



## Strengthening Western Gondwanan correlations: A Brazilian Dicynodont (Synapsida, Anomodontia) in the Middle Triassic of Namibia

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### ABSTRACT

Terrestrial Middle Triassic strata occur throughout continental Africa and are particularly well exposed in South Africa, Tanzania, Zambia, and Namibia. The youngest age for all these African deposits is widely accepted as early Middle Triassic (Anisian). Fossils collected recently from the uppermost strata of the upper Omingonde Formation in Namibia highlighted the presence of *Chiniquodon*, a carnivorous cynodont previously only found in Ladinian–Carnian aged rocks of South America. In addition, work in progress indicates that a large archosaur, originally reported as *Erythrosuchus*, also discovered from levels close to the top of this unit, is in fact a rauisuchian, a group of archosaurs well known from Ladinian–Carnian beds of southern South America. Here we present the first record of the tuskless dicynodont *Stahleckeria potens* from the top of the upper Omingonde Formation in central Namibia. This taxon was up until now only known from the Ladinian *Dinodontosaurus* Assemblage Zone of the Santa Maria Formation in southern Brazil. Thus, compelling evidence for a Ladinian age for the upper levels of the upper Omingonde Formation is provided by two therapsid and one archosaur taxa. The tetrapod fauna of the upper Omingonde Formation partially fills the gap of the well-documented hiatus (Ladinian gap), prevalent throughout the Karoo basins of south and central Africa. The presence of the same therapsid taxa in the Namibian Waterberg Basin and the Paraná Basin of Brazil during Middle Triassic suggests that these basins were biogeographically linked through a series of interconnecting lowlands, with no major ecological, climatic and/or physical barriers.

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### 1. Introduction

Dicynodonts are a diverse and widespread group of herbivorous therapsids, which constituted a key component of Permian and Triassic terrestrial tetrapod communities throughout Pangea (e.g. King, 1988; Fröbisch, 2009). In western Gondwana (southern South America and south-central Africa), dicynodonts are well represented and diverse. Accordingly, they have been extensively used as biostratigraphic markers mainly to correlate Triassic successions between western Argentina and southern Brazil and Permo-Triassic strata around south-central Africa (e.g. Bonaparte, 1966, 1969; Cox, 1968, 1969; Vega-Dias et al., 2004; Langer et al., 2007; Domnanovich, 2010; Kammerer et al., 2011). Nevertheless, faunal correlations between South America and Africa based on dicynodonts are scarce. Until recently, *Kannemeyeria* represented the only dicynodont taxon shared between Africa (South Africa and Namibia) and South America (Argentina); however, the taxonomic identification of

the Argentinian specimen has been questioned (Renaut and Hancox, 2001).

Conversely, cynodont therapsids have proven to be an important tool in western Gondwanan correlations, particularly Early-Middle Triassic strata. A recent revision of cynodonts from the upper part of the Middle Triassic upper Omingonde Formation of central Namibia found taxonomic links with tetrapod faunas of southern Africa and South America (Abdala and Smith, 2009). These included the cynodont *Luangwa* which is also present in faunas from Zambia and South America, *Aleodon*, also known from Tanzania, and the carnivorous cynodont *Chiniquodon* which also occurs in South America and Madagascar (Abdala and Smith, 2009; Kammerer et al., 2010).

To improve our understanding of the palaeobiogeographical connections in western Gondwana during the Middle Triassic we recently conducted fieldwork targeting the uppermost Omingonde strata exposed along the Omaruru River in central Namibia. Several therapsid fossils were discovered of which the most interesting is the skull and lower jaw of a relatively large tuskless dicynodont which we have identified as *Stahleckeria potens*, a species previously known only from a Ladinian-aged interval of the Santa Maria Formation of southern Brazil. This new specimen constitutes the first large tuskless

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dicynodont described from the Triassic of Namibia and only the second for the Middle Triassic of Africa. Tuskless dicynodonts are represented by four taxa in the Middle-Late Triassic successions of South America, one of them, *Ischigualastia*, being abundant. This new record not only strengthens correlations between Namibia and southern South America during early Mesozoic times but also supports previous suggestions of a late Middle Triassic (Ladinian) age for the fauna represented in the uppermost strata of the upper Omingonde Formation. Accordingly, these new vertebrate fossils from the upper Omingonde are hitherto the only positively identified Ladinian-aged fauna for continental Africa.

## 2. Geological setting

In southwestern Gondwana, during the Middle Triassic, the large Karoo foreland basin of South Africa was positioned around 55° S

(Fig. 1) and was bounded by the rising Cape Fold mountains to the south, east and west and a vast plateau to the north (Visser, 1991; Turner, 1999; Hancox and Rubidge, 2001; Catuneanu et al., 2005; Rubidge, 2005; Zeffass et al., 2005). At the same time this plateau was affected by crustal extension that opened up a broad belt of linear rift valleys stretching NE-SW across southern Gondwana (Tankard et al., 2009; Zeffass et al., 2004; Fig. 1) and it is in these rifts that various Karoo-aged (Permo- Carboniferous to Early Jurassic) successions have been preserved. The structural trend has been attributed to transtensional forces in the crust that were being released along deep-seated pre-Gondwanan sutures (De Wit et al., 1988). Zeffass et al. (2004) concluded that the en-echelon extensional basins of southern Brazil and southern African were formed in dextral shear zones sub-perpendicular to the Gondwanides orogen caused by oblique compression in the Sierra de la Ventana and Cape Fold belts. Alternatively Loffler

