compacted claystone. Higher up in the section the siltstone is more evenly laminated and contains minor flaggy-weathering tabular sandstone bodies, most of which have sharp basal contacts (Figure 3). The upper contact of the sandstone is invariably gradational with fissile weathering horizontally laminated siltstone. No evidence of bioturbation could be found in or on the mudrock laminae or within the tabular

sandstones which might suggest hostile benthic conditions. The question of whether this lack of bioturbation is due to anoxia or a low carbon content of the bottom sediments is discussed later.

The mudrock interval between these thin tabular sandstone sheets contains three "horizons" of light-grey coloured calcareous nodules. The nodules occur as discrete, sharply contacted, smooth-surfaced, biconvex and commonly elongate bodies which roughly delimit the shape of the skeleton around which they have formed (Figure 4). The outer surface of the nodules displays concentric colour banding reflecting the original light/dark laminae of the host siltstone, demonstrating that the nodules are formed by cementing the original sediment rather than displacing it (Figure 4). Not all the *Barasaurus* skeletons are permineralized with nodules, and in many cases the skulls and tail are preserved as highly compressed weathered bones on the bedding plane outside the nodule (Arduini 1993). The sedimentological interpretation of the formation of the *Barasaurus*-bearing nodule horizons must account for a death event followed by a period of intermittant suspension/ traction current sedimentation sufficient to bury the carcass before it could be destroyed. Finally, a change in porewater chemistry around the decaying carcasses

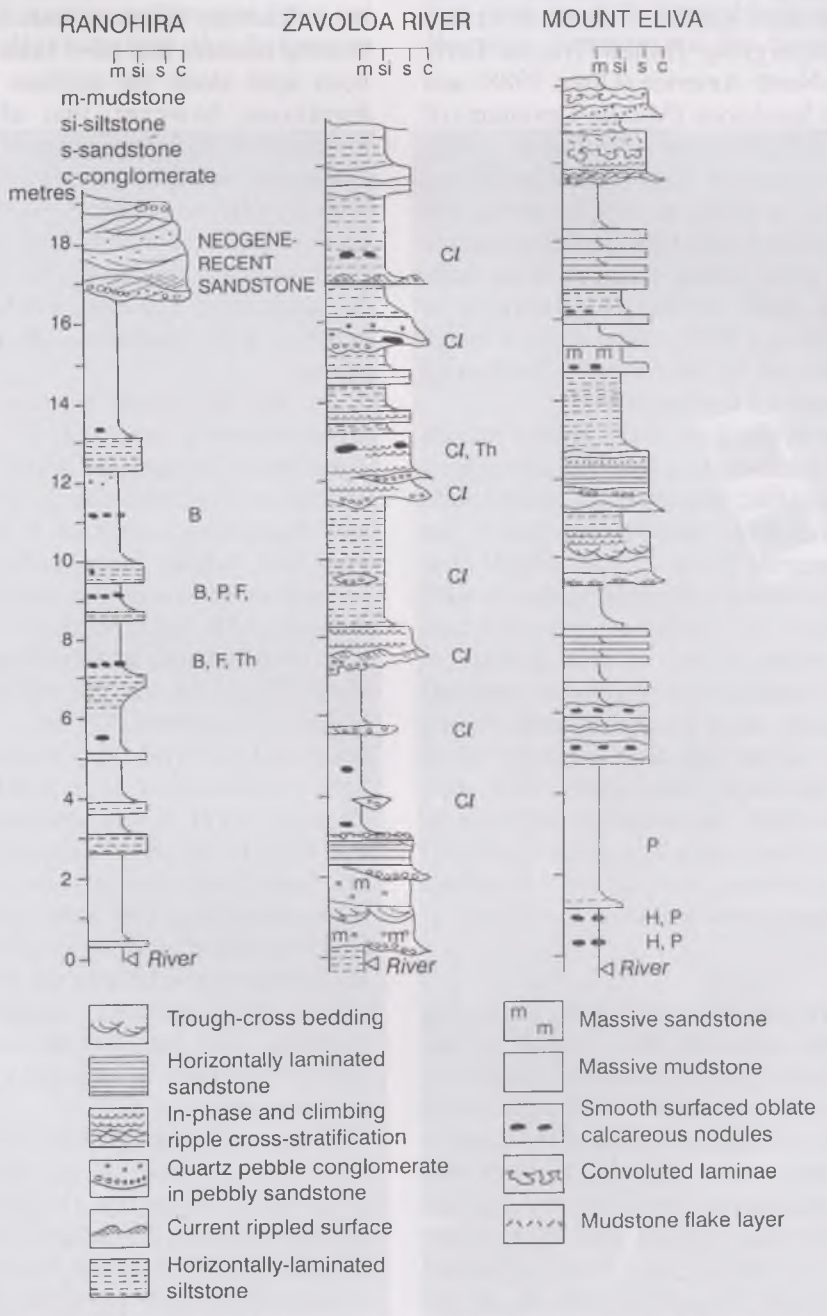


Figure 3. Lithology, sedimentology and fossils of 3 vertebrate fossil localities in the upper Lower Sakamena Formation of southwestern Madagascar. Legend to fossils B=*Barasaurus*, Cl=*Claudiosaurus*, Th=Therapsid, F=Actinopterygian , P=Glossopterid flora, H=*Hovasaurus*.

caused the localised precipitation of micrite. These nodule-forming processes and their controls are discussed later.

Above the three nodular intervals, the mudrocks become dominated by light greenish-grey and fissile-weathering claystone with no nodules or fossils. The upper 5m of the exposure at Ranohira comprises a Neogene crust of a single 2m-thick conglomeratic channel sandstone body overlain by smaller sand-filled scour channels (Figure 3). The base of the main channel is eroded into the fissile Sakamena mudrocks with wide, shallow scours filled with planar cross-bedded poorly sorted matrix-supported conglomerate.

