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2018-10-31
Evolutionary Studies Institute
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Fossil tree hollows from a late Permian forest of the Matinde Formation (Tete, Mozambique)

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Received 14 December 2017. Accepted 31 August 2018

Fossil tree hollows are seldom described in the literature and can often be elusive to the field paleobotanist. However, these structures may provide unique paleoecological, environmental and tree life history information that are essential for a more complete understanding of ancient forests. A stump from the 'late Permian' (Wuchiapingian–Changhsingian) of the Mágoè Fossil Forest in Mozambique (Tete Province) provides a rare example of fossilized tree hollows. These hollows were found near the base of the tree and are subcircular in shape, ranging between ~1.3 and 3.5 cm in diameter. Although thirty-one trees were densely sampled (i.e. no fossil trees were excluded from a given area, in our case ~2650 m^2) and inspected at the Mágoè Fossil Forest, only one (PPM2017-31) exhibited tree hollows, highlighting the scarcity of these structures in this fossil forest. In modern forests tree hollows are more likely to be found in old trees, likewise PPM2017-31 was among the largest trees found in the sample, suggesting this was an old tree. The subcircular morphology of the tree hollows indicates they resulted from fungal/bacterial activity rather than from a fire.

Keywords: Mágoè Fossil Forest, Lopingian, Cahora Bassa, paleobotany, tree stumps, Gondwana

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INTRODUCTION

Tree hollows are depressions on the outer surface of tree trunks that result from injuries caused by a variety of factors, such as branch or fire scars, fungal-animal-plant interactions, or complex environmental stressors (Mireku & Wilkes 1989; Lindenmayer *et al.* 2000a; Gibbons & Lindenmayer 2002). Once the sapwood is exposed after injury, hollows form by fungi-induced wood decay and subsequent degradation by saproxylic insects (Wilkes 1982). Tree hollows may vary greatly in size, from a few centimetres to nearly a metre in diameter (Gibbons & Lindenmayer 2002), however, tree hollow analyses in modern forests reveal that the development of these structures follows some general rules (Lindenmayer *et al.* 2000a). For instance, older trees typically have more tree hollows (e.g. Gibbons *et al.* 2000; Rayner *et al.* 2014) and, although tree hollow abundance may vary intraspecifically, it generally changes predictably according to geographic location (e.g. woodland extension or new tree availability; Lindenmayer *et al.* 1990; Bennett *et al.* 1994; Rayner *et al.* 2014). Furthermore, the majority of tree hollows found at the tree trunk base seem to derive from fire scars, whereas those near the tree crown typically result from broken branches (Lindenmayer *et al.* 2000a). Tree hollows have an instrumental ecological role, as they are often used as nesting places or resting refugia by a variety of different species, including saproxylic insects, small mammals, and birds (Lindenmayer *et al.* 1990, 2000b; Micó *et al.* 2012).

With its abundant and well-preserved tree fossil specimens, the Joggins Fossil Cliffs UNESCO World Heritage site (Nova Scotia, Canada) is a nearly complete snapshot in time of the tree hollows from ancient carboniferous environments (Grey & Finkel 2011). Surprisingly, at the Joggins Fossil Cliffs site no paleoecological studies concerning the tree hollows has yet been done. The tree hollows currently serve only to contextualize the animal fossils that lived within the hollows. Despite this remarkable example, tree hollows are only sporadically reported in the paleontological literature (e.g. Grey & Finkel 2011), because they are not being recognized by paleobotanists. Here, we describe tree hollows observed in the Mágoè Fossil Forest of Tete Province, in Mozambique. These fossil specimens were found in the Chicôa-Mucúcuè Basin, which is considered likely to be Lopingian in age on palynological evidence, i.e. Wuchiapingian–Changhsingian (GTK Consortium 2006; Pereira *et al.* 2016). Although the records of Mozambican fossil tree from the Tete Province date back to more than a century ago (Livingstone 1865), clear references to the Mágoè Fossil Forest were only published later, starting in the 1940s (Borges 1946;