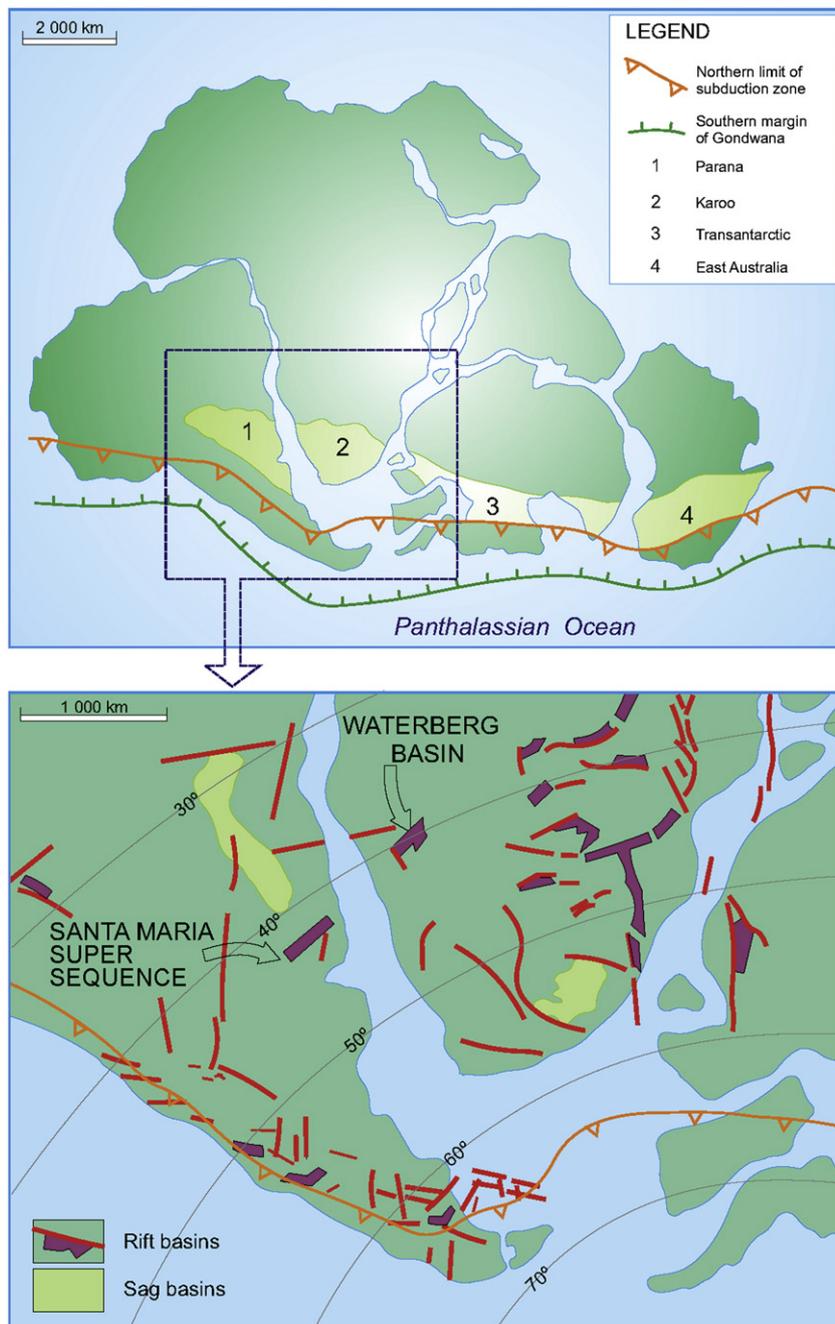


Fig. 1. Paleogeographic reconstruction of Western Gondwana during the Middle Triassic showing the relative position of the Waterberg Basin and the Santa Maria Supersequence of the Paraná Basin and their main structural elements.

(1998) interprets the lineament as a “failed rift” resulting from crustal upwarping as a precursor to the Early Cretaceous magmatism that accompanied the eventual break-up of western Gondwana.

The Omingonde Formation of central Namibia accumulated in a series of 3 parallel half-grabens in the region of south-western Gondwana that lay around 40° S (Fig. 1). These small basins have been named Waterberg and Erongo on the southern side and Otjungundu on the northern edge (South African Committee for Stratigraphy, 1980). The fossils and outcrops documented here (Figs. 2 and 3) all lie within the Waterberg Basin in the area around Mount Etjo (Stollhofen et al., 1998; Holzförster et al., 1999; Zeffass et al., 2005). Here, the 700 m-thick Karoo-aged succession lies directly on an uneven, glacially sculpted (Loffler, 1998) surface of Neoproterozoic granites and gneisses. The new dicynodont was recovered from the predominantly red fluvial floodplain deposits of the Upper Omingonde Fm., some 40 stratigraphic meters below the base of the predominantly aeolian Etjo Formation (Fig. 2). Global modeling (Hallam, 1985), as well as geological (Du Toit, 1948; Smith, 1995) and paleontological data (Grine et al., 1979, but see Kemp, 1982) indicate that the climate in the interior of western Gondwana during the Middle

Triassic was warm to hot, seasonally arid with mean annual temperatures of between 16 and 20 °C (Smith, 1995; Sellwood and Valdes, 2006).

### 3. Paleoenvironmental interpretation

In the upper Omingonde succession, the fluvial channel sandstone bodies gradually lose their gravel component yet retain high sinuosity characteristics and, as such, may be described as the preserved in-channel deposits of pebbly sand-bed meandering rivers. Fig. 3 is a measured sedimentological section of cliff exposures along the Omaruru River (see Fig. 2) in the vicinity of the new dicynodont and from which most of the associated fauna was recovered. This interval corresponds to the lower half of Unit 4 of Holzförster et al. (1999), which they interpret as floodplain facies with sheetflood deposits. The lower pebbly sandstone bodies display ribbon-shaped cross-sectional geometry and lateral accretion surfaces typical of meander-belt point-bar deposits (Friend, 1983). They have runneled basal scours and comprise mainly trough cross-bedded, coarse-grained sandstone or gritstone with

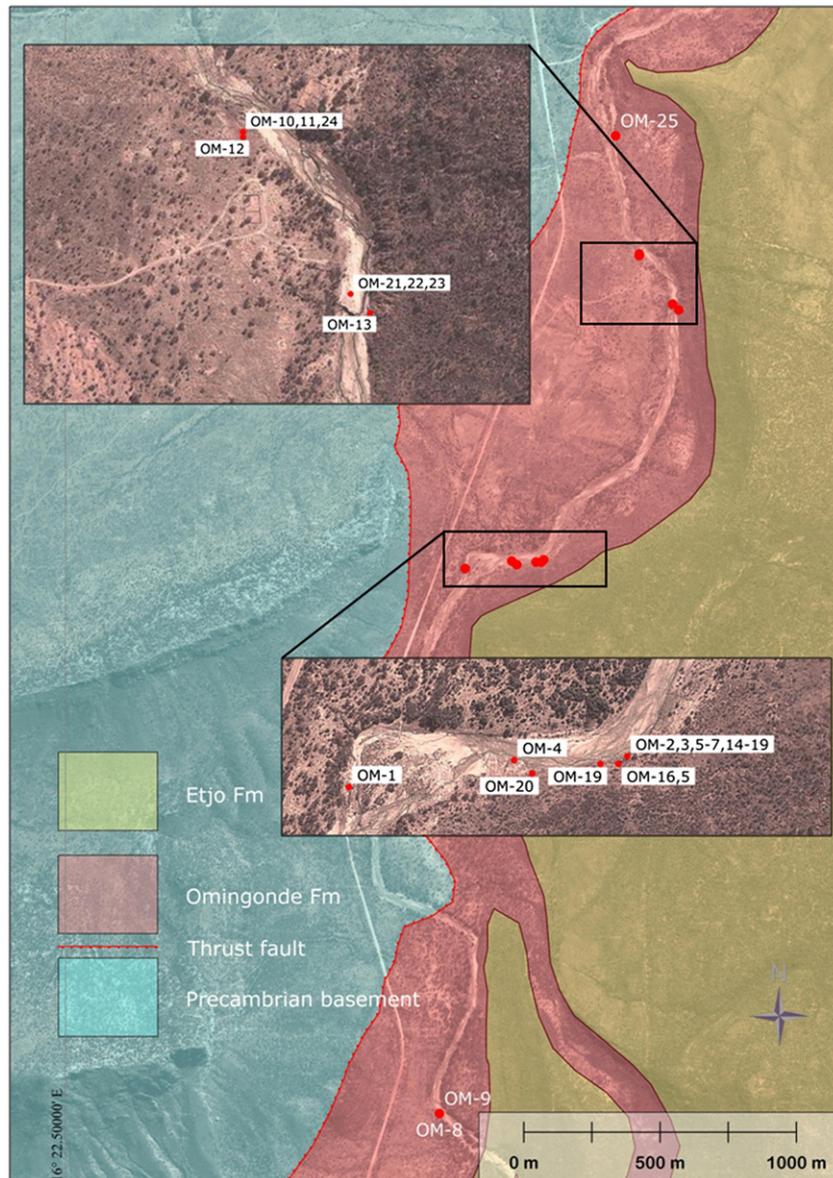


Fig. 2. Locality of the new *Stahleckeria* and associated fossil fauna in the Omaruru River, Otjiwarongo District, Namibia.