The lithologies and sedimentary sequences of the Sakamena Formation at Ranohira are interpreted as distal lacustrine turbidites similar to those described from the Newark Supergroup (MiddleTriassic-Early Jurassic) of eastern North America (Olsen 1988) and the Middle Old Red Sandstone (Middle Devonian) of northern England and Scotland (Donovan 1980; Trewin 1986). In such narrow fault-controlled basins, subsidence and uplift episodes as well as rising and falling lake water levels all affect the fluvial/lacustrine transition, creating rapid facies changes from fully terrestrial floodplain facies to marginal lacustine to offshore lacustrine (Cojan 1993). Similar rapid facies changes are evidenced in the Lower Sakamena between the three sections studied here.

Lake Turkana lies in the floor of the eastern branch of the African Rift System and is of similar dimensions and in comparable tectonic and climatic settings such that it may serve as suitable modern analogue to the Late Permian Sakamena basin. It has similar low organic content of profundal laminated mudrocks with minimal bioturbation and carbonate precipitation (Cohen 1989). The water column of Lake Turkana is unstratified, but it is subject to storm influxes, seasonal water level fluctuations, algal blooms in summer and seismic disturbance during volcanic eruptions. It is possible that the Sakamena lake waters were also unstratified and therefore permanently oxygenated. However the microlamination and preferential micritization of articulated vertebrates (described below) strongly indicate anoxic benthic conditions.

Taphonomy

In situ fossil-bearing nodules tend to be somewhat more convex on the underside than topside of the skeleton. This suggests that the chemical conditions that induced carbonate cementation of the enclosing mudrocks were either stronger or operated for a longer time below the buried carcass. The 56 *in situ* fossil-bearing nodules recorded at this locality had no preferred orientation, their attitude and shape being clearly determined by the organic material around which they had formed. Many but not all of the elongate smooth-surfaced nodules contain articulated remains of the procolophonid reptile *Barasaurus* (Figure 4). The larger flatter nodules contain articulated skeletons of the palaeoniscid *Atherstonia* (Figure 5). Some of the latter contain an assortment of plant debris including *Glossopteris* leaves, *Schizoneura* and *Lepidopteris* stems, and some woody fragments along with articulated *Barasaurus* limbs and other isolated post-cranial elements. The middle horizon contains more regular muffin-shaped ellipsoidal nodules that are similar in colour and composition but are difficult to break apart and contain no macrofossils.

Skeleton-bearing nodules part easily along the midline, causing most of the bones to break along their length. In the formation of the present-day landscape there has been a period during which groundwaters have flushed through the partings of these nodules and weathered the fossilized bone much more rapidly than the calcareous siltstone nodule. All the *Barasaurus*-bearing nodules that have been collected to date have been split along the midline of the skeleton. It is fortuitous, however, that after cleaning out the remnants of decomposed fossil bone, the fine-grained calcareous siltstone moulds are ideal for casting with latex or silicone rubber. Casting part and counterpart gives a perfect replica of both dorsal and ventral sides of the skeleton (Figure 6). This 3-dimensional view of the articulated skeleton would be very difficult to achieve with mechanical preparation of the fossil bones.

Of the 65 fossil bearing nodules that were taphonomically assessed, 57 contained articulated *Barasaurus* remains, of which only 5 had preserved skulls (see Figures 6 and 7). The orientation of loose and fragmentary nodules is difficult to determine. However, whole loose nodules are slightly more bulbous on the lower side and this makes it possible to determine the upper surface of these fossils. Twelve fossil-bearing nodules were found still embedded in the shale. Thus, the attitude of the skeletons could be reliably documented. Of these, 10 were lying on their belly, and two were lying on their backs, all with their legs spreadeagled in typical aquatic death pose (Weigelt 1989). Several nodules were found to contain two or three skeletons that were invariably curled-up and whose limbs were disassociated. This suggests that some scavenging may have taken place before burial. However, these multiple specimens most often contain the fully preserved skulls and distal sections of the tail, which are commonly missing from the single skeletons. The complete skeletons measured between 230-250mm from snout to tail tip and are considered to be adult size.

Clumps of rounded quartz pebbles occur within the abdominal region of all the *Barasaurus* fossils collected at Ranohira (Figure 7). The number of pebbles in each clump ranges from 2-15, although most contain 8-10. They tend to lie between vertebrae 16-19, on and slightly to the left of the midline of the abdomen. The pebbles are composed of opaque, grey, brown and white quartz ranging in maximum diameter from 8-13 mm. Some have dark coloured inclusions of tourmaline that suggests a granitic source. The clasts are in contact

with each other and there is a tendency for the larger pebbles to be confined to the anterior half of the clump. Pebbles range in shape from rod to ovoid to spherical, and surface textures may be rough, pitted, smooth with pits or completely smooth (Figure 7). A few of the pebbles are polished. Unlike the abdominal stones of *Hovasaurus*, the *Barasaurus* clumps have no associated grit- or sand-sized particles.

Zavoloa River, Ambohitra [GR. S 22° 46' 45.7" E 45° 20' 29.3"]

Sedimentology

This locality lies some 25km south of Ranohira on the eastern banks of the Zavoloa River just south of the river crossing to the village of Ambohitra (Figure 1). It consists of a series of erosion gullies that have cut through sub-recent alluvium into the Sakamena sediments below. The outcrop comprises at least 20 stratigraphic metres of laminated mudrocks with subordinate pebbly sandstone and conglomerate lenses in a ratio of 3:1(Figure 3). The section dips gently (20°) towards the west away from two N-S trending normal faults. The mudrocks are generally olive grey (5Y4/2), thinly bedded and finely- to micro- laminated. They contain light grey (5Y7/2) isolated smooth-surfaced oblate calcareous nodules up to 120mm in diameter, some of which contain articulated vertebrate fossils, although most are non-fossiliferous. Mudstone laminae are, in places, clearly visible as extremely thin (<0.2mm thick) dark-coloured organic claystone laminae separated by thicker (0.5-1mm) lighter-coloured silty layers with vague intermittent laminae. An obvious difference between this locality and Ranohira Cemetry are the bone-rich quartz pebble



Figure 4. Ranohira locality. Two *in situ* micrite nodules containing articulated *Barasaurus* skeletons. Note the similarity in the shape of the nodules, which is determined by the attitude of the skeleton inside. The preservation of the original siltstone laminae in the nodules indicates that the micrite precipitation was post-burial and non-displacive.