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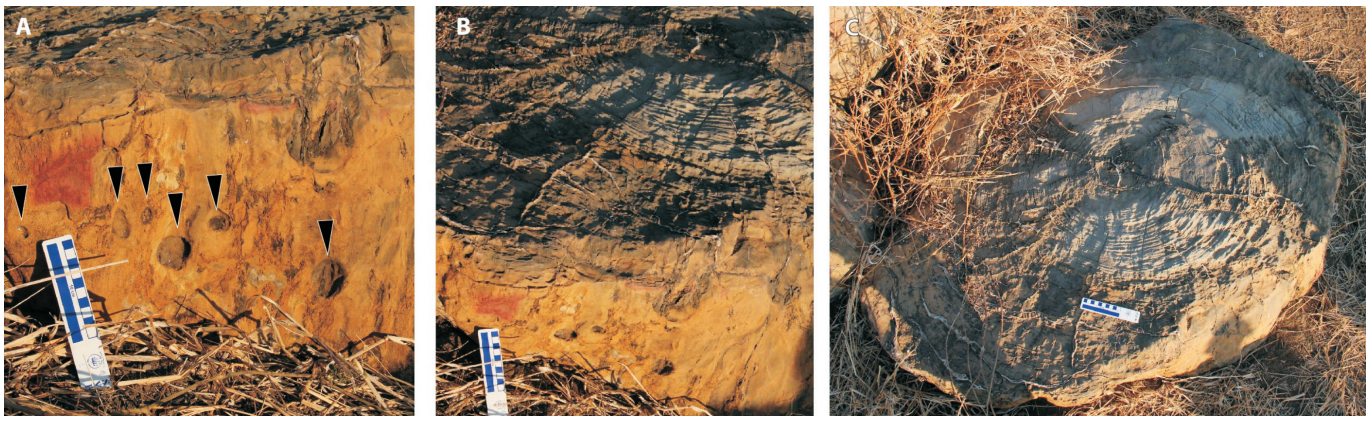


Figure 1. On the lateral side of the PPM2017-31 *in situ* tree trunk there are six subcircular tree hollows. **A**, Tree hollows are indicated by the arrows in lateral view; **B**, an oblique view of the tree stump; **C**, an orthogonal photograph of the same specimen in cross-section. Scale bars in A, B and C equal 10 cm.

Silva *et al.* 1967). This fossil forest extends for more than 75 km in length (Ferrara 2004), indicating this is the largest fossil forest in Africa published to date. Other fossil forests in Africa are present in Zambia, Zimbabwe (Barbolini *et al.* 2016) and Namibia (Schneider 2008).

The Mágoè Fossil Forest is a unique site for studying the floras and ecosystems that existed prior to the end-Permian mass extinction, however, despite its vast area and abundance of fossil trees, this fossil forest remains mostly unexplored. Tree hollows are important for understanding various aspects of forest ecology and plant–environment interactions but are seldom reported in the fossil record. In this study, we discuss a fossil stump with preserved tree hollows from the Mágoè Fossil Forest, thereby opening the way for future research into the paleoecology of Permian ecosystems in Gondwana (Fig. 1).

MATERIALS AND METHODS

We sampled two distinct locations at the Mágoè Fossil Forest totalling 31 *in situ* fossil trees. The fossil trees from the two different areas were sampled exhaustively, meaning that from that particular area no exposed tree was left unmeasured. The area from which PPM2017-31 was collected was mapped (Fig. 2). The stump diameters were only measurable for 27 logs ($n = 27$). For each of the trees we registered precise geographic coordinates (precision ±1 m) using a hand-held GPS, orientation of the fallen tree stem using a field compass, and maximal diameter of the tree stumps at the base. Photographic evidence and a sample of each specimen were also collected. Linear measurements were taken with a measuring tape (precision of 0.5 cm) and angular measurements (i.e. orientation were registered using a field compass oriented according to the magnetic north; precision of 0.5°). The only sampled fossil tree stump presenting tree hollows was PPM2017-31 (precise geographic coordinates may be available by direct contact with the corresponding author). The tree hollow diameters were calculated using an orthogonal photograph of the specimen and measured using the linear measurement 'straight line' tool upon image calibration in ImageJ2 (Schindelin *et al.* 2015). The tree hollow areas were calculated using the area measurement

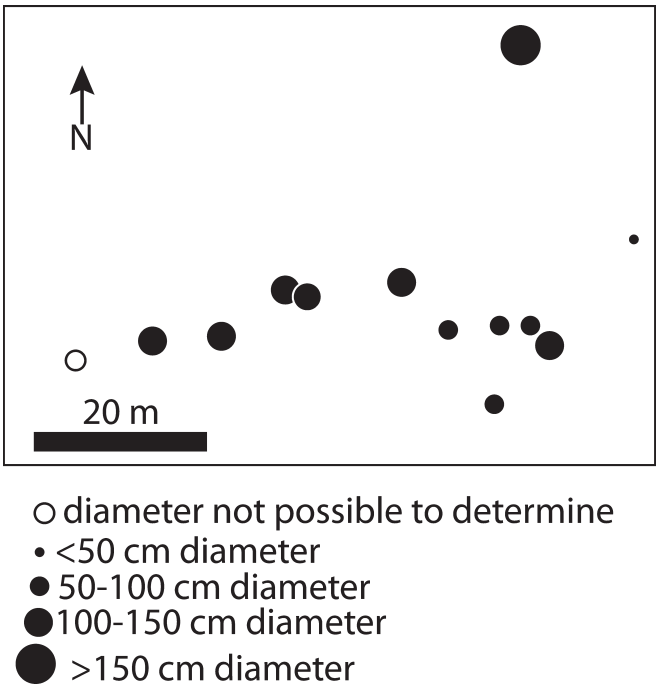


Figure 2. Map of the exhaustively sampled area from where PPM2017-31 was collected from.