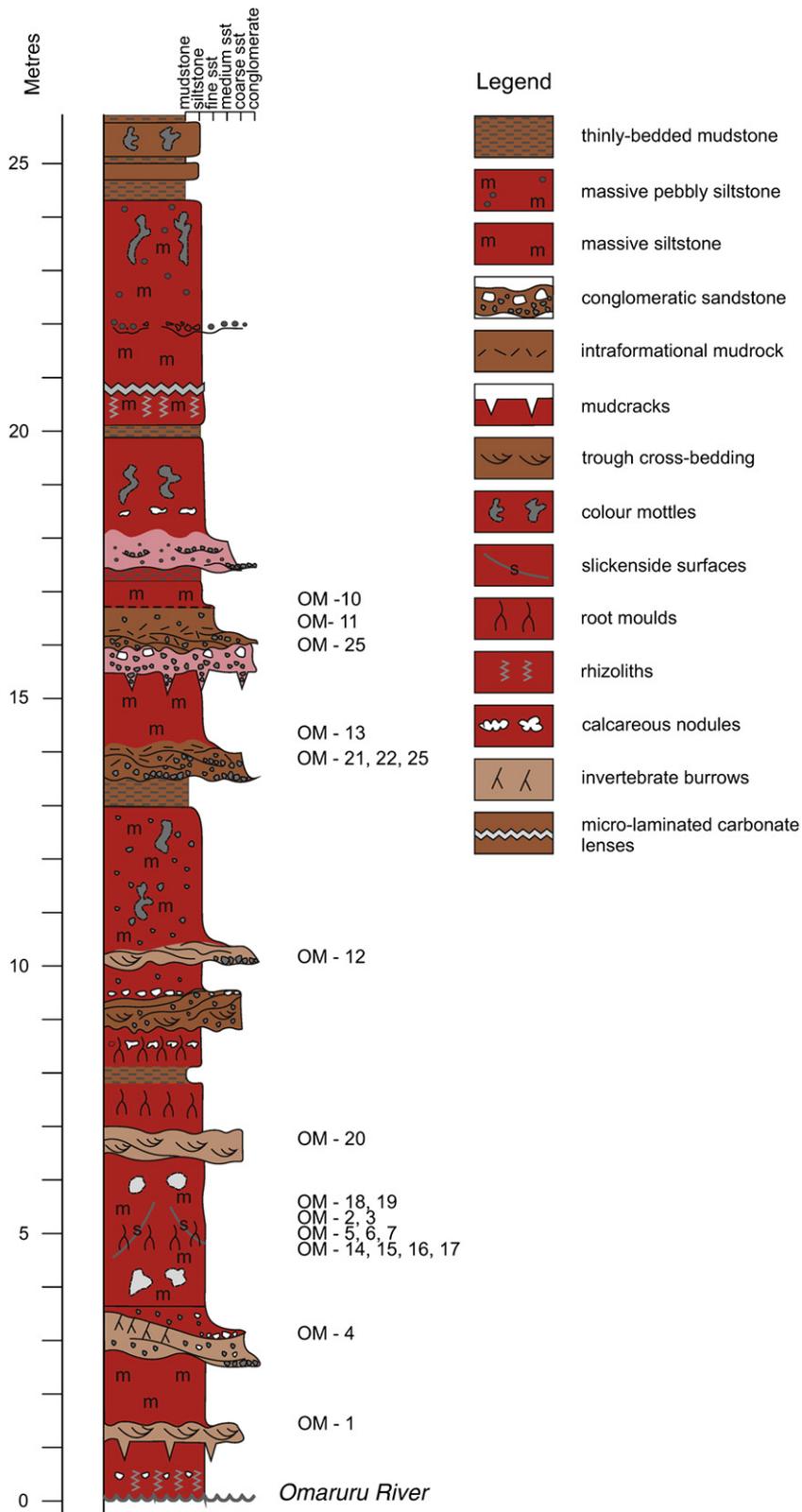


Fig. 3. Sedimentological section of the new *Stahleckeria* locality.

scattered maroon mudrock pebbles and lenses of matrix supported white quartz and rare basaltic pebble conglomerate.

The sandstone-to-mudrock ratio in the logged interval is 1:6. The overbank fines are dominantly thickly bedded, pale red, massive siltstone with some horizontally laminated fine-grained sandstone sheets

containing minor mudrock flakes. Colour mottling and horizons of calcified arcuate planes are common in the massive mudrock. These homogeneous siltstone beds are interpreted as loessic in origin, each having been deposited rapidly, possibly in a single duststorm (Pye, 1995), then overprinted with immature vertisols (Smith and Swart, 2002).

**Table 1**

List of fossils found in the Omaruru River in levels representing the uppermost strata of the upper Omingonde Formation. See Fig. 2 for localities and Fig. 3 for stratigraphic position.

Field number	Southings	Eastings	Field identification
OM-1	21 deg 03.659	16 deg 23.450	Dicynodontia ulna
OM-2	21 deg 03.705	16 deg 23.445	Luangwa snout
OM-3	21 deg 03.705	16 deg 23.445	Chiniquodon skull and skeleton
OM-4	21 deg 03.659	16 deg 23.450	Rauisuchian skeleton
OM-5	21 deg 03.705	16 deg 23.445	Traversodontidae skull
OM-6	21 deg 03.705	16 deg 23.445	Luangwa snout
OM-7	21 deg 03.705	16 deg 23.445	Cynodontia indet.
OM-8	21 deg 04.731	16 deg 23.239	Dicynodontia postcrania
OM-9	21 deg 04.731	16 deg 23.239	Dicynodontia terminal phalanx
OM-10	21 deg 03.138	16 deg 23.634	Stahleckeria
OM-11	21 deg 03.141	16 deg 23.634	Dicynodontia skull elements
OM-12	21 deg 03.141	16 deg 23.634	Small mandible
OM-13	21 deg 03.242	16 deg 23.712	Luangwa skull and scattered skeleton
OM-14	21 deg 03.705	16 deg 23.445	Traversodontidae snout
OM-15	21 deg 03.687	16 deg 23.445	Luangwa snout
OM-16	21 deg 03.687	16 deg 23.448	Cynodontia scattered skull and post cranium
OM-17	21 deg 03.687	16 deg 23.445	Cynodontia lower jaw
OM-18	21 deg 03.687	16 deg 23.448	Traversodontidae maxilla
OM-19	21 deg 03.709	16 deg 23.430	Traversodontidae skull
OM-20	21 deg 03.714	16 deg 23.392	Large bone indet
OM-21	21 deg 03.231	16 deg 23.700	Dicynodontia large tusked skull
OM-22	21 deg 03.231	16 deg 23.700	Small cranial element
OM-23	21 deg 03.231	16 deg 23.700	possible basicranium
OM-24	21 deg 03.138	16 deg 23.634	Dicynodontia large ?ilium
OM-25	21 deg 02.919	16 deg 23.587	Dicynodontia post crania

The vertical profile through the new dicynodont locality (Fig. 3) shows that most of the vertebrate fossils in these strata are found in the dark red (10YR3/6) massive siltstone overbank facies. It is interpreted that many of these tetrapod remains, including the new dicynodont (OM-10) described here, were buried as disarticulated but associated skeletons beneath layers of loessic silt dumped on the floodplain surface during windstorms. The new dicynodont skull is distorted due to it having been buried in an unusual postero-lateral-up attitude which is attributed to the “self burial” mechanism that is common on windswept loessic plains (Behrensmeier, 1975). Isolated and abraded transported post-cranial elements (OM 21–23), and very rarely more fully articulated skeletons, such as the skull and disarticulated but still associated post crania of a medium sized cynodont (OM-13) and the large semi-articulated rauisuchid skeleton (OM-4), are found within the upper levels of coarser-grained ephemeral stream channel fills (see Fig. 3).