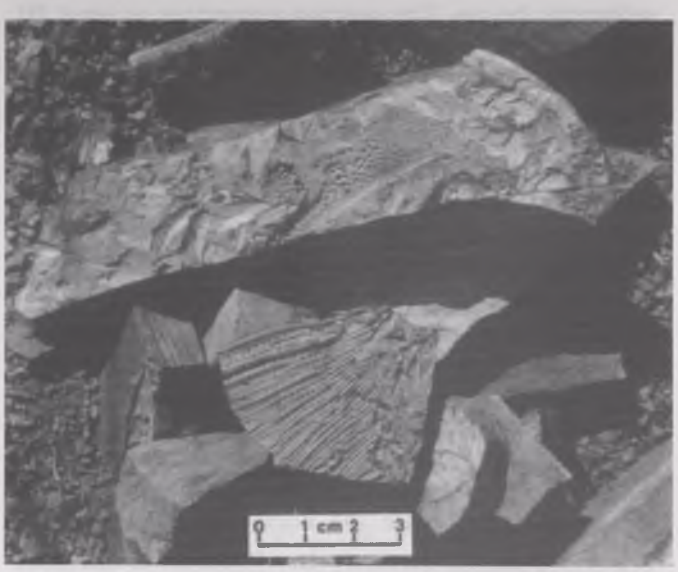


Figure 5. Ranohira locality: Fragments of a calcareous siltstone nodule containing an articulated palaeoniscid fish, probably *Atherstonia*.

conglomerate lenses within most of the sandstone beds in the lower part of the section (Figure 8). At the bases of the sandstones, longitudinal runnels that have been scoured up to 60cm into the underlying argillaceous sediments are floored with stringers of clast-supported pebble conglomerate and filled with medium grained pebbly sandstone displaying undulating "swaley" laminae. Thin sheets (<20cm) of well-sorted matrix-supported pebble conglomerates occur within the 2-3 metre-thick tabular sandstone bodies that overlie the basal scour. These sheet conglomerates (Figure 8) are sharply bounded. Larger intraclasts of well-rounded chert and quartz pebbles and post-cranial bones of *Claudiosaurus* commonly protrude from their upper surfaces. The matrix of fine- to medium-grained sandstone appears to have been dense enough to support these larger clasts during and after sedimentation, a feature that is indicative of cohesive debris flows. In places the gravel stringers are structured into planar-convex barforms displaying high angle epsilon cross-stratification. *Claudiosaurus* long bones and ribs are aligned with their long axes parallel to the dip of the foresets, indicating that these



Figure 6. Ranohira locality: Silicone cast of the moulds of part and counterpart of a *Barasaurus*-bearing nodule. Note the intricate details of the maxillary teeth and skull roof bones in the close-ups (scale bars=1cm).

bars were, at least in part, accreted laterally. Each conglomerate sheet is sharply overlain by horizontally-laminated pebbly sandstone which grades upward into ripple cross-laminated sandstone. This sandstone is rarely capped by a mega-rippled surface that resembles hummocky cross-stratification (which is commonly attributed to submarine reworking during storm surges) (Figure 9).

The larger conglomerate-based, trough cross-bedded sandstone bodies are interpreted as subaerial braided river channel deposits, and the thinner matrix-supported conglomerate and horizontally laminated sandstone units are interpreted as overbank splays lateral to the braid channels on the distal surface of an alluvial fan. Rarely, thin sheets of granule conglomerate occur as discrete beds within the mudrock sequences. They have been deposited as low amplitude starved megaripples. These are interpreted as subaqueous debris flow lobes that have been locally reworked, either at the time of emplacement or sometime later, by storm-generated wave action. The rapid interdigitation of coarse-grained, fluvially-generated sands and gravels with laminated fines suggests that this succession lies in the distal parts of a sublacustrine fan that prograded from the tectonically inactive margin of the lake onto a relatively shallow shelf (Wescott and Diggens 1998). Similar facies sequences have been reported from cores drilled into the margins of Lake Turkana in northern Kenya, a modern rift valley lake (Cohen 1989). It is notable that the coarse clastics enter the lake from rivers entering along its narrow shoreline but they rarely get transported more than 1km offshore. These sands and gravels accumulate in narrow bodies parallel to the shoreline. The gravels are typically matrix-supported with angular to sub-angular quartz and volcanic rock pebbles. A similar setting is interpreted for the Sakamena facies sequences at Zavoloa River.