Another taphonomically interesting occurrence is the concentration of cynodont remains in a 2.5 m thick × 40 m wide cliff exposure of loessic siltstones (see Fig. 2, OM 2–3, 5–7 and 14–19; Table 1). The 10 specimens are mostly traversodontids and one chiniquodontid, showing a range of body sizes with all states of disarticulation and all are preserved without any calcareous nodular encrustation. Their distribution is clearly associated with the top and margins of a narrow, fine-grained, shoe-string channel-fill sandstone. Thus, it is proposed that vegetation along the channel banks attracted the animals to this floodplain depression, which then promoted rapid burial of their carcasses by acting as a loess trap.

#### 4. Systematic palaeontology

Therapsida Broom, 1905  
Anomodontia Owen, 1859  
Dicynodontia Owen, 1859  
Stahleckeriidae Lehman, 1961  
*Stahleckeria potens* von Huene, 1935

##### 4.1. Modified diagnosis

Large sized tuskless dicynodont presenting the following combination of characters: skull wider than longer, snout robust and blunt, frontal with narrow anterior processes intruding between the nasals; interorbital skull roof very wide, with orbits not visible in dorsal view, postorbital region reduced representing less than the 40% of the cranial length, intertemporal skull roof remarkably wide, mostly formed by the parietal, and positioned approximately horizontal in lateral view, preparietal absent, occipital plate vertical and remarkably widened by the lateral extension of the squamosal wings (which form almost half of the width of the occiput).

##### 4.2. Comments

There is no original specific diagnosis for *Stahleckeria potens*. The only available diagnosis is for *Stahleckeria* and was presented by Keyser and Cruickshank (1979). Some characters proved to be problematical after the new detailed anatomical study and reconstruction of the skull of *S. potens* by Maisch (2001). The diagnosis above presented for *S. potens* includes diagnostic features proposed by Maisch (2001) for Stahleckeriidae Lehman, 1961, and Stahleckeriinae Lehman, 1961.

##### 4.3. Lectotype

Complete articulated skull number one described by Huene (1935) at the Institut und Museum für Geologie und Paläontologie der Universität Tübingen (GPIT/RE/7107). Designated by Maisch (2001).

##### 4.4. Paralectotype

Incomplete skull number two described by Huene (1935) (GPIT/RE/7106). Designated by Maisch (2001).

##### 4.5. Locality and horizon

Chiniqua, São Pedro do Sul Municipality, Rio Grande do Sul State, southern Brazil. *Dinodontosaurus* Assemblage Zone, Santa Maria Formation considered to be deposited during the Middle Triassic (Langer et al., 2007).

##### 4.6. New Material

The specimen described, GSN field number OM-10, is deposited in the paleontological collection of the Geological Survey of Namibia, and consists of a nearly complete skull with the mandible in articulation

that was separated after preparation (Figs. 4 and 5). Scattered post-cranial bones were found in association.

#### 4.7. Locality and horizon

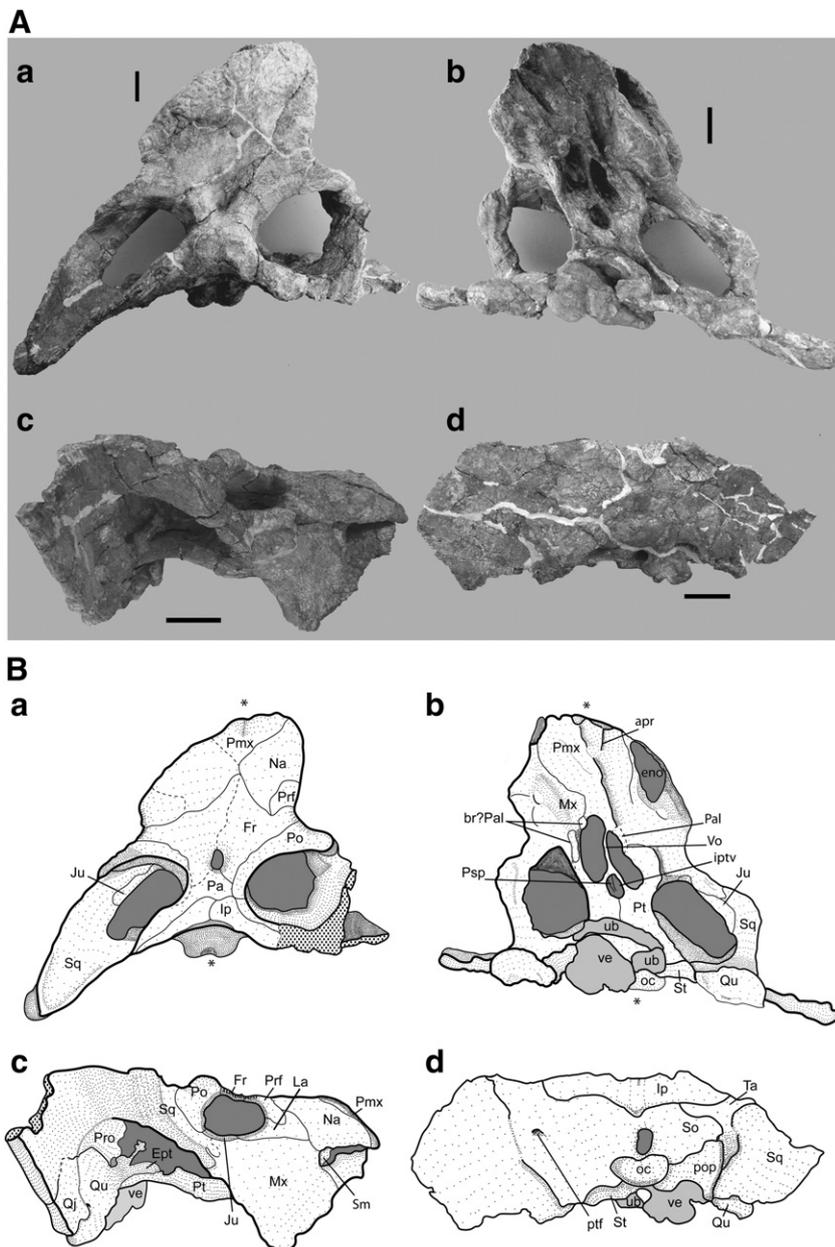
The specimen was collected from low exposures on the eastern bank of the Omaruru River (S 21° 03.141, E 16° 23.634), Otjiwarongo District, central Namibia (Fig. 2). Stratigraphically the specimen lies 40 m below the base of the Etjo Formation in strata assigned to the Unit 4 of the upper Omingonde Formation by Holzförster et al. (1999) and considered to be of Middle Triassic age (Abdala and Smith, 2009).

## 5. Description

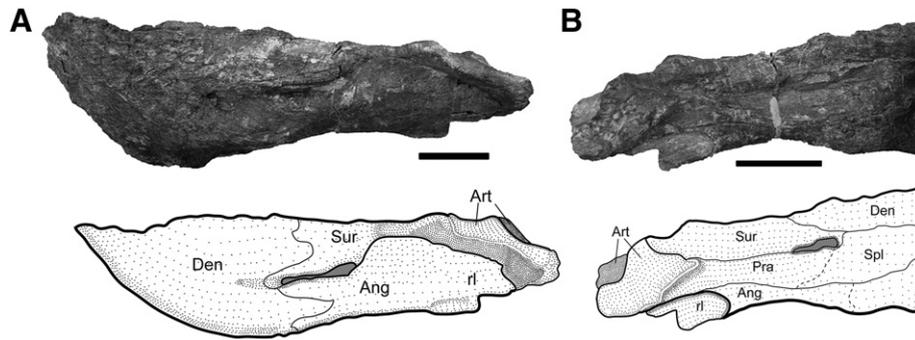
### 5.1. Skull

#### 5.1.1. General preservation

The specimen shows a strong postero-lateral distortion that affected particularly the left side, which has suffered from compaction and thus appears to be antero-posteriorly elongated (Figs. 4a and b). The occipital plate on the left side is also remarkably deformed (Fig. 4d). This distortion has resulted in the loss of bilateral symmetry in the skull (see asterisks in Figs. 4a and b) and mandible. In spite of this, the bone tissue structure is well preserved and several sutures can be traced in one or both sides of the skull.



**Fig. 4.** *Stahleckeria potens* (GSN OM-10) from the upper Omingonde Formation, Namibia. (A) Photography and (B) interpretative drawing of the skull. (a) Dorsal. (b) Ventral. (c) Lateral. (d) Occipital views. Abbreviations: apr, anterior palatal ridges; br?Pal, broken palatine; Bs, basisphenoid; eno, external narial opening; Ept, epipterygoid; Fr, frontal; Ip, interparietal; iptv, interpterygoid vacuity; Ju, jugal; La, lacrimal; Mx, maxilla; Na, nasal; oc, occipital condyle; Pa, parietal; Pal, palatine; Pmx, premaxilla; Po, postorbital; pop, paroccipital process; Prf, prefrontal; Pro, prootic; Psp, parasphenoid; Pt, pterygoid; ptf, posttemporal fenestra; Qj, quadratojugal; Qu, quadrate; Sm, septomaxilla; So, supraoccipital; Sq, squamosal; St, stapes; Ta, tabular; ub, unidentified bone; ve, vertebra; Vo, vomer. Asterisks indicated the sagittal axis of the skull anterior and posteriorly. Dot pattern indicates bone breakage. Scale equals 5 cm.



**Fig. 5.** *Stahleckeria potens* (GSN OM-10) from the upper Omingonde Formation, Namibia. Photography and interpretative drawing of the lower jaw. (A) Lateral. (B) Medial views. Abbreviations: Ang, angular; Art, articular; Den, dentary; Pra, prearticular; rl, reflected lamina; Sp, splenial; Sur, surangular; Scale equals 5 cm.

### 5.1.2. Dorsal view

The skull is fairly wide, with the maximum width across the squamosals of approximately 420 mm and the basal skull length of circa 360 mm. The postorbital length is shorter than the length between the tip of the snout and the pineal foramen (Fig. 4a). The facial surface of the premaxilla, maxillae, nasals and prefrontals is ornamented by coarse rugosities that are particularly well developed on the premaxilla, where there is also a low longitudinal crest. The snout is short (approximately one third of the length of the skull) and blunt. The premaxilla has a 'V'-shaped contact with the nasals and behind this contact the nasals form a short suture, thus preventing a premaxilla-frontal contact. The interorbital region is particularly wide so that the orbits are not visible in dorsal view (Fig. 4a). The temporal openings are nearly rounded, slightly wider than long, and the intertemporal bar is antero-posteriorly short and also wide (Fig. 4a). The pineal foramen is located just behind the anterior margin of the temporal openings. The frontals are projected posteriorly thus forming the anterolateral margin of the pineal foramen, and extend laterally, between the prefrontals and postorbitals, into the dorsal margin of the orbits (Fig. 4a). The parietals are small, nearly pentagonal-shaped bones, located in the middle part of the intertemporal bar at the same level of the bones forming the margins of the temporal openings. The anterior margin of the interparietal is bilobed and a medial suture is visible in dorsal view (Fig. 4a) and in the upper third in occipital view, thus indicating it is a paired bone, a condition unusual in therapsids, but present in *Stahleckeria potens* (see Maisch, 2001). The postorbitals make up the postorbital bar presenting a long posterior process onto the dorsal medial border of the temporal opening, reaching the squamosals and interparietals.

### 5.1.3. Palatal view

The palate is nearly 40% of the total length of the skull and is formed by the premaxilla that bears a pair of low longitudinal ridges anteriorly (Fig. 4b). These ridges fade away posteriorly where only a strong medial ridge is present. The medial margin of the maxilla is excluded from the margin of the internal nares by the palatine. The choanae are elongated and wide, surrounded by palatines, pterygoids and, in the midline, by the vomer. The vomer also limits anteriorly a rounded interpterygoid vacuity (Fig. 4b). Behind the vacuity the pterygoids contact widely forming a flat and smooth surface. The remaining bones of the basicranium are covered by displaced postcranial elements, including a vertebra and other unrecognized bones (Fig. 4b). In ventral view, the infraorbital bar is formed mostly by the maxilla and medially by the jugal, whereas the zygomatic arch has a large contribution of the squamosal. Both quadrates are preserved and bear broad and wide articular facets separated by a shallow central trough. The left stapes is poorly preserved but is possible to observe the absence of a stapedia foramen (Fig. 4b).

### 5.1.4. Lateral view

The septomaxilla borders the posterior margin of the external nares; thus, there is no inclusion of the lacrimal in the border of the nares. As a

consequence of deformation, the nasals protrude and overhang the nares, partially obscuring them in lateral view (Fig. 4c). The maxillae are relatively broad, triangular bones bearing strong tuskless, ventrally projected maxillary processes located at the level of the anterior border of the orbit and oriented nearly vertical (Fig. 4c). The prefrontals are nearly rectangular-shaped, forming the anterior half of the dorsal margin of the orbit (Fig. 4c). The lacrimal has a well-developed facial portion and a posterior projection that forms the anteroventral margin of the orbit and contacts a thin jugal, which represents the posteroventral margin orbital. A digitated suture between the maxilla and the squamosal is clearly represented at the level of the posterior margin of the orbit. A partially preserved, thin epipterygoid and prootic are representing the lateral wall of the skull. There is a long horizontal suture between the ventral portion of the epipterygoid and the pterygoid.