Taphonomy

The common vertebrate fossils at Zavoloa River locality are of the medium-sized (total adult body length approximately 640mm) sauropterygian reptile *Claudiosaurus germaini*. They occur rarely as fully articulated skeletons and far more commonly as disarticulated, transported and sorted bones within quartz pebble conglomerates. The articulated skeletons are found inside calcareous siltstone pods that occur within the olive grey mudrocks and within the lower parts of the thin tabular splay sandstones (Figure 10). The biscuit-shaped calcareous pods are approximately 10 cm thick with flattened upper and lower surfaces, and are up to 45cm in longest diameter. Unlike the *Barasaurus*- bearing nodules at Ranohira Cemetery, these nodules show no parting on the outer surface as a telltale sign that there is a skeleton inside. The pachyostotic postcranial bones are characteristically very dark grey (2.5Y3/0) sometimes with a greyish brown (2.5Y3/2) colour and preserved uncrushed and unweathered (Figure 10). As with the Ranohira locality, there are many calcareous nodules that do not contain macrofossils, although there is no record of any

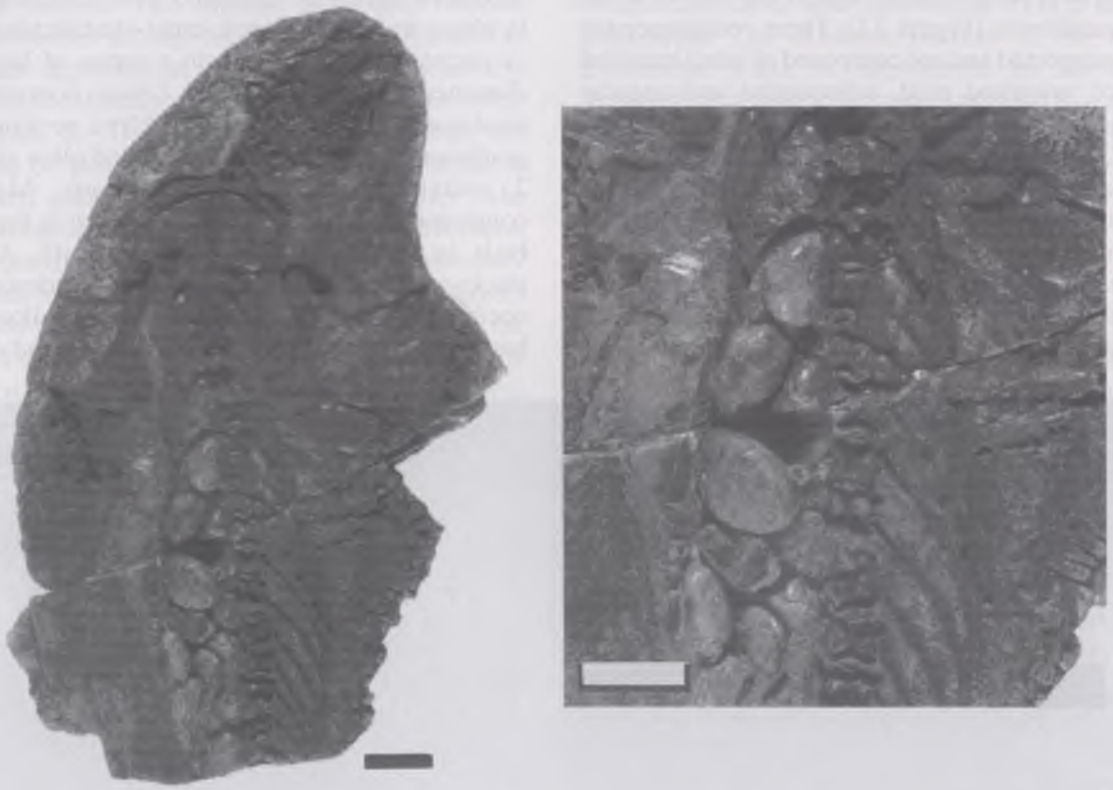


Figure 7. Ranohira locality: Anterior half of a *Barasaurus* skeleton preserved in dorsal-up attitude. Note the clump of roughly equal-sized quartz pebbles lying lateral to the mid-line (right side in life) in the abdomen. The close-up shows that unlike *Hovasaurus*, *Barasaurus* pebble masses do not have any grit or sand-sized clasts.

articulated *Claudiosaurus* skeleton that was not contained inside a nodule. The skeletons are mostly preserved in dorsal-up attitude with limbs trailing backwards along the sides of the body, in a pose similar to the inferred swimming position (Carroll 1981). Rarely are the skulls or distal portions of the tail preserved within the nodules, suggesting that decomposing tissue and muscle, rather than skin, determined the distribution and degree of micrite precipitation. The few skulls that are preserved are lying lateral-up and are inevitably crushed with slight displacement of the lower jaw elements (Carroll 1981, Figure 11).

Isolated post-cranial elements such as ribs, vertebrae, interclavicles, and long bones occur scattered within the olive-grey mudrocks. These are generally well preserved, showing little signs of abrasion or weathering. Adult *Claudiosaurus* long bones and ribs are comparatively heavy and brittle because they were originally composed of more compact bone tissue. This was possibly a buoyancy adaptation that evolved after the animal re-entered an aquatic niche (de Ricqlès 1974; de Buffrénil & Mazin 1989). A scattered skeleton of a dicynodont therapsid was found in the mudrocks at this locality. Unfortunately, no skull material could be located, but the post-cranial elements are of the size of *Oudenodon*, which is the only therapsid to have been identified in this basin (Mazin & King 1991).

In the lower half of the section exposed at Zavoloa River, bonebed type accumulations of disarticulated *Claudiosaurus* post crania and plant debris are associated with conglomerate lags at the base of some channel sandstones (Figure 12). These conglomerates are clast-supported and are composed of small rounded pebbles of reworked mud, subrounded and angular quartz, feldspar and mica set in a coarse dirty arkose matrix. On the upper surface of the conglomerate lenses, patches of disarticulated bones lie along the axes of troughs and on the downstream-fining "tails" of side-accreted gravel bars. They comprise mainly ribs, vertebrae, long bones and girdles in a chaotic melange with a relatively weak current alignment (Figure12). The ribs appear to be the most strongly orientated with their proximal ends upstream. Most of the long bones are unbroken but show slight abrasion of the articular surfaces; a few are broken and well worn to the extent that they resemble rounded pebbles. The associated plant trash consists of impressions of *Schizoneura*-like leaf and woody stem fragments. Rounded clasts of silicified wood are a rare intraclast in the conglomerates, although a few metre-long silicified logs were recovered from the intervening mudrocks. Dr Marion Bamford (University of Witwatersrand) has made a preliminary identification of the wood as *Araucarioxylon africanum*, which is a relatively common conifer that occurs in Late Permian to Mid-Triassic sediments throughout southern Africa.

Mount Eliva, Andamilamy District [G.R. S 23°59'41.4" E44°25'55.0"]

Sedimentology

The strata exposed at Mt Eliva are the most southerly outcrops of the Lower Sakamena Formation, and they lie stratigraphically nearer to the top of the formation than in either of the previously described localities (Figure 1). They comprise roughly 1:1 ratio of sandstone to mudrock, and are interpreted as having accumulated on a submerged lacustrine delta at the southern end of the Sakamena lake (Figures 2 and 13). Predominantly fine to medium-grained light yellowish-brown (2.5Y 6/4) sandstones form tabular sheets between 0.5-1.25m thick, which are traceable up to 1km. They have flat basal surfaces with shallow scour troughs filled with clast-supported clay- and quartz-pebble conglomerate. The main body of the sandstone sheets is structured with lenticular beds of in-phase and in-drift ripple cross-stratification, which, in places, has deformed into a series of large (1-2m diameter) pillow structures. Upper contacts of the sandstone bodies in the Mt Eliva section are all gradational into rhythmically bedded olive grey (5Y5/2) siltstone/mudstone alternations. Mud flake conglomerate lenses 2-5 cm thick occur in the siltstone beds in the lower part of these units. Arthropod trackways of the *Umfolozia*-type (Anderson 1975) occur on some of the flaggy weathering siltstone beds but the majority of surfaces are smooth and devoid of



Figure 8. Zavaloa River locality: Vertical section of matrix-supported quartz pebble and bone conglomerate that fills isolated scour troughs at the base of tabular low sinuosity channel sandstone units.



Figure 9. Zavoloa River: Wave-rippled surface of a fine grained splay sandstone interpreted as part of the submerged distal facies of an alluvial fan entering the side of the Sakamena lake.

trace fossils. The rhythmites commonly grade upwards into a 2-4m thick interval of olive (5Y4/3), very finely laminated siltstone with scattered small oblate calcareous nodules, some of which contain vertebrate and plant fossils. The tabular lenticular bedded sandstone bodies at this locality are interpreted as having been deposited in wide shallow low-sinuosity channels on the distal portion of a large sub-lacustrine delta (Figure 2). The lack of significant scour, the dominance of unidirectional ripple cross-laminated, fine-grained sand, and the gradational rather than interdigitating upper contact with essentially overbank facies are good indications that this was a low sinuosity system with high suspended sediment load. The layers of slumped laminae that occur near the top of the uppermost sandstones in the Mt Eliva section show the characteristics of post-depositional soft sediment deformation caused by gravity sliding of waterlogged fine sand soon after it was deposited. The lack of any emergence or desiccation features in the section suggests a sub-aqueous setting for the entire section. Rapidly alternating siltstone/mudstone rhythmites and mud flake conglomerate lenses are the commomly associated "overbank" facies deposited on the flanks of the channels in the middle and distal parts of the delta slope. The rhythmites are interpreted as having been deposited by episodic density underflows and are similar to the interdistributary bay facies of large deltas. The very finely laminated mudstone facies is indicative of the "background" sedimentation of suspension fines that characterises a closed lake system with restricted circulation and probably for most of the time, a thermally-stratified water column. In the geological record of rift valley lakes, the Devonian Escuminac Formation of southern Quebec (Dineley and Williams 1968) has similar lithologies, sedimentary facies and taphonomic style to the Lower Sakamena. The offshore portion of the elongate Escuminac Lake is interpreted as having been stratified, with anoxic bottom conditions that gradually become more fluvially influenced towards the axial ends of the lake where distal turbidites grade into deltaic and sub-aerial floodplain facies. This scenario could well describe the geomorphology at the southern end of the Sakamena lake.

Taphonomy

The fossil assemblage in the Lower Sakamena at Mount Eliva is dominated by the aquatic younginiform *Hovasaurus* along with rare palaeoniscid fishes, glossopterid fructifications and *Schizoneura* leaf fragments. They are preserved within oblate, smooth-surfaced, calcareous nodules similar to those at Zavoloa River and generally larger than those at Ranohira (Figure 14). The nodules are scattered within the fine-grained laminated siltstone facies only. None were found within the sandstone facies. The *Hovasaurus* skeletons are fully articulated, although rarely entirely enveloped by the nodule. The skull and tail are usually missing, suggesting that nodule formation in the surrounding matrix is controlled by the amount of decomposing soft tissue in the carcass. Currie (1981) estimated the length of an adult *Hovasaurus*, based on the largest incomplete specimen

in Piveteau's collection, to be approximately 900mm. The calcareous cement that forms the nodule is most thickly developed around the quartz pebble mass within the abdomen of *Hovasaurus* specimens. Piveteau (1926) considered the abdominal pebble masses to have provided the nucleus of the nodule formation. It is interesting to note that all the articulated *Barasaurus* skeletons at the Ranohira locality also have abdominal pebbles, but they are fewer in number and do not have any grit-sized clasts. Currie (1981) concluded that the pebbles were deliberately ingested and may have been used in a gastric mill as an aid to digestion, but he considers them more likely to have been used as ballast to assist swimming. No plant fragments have been observed in any of the pebble masses of either *Barasaurus* or *Hovasaurus*, although several nodules have lycopod stems and *Schizoneura* leaf fragments preserved next to the skeletons. Although it is negative evidence, the presence of a gastric mill would imply that the animal was eating fibrous plant tissue. Therefore, plant trash remains should be preserved within the pebble mass. The lack of such remains favours the ballast stone interpretation.