### 5.1.5. Occipital view

The occipital plate is vertical with the flaring lateral flanges of the squamosals (Fig. 4d). The occiput is approximately two times wider than high, with a relatively narrow foramen magnum and a robust and wide occipital condyle (Fig. 4d). Only in a restricted area near the dorsal margin of the interparietals is it possible to recognize the suture between these bones on occipital view. The interparietals occupy a relative extended area on the dorsal part of the plate and extend ventrally forming a V-shape suture with the supraoccipital. This bone contacts ventrally with a large paroccipital process. Both bones and also possibly the squamosal contribute to form the margin of a tiny posttemporal foramen. There is a lateroventral projection of the paroccipital process which ends close to the medial border of the quadrate trochlea (Fig. 4d). The lateral margin of the paroccipital process is separated from the squamosal by a well-developed crest. The squamosals are broad and greatly contribute to extend laterally the occipital plate (Fig. 4d).

### 5.2. Mandible

Both rami of the lower jaw are nearly complete but the right ramus is severely affected by deformation, being approximately two-thirds of the length of the left ramus. The dentary is a massive bone with a dorsally projected and pointed anterior tip (Fig. 5A). The labial surface of the dentary is coarsely rugose as is the surface of the snout. The dorsal surface of the dentary shows two parallel longitudinal ridges along its length, with the medial one higher than the lateral. In lateral view the dentary develops two posterior processes, the dorsal, in contact with the surangular, and the ventral, forming a spur that is contacted by the angular (Fig. 5A). Surangular and angular enclose the mandibular foramen laterally. The angular extends posteriorly in a long, flat reflected lamina, which nearly reaches the retroarticular process (Fig. 5, A and B). This process is partially deformed but it possible to confirm that it bends downwards. The articular surface for the quadrate trochlea is long and wide, showing a longitudinal crest that divides the surface in the lateral and medial areas (Fig. 5B). In medial view, the mandibular

foramen is limited by the surangular dorso-anteriorly and by the prearticular, ventrally (Fig. 5B).

## 6. Discussion

### 6.1. Taxonomy

The new tuskless Namibian dicynodont is here assigned to the Brazilian species *Stahleckeria potens*. This assignment is based on the presence in the Namibian specimen of a mixture of diagnostic characters of Stahleckeriidae and Stahleckeriinae that are typical of *S. potens* (see comments in diagnosis above): presence of a skull wider than longer, a snout robust and blunt, an interorbital region extremely wide with the orbits not visible in dorsal view, a postorbital region reduced representing less than the 40% of the cranial length, an intertemporal bar remarkably wide (mostly formed by the parietal) and positioned approximately horizontal in lateral view, and the presence of the vertical occipital plate which is distinctively widened by the lateral extension of the squamosal wings.

Most of the recent phylogenetic analyses that included Triassic dicynodonts (kannemeyeriiforms) consistently recovered a monophyletic Stahleckeriidae (Maisch, 2001; Vega-Dias et al., 2004; Damiani et al., 2007; Kammerer et al., 2011), a group of dicynodonts which includes the Brazilian *Stahleckeria*, the South American *Jachaleria*, the Argentinean *Ischigualastia*, the North American *Placerias*, the Zambian *Sangusaurus*, the Namibian *Dolichuranus* and the African *Angonisauros* (Fig. 6). The first four genera were recovered in all the hypotheses (Fig. 6), the only exception being that of Damiani et al. (2007) in which *Jachaleria* and

*Placerias* were not included in the analysis. In addition, Maisch's (2001: 145) taxonomic arrangement of Stahleckeriinae includes the African dicynodonts *Angonisauros* and, with some reservations, *Zambiasaurus*. Vega-Dias et al. (2004) included the South African taxon *Angonisauros* that was recovered as the sister-taxon of *Stahleckeria*; however, in a more recent phylogenetic analysis *Angonisauros* resulted in a basal position outside Stahleckeriidae (Kammerer et al., 2011; see Fig. 6). The same occurred with the Namibian taxon *Dolichuranus* which was considered the sister-taxon of the clade Stahleckeriidae (Damiani et al., 2007), but was recovered as a basal kannemeyeriiform by Kammerer et al. (2011). The later authors found a sister group relationships between *Stahleckeria* and *Sangusaurus* from Zambia (Fig. 6), a taxon usually considered among kannemeyeriids (Cox, 1969; Keyser and Cruickshank, 1979) or as *incertae sedis* (Cox and Li, 1983; King, 1988). Kammerer et al. (2011: 135) however caution that the Zambian taxon is poorly known and mostly coded with "?" for the synapomorphies supporting stahleckeriids.

The Namibian *Stahleckeria* shows clear differences with these proposed most-closely related taxa. The Namibian *Dolichuranus* shows, among other differences with *Stahleckeria*, the presence of tusks and of nasal bosses, a narrow intertemporal bar oriented dorsally, an interpterygoid vacuity placed posteriorly and near to the posterior margin of the temporal opening, the presence of a postorbital process that contributes to the suborbital bar anteriorly, and a prominent *processus depressor mandibulae* on a well-developed ventral tympanic ridge (Damiani et al., 2007). The skull morphology of *Zambiasaurus*, considered by some authors as closely related to *Stahleckeria*, was interpreted from eighty-five separate skull fragments (Cox, 1969). The principal differences of this taxon with *Stahleckeria* is that *Zambiasaurus*

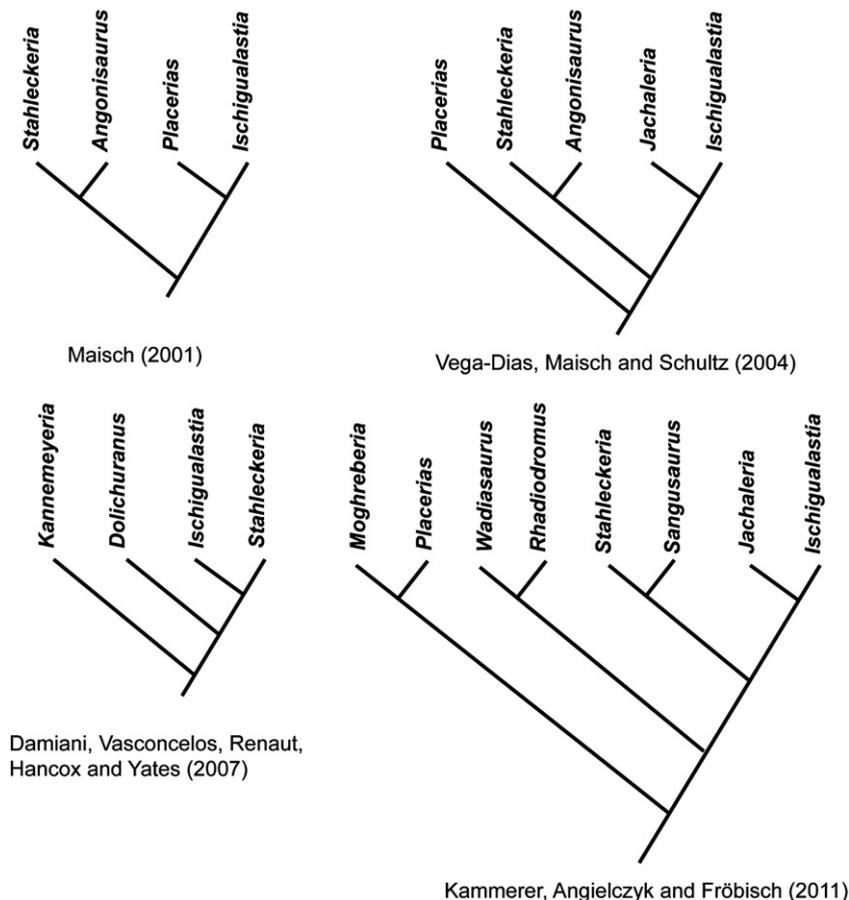


Fig. 6. Placement of *Stahleckeria* in different phylogenetic analyses. The trees in the figure are reduced versions of the trees originally presented, only including taxa close related to *Stahleckeria*. Cladogram by Kammerer et al. (2011) is representing result of their primary phylogenetic analysis.