The attitude of the smooth-surfaced siltstone nodules and the fossils contained within can only be determined whilst they are still embedded. Unfortunately, Piveteau did not record attitude for his collection that resides in Paris. Therefore, the original orientation can only be determined on the few specimens that were excavated during fieldwork for this study. Only three *Hovasaurus*-bearing siltstone nodules were collected in situ and all three contained skeletons that were buried dorsal-up. This was determined in the field after splitting the nodule and noting that the ribs and vertebrae overlie the gastralia and are slightly displaced. In these orientated

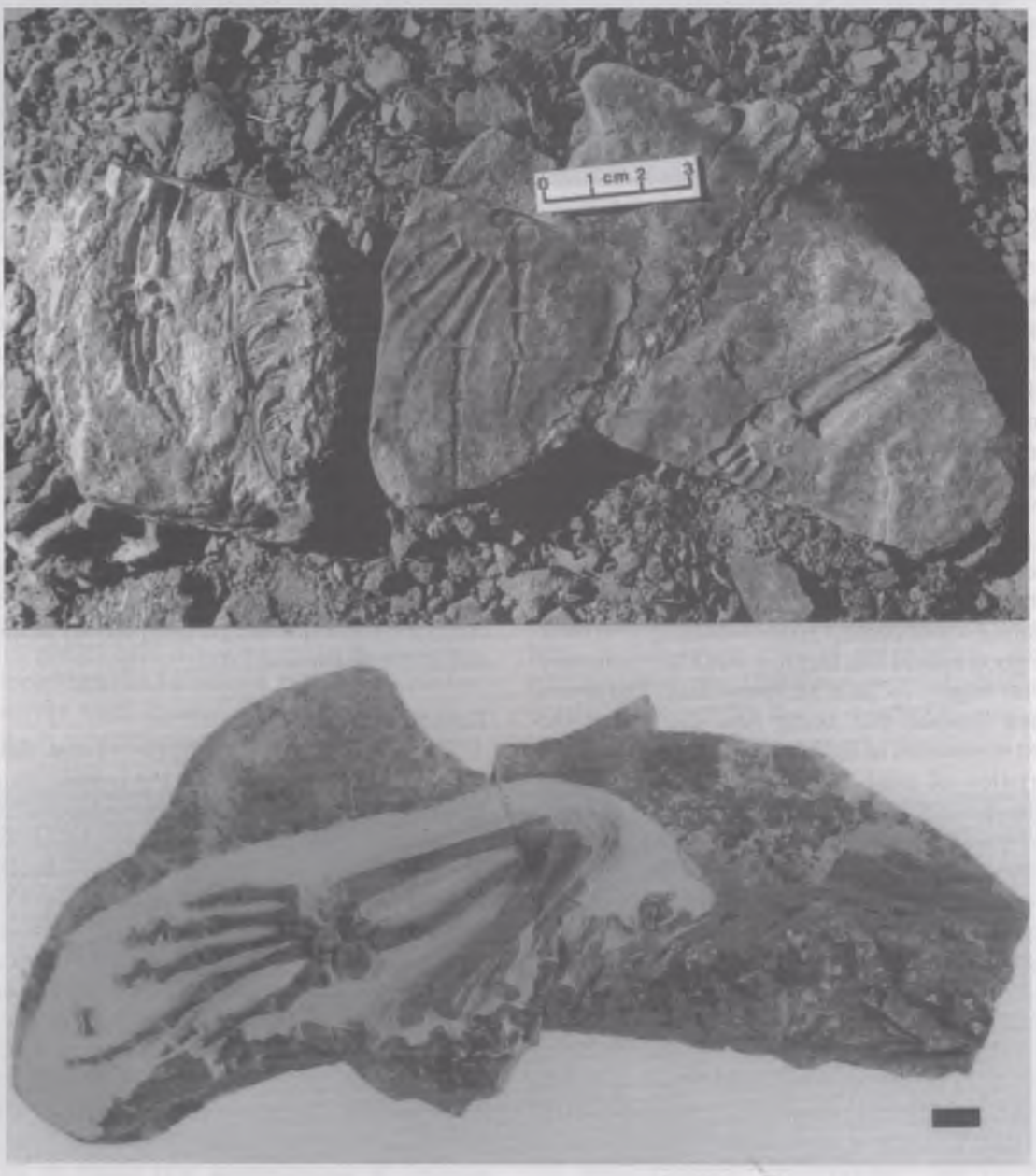


Figure 10. Zavaloa River: *Claudiosaurus*-bearing calcareous nodules in the field and after preparation a right arm and manus of the semi aquatic reptile *Claudiosaurus* (scale bar=1 cm)

specimens, the pebble mass is parted by the ribs and the gastralia are not visible. One specimen of a juvenile *Hovasaurus* collected by Piveteau from Mt Eliva (numbered 1925-5-20) is preserved lateral-up and clearly shows a mass of small quartz pebbles lying ventral to the spine just anterior to the pelvic girdle and dorsal to the gastralia. Incidentally this specimen also shows a possible tail "fin" impression above the neural spines of the caudal vertebrae. From taphonomic evidence it is concluded that *Hovasaurus* was aquatic and ingested quartz pebbles and grit to weigh down and stabilise the abdomen in an effort to counteract the upward thrust generated by the lungs (Laurin pers. comm.) and/or tail (Currie 1981) when swimming.