presents a narrow and longer intertemporal region, the frontal is on the anterior dorsal margin of the orbits (Cox, 1969: Fig. 20B), there is a sharp transition between dorsal and occipital surfaces and the squamosal wings of the occiput are extended laterally and somewhat posteriorly (Cox, 1969: 260). All these differences should be considered with caution, because *Zambiasaurus* is not only based in fragmentary material, but they are most likely of juveniles (Cox, 1969).

*Sangusaurus* is represented for a few cranial fragments, the most significant being an incomplete intertemporal bar, a partial premaxilla and a partial maxilla (Cox, 1969: Figs. 21–23). Differences with *Stahleckeria* include the presence of a low boss behind the pineal foramen and intertemporal bar directed postero-dorsally (this last character contingent of a correct interpretation of directionality in the intertemporal fragment; Cox, 1969: 289). In addition, the intertemporal bar appears to be narrower in *Sangusaurus*.

Major differences with *Angonisauros* is that the latter has a caniniform process with a stout and straight posterior edge, an intertemporal bar tapering upwards to a narrow crest, a postorbital region of the skull longer than preorbital, strong nasal bosses, and an occiput slightly oblique (Cox and Li, 1983). Another partial skull, identified as *Angonisauros*, was also described for the youngest sub-assembly of the *Cynognathus* Assembly Zone in South Africa (Hancox and Rubidge, 1996). Differences between this specimen and the Namibian *Stahleckeria* include the presence of a deep triangular depression including, anteriorly, the extremely large pineal foramen in the South African taxon, also the presence of two strong diverging crests in the posterior portion of the temporal region, and a frontal occupying most of the dorsal margin of the orbit. The Argentinean dicynodont *Ischigualastia* is strikingly different from the Namibian *Stahleckeria*, including, among other differences, a long and narrow intertemporal bar, a convex dorsal margin of the occiput and a pointed snout (Domnanovich, 2010). Clear differences between *Stahleckeria* and *Placerias* are the presence of a sharp snout, pronounced upright temporal bar, comparative longer postorbital region, the extreme development of a blade-like caniniform process with reduced canines and short parietal process of the postorbital extending only to the level of the pineal foramen in the Late Triassic taxon from USA (Keyser and Cruickshank, 1979). Finally, the Late Triassic *Jachaleria* from South America also differs markedly from *Stahleckeria*. *Jachaleria* shows an extra bone between nasals and frontals, well-developed rugosities in the orbital margins of the prefrontals and postorbitals, a furrow on the dorsal face of the postorbital, a horizontal ventral margin of the maxilla in lateral view, a narrow intertemporal bar which is upright in relation to the interorbital bar, and the presence of a preparietal bone in front of the pineal foramen (Vega-Dias and Schultz, 2004; Domnanovich, 2010).

In summary, the new specimen described herein constitutes a new representative of *Stahleckeria potens* only known, until now, from specimens collected from the Santa Maria Formation of southern Brazil. The only difference between the Brazilian specimens and the individual from Namibia is in their size. The largest Brazilian specimen has a basal skull length of 490 mm (Cox and Li, 1983), against the 360 mm of the Namibian skull, thus being approximately 27% smaller. Size per se is not a reliable indicator of taxonomic distinction, and could simply indicate ontogenetic-age difference, a feature that has already been observed amongst the Brazilian specimens (Vega-Dias et al., 2005).

## 6.2. Biostratigraphy and correlations

The Middle Triassic fauna from the upper Omingonde Formation was originally described by Keyser (1973a,b). The fauna included several cynodont and dicynodont therapsids and a temnospondyl amphibian. Dicynodonts were important components in the first discoveries by Keyser (1973a,b), who recognized *Kannemeyeria*, a typical representative of the *Cynognathus* Assembly Zone of the main Karoo Basin in South Africa (Keyser, 1973a,b). However he also proposed a slightly younger age for the Namibian fauna based on the presence of the large cynodont *Titanogomphodon* and some dicynodonts presenting more

advanced characters than the South African. In addition, Keyser (1973a) interpreted the Omingonde Formation as older than the Manda and upper Ntawere Formations because of the absence of traversodontid cynodonts. Since 1973 at least three research teams have conducted fieldwork on the Omingonde outcrops, which has resulted in the discovery of several new taxa. There has also been a critical review by one of the authors (FA) of the identification and stratigraphic position of all the fossils collected to date. The new records included several cynodonts, mostly represented by traversodontids, and a large archosaur, all collected from the upper part of what was defined as the upper Omingonde Formation (Pickford, 1995; Holzförster et al., 1999; Smith and Swart, 2002). The age of the Omingonde Formation was considered to be lower Middle Triassic (Anisian) based on faunal correlations with the main Karoo Basin, and the east African Ruhuhu and Luangwa basins. A recent taxonomic review of a series of cynodonts collected by Smith and Swart (2002) has identified a heterogeneous mixture of cynodonts in the fossil assemblages from the top of the upper Omingonde Formation. This mixture included cynodonts known from Anisian levels of Tanzania and Zambia but also from the Ladinian of South America (Abdala and Smith, 2009). The most striking finding was the presence of *Chiniquodon*, a typical Ladinian-Carnian cynodont from South America, recently described from Ladinian-Carnian strata of Madagascar (Kammerer et al., 2010). In addition, the archosaur skeleton originally interpreted as *Erythrosuchus* (Pickford, 1995), a typical taxon from the *Cynognathus* AZ of South Africa, has been re-identified as a raiusuchid (Abdala and Smith, 2009; Arcucci and Smith, 2011), a group well represented in Ladinian-Carnian faunas of South America. Accordingly, Abdala and Smith (2009) suggested the possibility that the fauna represented in the uppermost part of the upper Omingonde Formation was of upper Middle Triassic (Ladinian) age (Fig. 7).

Until now, continental Ladinian strata were unknown from southern Africa (Hancox, 2000), where a regional tectonic unconformity separates the top of the Beaufort Group from the overlying Molteno Fm. (see Catuneanu et al., 2005). In this context, the Omingonde Fm. tetrapods are the only representatives of this age in the entire region and they partially fill the gap between the Early-Middle Triassic Beaufort Group therapsid-dominated faunas and the Late Triassic Elliot Formation dinosaur-dominated faunas. This finding is therefore of great importance in understanding the evolution of the tetrapod faunas in this part of western Gondwana during the Triassic.