DISCUSSION OF MODE OF DEATH, BURIAL AND PRESERVATION OF SAKAMENA AQUATIC VERTEBRATES

Mode of death

In modern large, deep lakes, perhaps the most common cause of mass mortality among teleosts is oxygen deficiency and thermal shock when large volumes of cool anoxic bottom water mix with warm oxygenated surface water. This breakdown of thermal stratification, or overturn, is most commonly caused by sudden influx of cold sediment-laden floodwaters during and immediately following thunderstorms in the catchment area. Within hours large numbers of fish suffocate, especially when plumes of suspended silt and clay effectively clog the gills (Eric Anderson, pers.comm.). The thermocline in small, deep lakes may also be destabilised during extended periods of drought, as the lake becomes shallower (Behrensmeyer and Hooke 1992). Other common causes of mass fish kills in lakes are poisoning by algal blooms (McGrew 1975), and sudden cold winds and rainstorms (Perkins 1970). Rarely, seismically induced degassing of the anoxic bottom sediments can cause mass mortality in and around the lake. The presence of thick sequences of microlaminated and non-bioturbated mudrock containing horizons of fully-articulated, non-scavenged and undisturbed aquatic vertebrate fossils is compelling evidence that the bottom conditions in the centre of the Sakamena lake were anoxic for much of the year.

Despite the bias caused by preferential collecting of nodules, it is evident that the most common taphonomic mode of aquatic reptiles and fishes in the Lower Sakamena is as complete articulated skeletons lying dorsal-up. It is also evident that many individuals of all ages died within a short-term event and that they were buried soon after death, before complete decomposition and before significant skeletal disarticulation took place. There is no evidence of macro-predation or scavenging on these carcasses. Scale impressions on some specimens and abdominal stone clumps confirm that most individuals were intact when they arrived at their final burial site. The most plausible cause of death in this setting is overturn of the thermocline caused by storm-generated flooding. Sedimentological evidence suggests several sources of sediment-laden braided channels issued into a linear standing water body. Fresh plant material and newly drowned carcasses of terrestrial animals such as *Oudenodon* would have floated further offshore before sinking beyond the influence of bottom traction currents.

Unlike the actinopterygians, *Barasaurus*, being an air-breathing, potentially amphibious or fully-aquatic reptile, would not have been suffocated by an overturn event but may have been debilitated by the sudden drop in temperature of the surface waters. Immediately after death, the ballast-weighted cadavers sank, belly-down, to the lake floor, where they lay with limbs spread-eagled in a dorsal-up attitude. The newt-like "tail fin" came to rest on its side and it would have tended to rotate the abdomen until the pelvic girdle fell apart. Methane generated by bacterial decomposition of the stomach contents would have bloated the abdomen but this was clearly not enough to re-float the cadaver. Studies of modern fish cadavers in similar settings show that in water temperatures of less than 16°C, anaerobic decay of the gut contents does not generate enough buoyancy to re-float the cadaver (Elder and Smith 1988). Further anaerobic decay of the flesh and muscle tissue continued for an estimated 2-5 years, during which time the carcass was undisturbed by scavengers or turbulent bottom currents until it simply collapsed on itself. Before complete decomposition of the soft tissue, the carcasses had become completely covered with a layer of microlaminated silt. The silt drape settled from clouds of suspended fines that were rafted offshore on the thermocline during subsequent flood events. Anaerobic bacterial decay generated a sulphate-rich halo in the surrounding sediment that in some cases became the locus for early diagenetic precipitation of micrite from groundwater. Details of the controls and timing of this nodule formation are discussed later.



Figure 11. Zavoloa River: Severely crushed skull and lower jaw of *Claudiosaurus* preserved in a tabular sandstone but without having been peri-mineralized with a calcareous nodule (Scale bar=0.5cm)

Towards the margins of the Sakamena lake, the bottom waters were permanently oxygenated and, following thunderstorms in the catchment, were subjected to high-energy mass transport episodes. Sheet wash and flood discharge resulted in the injection of sand and poorly sorted gravels into the lake, where they accumulated in sheets parallel to shore. These short-lived debris flows transported pebble-sized basement rock fragments and numerous disarticulated skeletal elements of another aquatic reptile, *Claudiosaurus*. The repeated occurrence of conglomerates rich in *Claudiosaurus* bones suggests that this taxon was also a victim of mass mortality but in an environment that was not conducive to preservation. It is likely that *Claudiosaurus* preferred to forage in shallower waters and was possibly semi-terrestrial (Carroll 1981), spending time on the shore alongside *Oudenodon* and other therapsids (Mazin & King 1991). However, it too probably suffered from thermal shock during overturn events that resulted in numerous cadavers in the nearshore parts of the lake, which were then reworked by low-density turbidity currents. Those fully articulated skeletons preserved in the thicker sheet sands were entombed soon after death, possibly in the same depositional episode, and have escaped subsequent reworking.

Nodule Formation

It is evident that in the chemical environment that existed in the Sakamena lake sediments soon after deposition, decomposing organic matter was preferentially enveloped in calcareous nodular material. This preferential perimineralization occurred after burial and before compaction, and possibly before replacement of the carbonate component of the bone. This implies an early diagenetic origin for the nodules, which is almost certainly linked in some way to the bacterial decomposition of the organisms. A tendency



Figure 12. Zavoloa River: *Claudiosaurus* bone conglomerate lining the axis of a trough in a braided channel sandstone. Note the weak orientation of long bones and the stronger alignment of ribs with their proximal ends upstream.



Figure 13. Mount Eliva locality: View of the *Hovasaurus* collecting grounds, closely guarded by the local residents, with Mount Eliva in the background.

for nodules to thicken on the underside suggests that the reducing conditions necessary for precipitation of calcium carbonate out of the interstitial water in the sediment occurred whilst the topside was still exposed. Only later, after burial of the organic remains, was calcification of the overlying sediment able to take place. It is clear that the calcium carbonate precipitation was not displacive because the original fine sedimentary structures remain undisrupted within the nodules. The sharp outer boundary of the nodules indicates that the calcium carbonate precipitation was probably incremental and the nodule grew outwards from the decaying organic matter over an extended period. The lack of compaction of the enveloped fossils indicates early lithification of the calcareous sheath that increased mechanical strength and prevented vertical compaction resulting from continued accumulation of sediment.