From the Middle Triassic faunas of east Africa, the Lifua Member of the Manda Fm. has yielded traversodontid cynodonts with postcanine teeth morphologically similar to Anisian forms and some taxon with the dentition resembling Ladinian and Carnian forms (Abdala and Ribeiro, 2003). Based on these differences of features in the dentition of traversodontid species it was proposed that different ages were represented in the Manda fauna and that the youngest fauna might be Ladinian (Fig. 7; Abdala et al., 2005). However, this conclusion was only based on differences in evolutionary stages of the dentition of cynodonts, not in the presence of taxa shared with Ladinian faunas. Recent field trips to the Ruhuhu Basin resulted in numerous new fossil findings (Sidor et al., 2008; Sidor, 2011) whose study will provide additional evidence for the presence of putative Ladinian faunas in Tanzania.

The Middle Triassic faunas from South America includes the Puesto Viejo fauna from Mendoza Province, Argentina which has records of *Cynognathus* and *Diademodon*, cynodonts also known from the *Cynognathus* AZ of South Africa and the assemblages of lower and middle levels of the upper Omingonde Formation. The Puesto Viejo fauna is generally interpreted as Anisian (Fig. 7; Martinelli et al., 2009). A second fauna from Mendoza Province is recorded in the Cerro de las Cabras Formation. This endemic fauna is usually correlated to the Puesto Viejo Assemblage (Martinelli et al., 2009). Recent radiometric dates are consistent with an Anisian age for the fossil assemblage of the Cerro de las Cabras Formation (Fig. 7; Ávila et al., 2006; Abdala et al., 2009). The Chañares fauna from the Ischigualasto-Villa Union Basin, north-western Argentina show traversodontid cynodonts more advanced than those

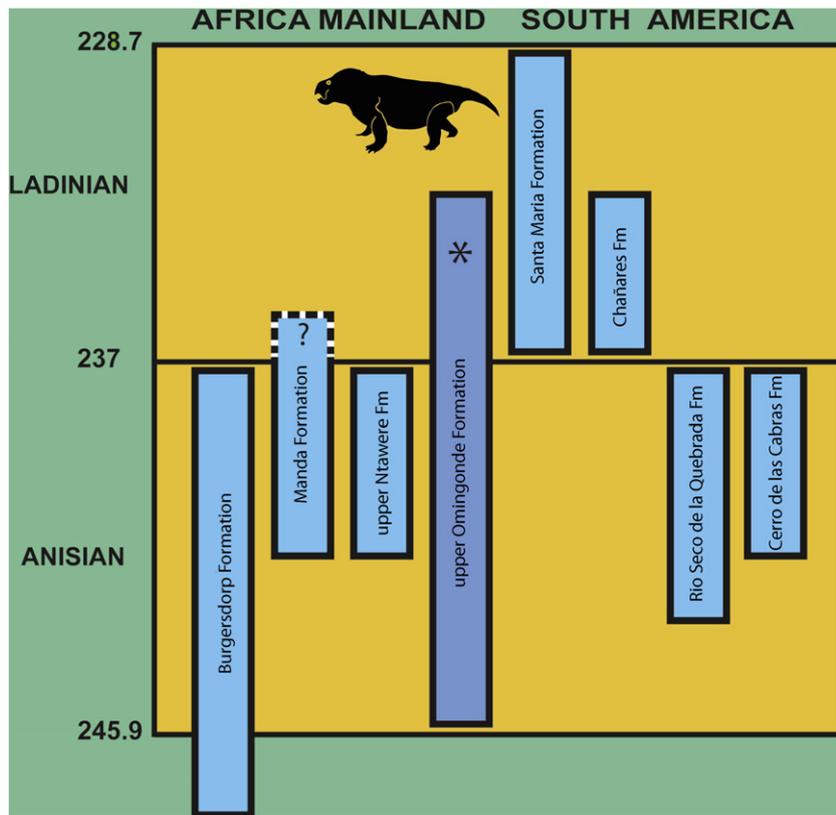


Fig. 7. Biostratigraphic chart of Middle Triassic units from South America and southern, eastern Africa discussed in the text. Asterisk indicates fauna of the uppermost strata of the upper Omingonde Formation. Geologic time scale after Gradstein et al. (2004).

from the Puesto Viejo and the Cerro de las Cabras faunas and an explosive radiation of archosauriforms (Abdala et al., 2009). In Brazil, the *Dinodontosaurus* assemblage zone of the Santa Maria Formation is considered contemporaneous to the Chañares fauna because they share several taxa at genus level (e.g. *Massetognathus*, *Dinodontosaurus*). Dicynodonts are abundant in the Brazilian fauna, with *Dinodontosaurus pedroanum* being by far the most common taxon represented by hundreds of specimens. Another dicynodont known from this Brazilian assemblage zone is the large tuskless *Stahleckeria potens* which is only known by five specimens (Maisch, 2001; Vega-Dias et al., 2005). Strata of the Santa Maria Formation bearing fauna of the *Dinodontosaurus* assemblage zone are considered as Ladinian (Fig. 7; Langer et al., 2007).

The description herein of the dicynodont *Stahleckeria potens* from Namibia strengthens the Ladinian age hypothesis advanced by Abdala and Smith (2009) for the fauna represented in the uppermost part of the upper Omingonde Formation. In this context, there is no paleontological evidence suggesting an age younger than Ladinian for these strata in contrast with suggestions by Holzförster et al. (1999: Fig. 2) and Zerfass et al. (2005: Fig. 2).

*Stahleckeria* is the first mid-Triassic dicynodont to be found in both Namibia (Waterberg Basin) and Brazil (Paraná Basin). This evidence together with the common presence of the cynodont *Chiniquodon* in the same strata (Abdala and Smith, 2009) strongly suggests faunal interchange between these two regions of western Gondwana during middle Triassic times. The interchange not only involved medium-sized carnivorous animals but also relatively large specialized herbivores. This suggests that there were no major ecological, climatic and/or physical barriers to faunal migration before the opening of the south Atlantic in this part of southwestern Gondwana during the pre-rift phase (Macdonald et al., 2003), and the vegetation was similar (Spalletti et al., 2003), stable and relatively continuous in the lowlands that linked both basins.

## 7. Conclusion

A new relatively large tuskless dicynodont is described for the upper Omingonde Formation (central Namibia) and it is identified as a new specimen of *Stahleckeria potens*, previously known only from Ladinian-aged strata of the Santa Maria Formation of southern Brazil (Paraná Basin). This new finding together with the co-occurrence of the cynodont *Chiniquodon* and a rauisuchian archosaur supports a Ladinian age of deposition for the uppermost unit of the upper Omingonde Fm. A well-documented hiatus, dubbed the “Ladinian gap,” is prevalent throughout the Karoo basins of south and central Africa, which means that the fauna described here, is the first confirmed Ladinian-aged terrestrial fauna from this region.

*Stahleckeria* is the only dicynodont proven to occur in Middle Triassic rocks from central Namibia and southern Brazil and as such constitutes the first correlation between these two Gondwanan basins based on this group of large therapsids. This finding, together with the common presence of the cynodont *Chiniquodon*, suggests a degree of faunal interchange during Middle Triassic (Ladinian) times, which included both small carnivores and relatively large specialized herbivores and that a relatively stable lowland vegetation belt existed between these basins with no major ecological, climatic and/or physical barriers.

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