Arduini (1993) noted that several articulated *Barasaurus* skeletons were preserved on bedding planes within the nodular horizons but without any associated nodule formation. He also noted that in some cases only the girdle sections of the skeletons are perimineralized, with the rest of the skeleton preserved outside the nodules, on the siltstone bedding planes. Arduini (1993) interprets this as evidence that the nodule formation was centred on the products of bacterial decay of cartilage within the pelvic and pectoral girdles. It is clear from the field results that collecting bias has distorted the importance of nodule

formation in the preservation of the Late Sakamena flora and fauna. Many articulated skeletons and plant fossils have no associated nodule formation and were overlooked by previous workers (with the exception of Arduini (1993)). Even within the three nodular "horizons," the perimineralization is rarely complete, so that many partial skeletons of *Barasaurus* have been collected because only the nodular portion was recovered. It is also apparent that the particular chemical conditions that led to early diagenetic precipitation of calcium carbonate in interstitial spaces surrounding decomposing organic remains occurred at least three times in the Sakamena lake sediments.

After death, the carcasses settled into an anaerobic environment on the lake bottom. Bacterial decomposition of the soft tissues released hydrogen sulphide into the overlying water column and underlying sediments. Silt and clay-sized fines, originating from rivers feeding into the lake and rafted on the thermocline into the offshore regions, slowly draped the decomposing carcasses. Most were buried fully articulated, but in some cases, after the skin had rotted, the limbs became detached at their proximal ends to lie next to the carcass. After burial to a depth of 2-3 cm below the sediment/water interface, the ligaments and cartilages rotted and the rib cages collapsed. At the same time, hydrogen sulphide continued to accumulate in the interstitial fluids of the surrounding sediment. With further sediment accumulation, the skeletons passed slowly through the zone of bacterial decarboxylation around 10cm below surface, further concentrating the halo of diffused hydrogen sulphide-rich fluids around the carcass. Under normal circumstances bacterial activity would result in complete decomposition of the organic tissues including the collagen networks of the skeletons, leaving the bones brittle and vulnerable to compression. Plant material was for the most part completely denatured, leaving only impressions; only the lignin-rich stems remained intact.

However, on at least three occasions, this process was interrupted by the interstitial precipitation of calcium carbonate within the sulphide-rich halos around the decomposing organic matter. The micrite crystallised in response to the lowered pH in the diffusion gradient around each decomposed carcass. The threshold for precipitation was determined by the sulphide concentration in the halo. Thus, those carcasses that were buried quickly had thicker and more continuous micrite nodules, whereas those buried more slowly had not enough organic matter left to form a continuous micrite envelope. This resulted in selective micritization around the cartilage-rich parts of the skeleton such as the girdles.

What caused the "micritization events" that resulted in the three calcareous nodule horizons in the upper Lower Sakamena? Evidence suggests that these were periods when the generally anoxic sediments situated in the offshore areas of a linear rift valley lake became oxygenated. It appears that each micritization event resulted from oxygenated water penetrating at least 0.1m below the sediment water interface over a large area, suggesting that they could have been the result of prolonged lowstand. During periods of low lake level, the thermal stratification could not be sustained, and oxygenated bottom waters with carbonate in solution percolated through the upper layers of sediment, precipitating Mg-rich micrite around all partially decomposed organic remains. Similar calcareous precipitates have been detected on decomposing fishes in thermally stratified lakes (Elder and Smith 1988), which are the result of algal blooms depleting the water of carbon dioxide. This mechanism is most effective during lowstand when the water volume is insufficient to dissipate the algal toxins (Prescott 1948). If such lowstand events were climatically controlled, they should prove to be useful timelines to accurately correlate strata within and between these ancient rift valley lakes both in Madagascar and Tanzania.

SUMMARY

The upper Lower Sakamena Formation in southwestern Madagascar was deposited in open-ended rift valley lakes that formed in the axial regions of two half grabens some 255 million years ago. Three discrete sediment/fossil associations reflect contemporaneous subenvironments of the Sakamena lakes. Restricted circulation and thermal stratification of the relatively deep offshore waters resulted in thick



Figure 14. Mount Eliva locality: Local residents demonstrating how they excavate nodules in the search for *Hovasaurus* fossils that are sold to a foreign dealer on his yearly visit.

deposits of microlaminated muds which contain at least three mass mortality horizons of an aquatic procolophonid reptile, *Barasaurus*. Nearer to the lateral margins of the lake, especially on the inactive side of the half-graben, numerous transported remains of *Claudiosaurus* are commonly preserved in braided stream channel conglomerates. This diapsid, possibly sauropterygian reptile is believed to have been semi-aquatic, a conclusion corroborated by the nearshore environment of preservation and the taphonomy of its fossils. Another younginiform reptile, *Hovasarus*, is believed to have been fully aquatic. It is found in abundance in sediments deposited on a sub-aqueous delta that prograded into the southern end of the Sakamena lake (see Figure 2).

In large, deep, thermally stratified lakes, thermal shock from periodic overturn and poisoning from algal blooms are the most likely causes of mass mortality among the aquatic fauna. Sulphides released from anaerobic bacterial decay of soft tissue and girdle cartilage formed reduction halos around the newly buried reptile carcasses. At least three times during the infilling of the lake, oxygenated waters flushed through the bottom sediments to precipitate carbonate nodules in the reduction halos. These 3 "micritization episodes" are interpreted as extended periods of lowstand when thermal stratification could not be maintained and oxygenated waters came into contact with previously anoxic sediments. If such lowstand events were climatically controlled, they may be useful timelines to accurately correlate strata within and among these ancient rift valley lakes both in Madagascar and Tanzania.

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