'polygon selections' tool upon image calibration in ImageJ2 (Schindelin *et al.* 2015)

Although the trees from this location have been attributed previously to *Dadoxylon nicoli* (Walton 1956), this species is a *nomen dubium* at present (Merlotti & Kurzawe 2006). The species *Dadoxylon nicoli* is currently attributed to *Australoxylon teixeirae* (Marguerier 1973; Merlotti & Kurzawe 2006; Bamford 2016). However, the fossilized wood anatomy of the Permian trees from the Mágoè Fossil Forest is currently being revised and in need of a significant reinterpretation and taxonomic update. Nevertheless, preliminary results from thin sections performed in PPM2017-31 indicate that this specimen can be ascribed to the gymnosperm species *Agathoxylon* sp. In transverse section the fossil wood has regular, almost square tracheids and wide growth rings. In longitudinal section the rays are uniseriate and about 10–15 cells high. There is some resin or gum in the tracheids and there is no spiral thickening. The tracheids and general appearance

are the same as that of other specimens in this collection that can be identified as *Agathoxylon* sp.

RESULTS

The fossil tree stump PPM2017-31 is 180 cm in diameter and has a perimeter of ~450 cm. By using the equations of Creber & Ash (2004), PPM2017-31 had a critical height of 144 m ($H_{crit} = 95.75D^{2/3}$), and by applying the equations from Niklas (1993, 1994a,b), an estimated height of 35.8 m ($H_{est} = 27.8D^{0.430}$). This large calculated difference between the equations is expected because the critical height is the maximum height to which a vertical trunk can be elevated before it theoretically undergoes buckling (i.e. a tree never reaches this size), whereas the Nikla's estimated height is based on various different mechanical proprieties of wood.

The sample of the tree trunk diameters has a normal distribution (for a level $\alpha = 0.05$, Shapiro-Wilk test *P*-value = 0.146, Anderson-Darling test *P*-value = 0.2, and Lilliefors test *P*-value = 0.335), yet it is positively skewed (Pearson skewness = 0.512; Fisher skewness = 0.542), in line with what is observed in modern forests (e.g. Kohyama *et al.* 1990). The average diameter of the base of the trees is 92 cm ($\sigma = 48.74$ cm, where σ is the standard deviation here and throughout), with a minimum diameter of 20 cm (PPM2017-10) and a maximum diameter of 190 cm (PPM2017-1), see Table 1. In the boxplot PPM2017-31 is in the last quartile of the dataset (Fig. 3), indicating that the specimen preserving the tree hollows was an old tree based on the collected data sample.

There are only six tree hollows found and all are in one side of the stump (Fig. 4). All the hollows occur at approximately the same distance from the ground. The tree hollows are subcircular in shape, averaging 2.1 cm in diameter ($\sigma = 1.16$ cm) and are no more than ~1.5 cm deep (Fig. 1, 4). The smallest tree hollow is 1.1 cm in diameter (1.15 cm^2 in surface area) and the largest 3.6 cm in diameter (10.75 cm^2 in surface area) (Table 2). The Pearson correlation coefficient between the surface area and diameter of the hollows is very high (0.993≈1), which is a consequence of the low number of tree hollows that are present and an indication that the tree hollows are subcircular (Fig. 1). The relationship between area and diameter is a measure of eccentricity of the hollows, which is relevant because different tree hollow shapes indicate different origins

Table 1. Sampled tree trunk diameters (cm) from the Mágoè Fossil Forest. Specimen PPM2017-12 through PPM2017-15 could not be measured due to incomplete preservation.

Specimen	Diameter (cm)
PPM2017-1	190
PPM2017-2	40
PPM2017-3	20
PPM2017-4	120
PPM2017-5	70
PPM2017-6	65
PPM2017-7	60
PPM2017-8	55
PPM2017-9	90
PPM2017-10	20
PPM2017-11	70
PPM2017-16	180
PPM2017-17	90
PPM2017-18	40
PPM2017-19	170
PPM2017-20	130
PPM2017-21	120
PPM2017-22	100
PPM2017-23	120
PPM2017-24	105
PPM2017-25	60
PPM2017-26	90
PPM2017-27	60
PPM2017-28	80
PPM2017-29	140
PPM2017-30	45
PPM2017-31	180

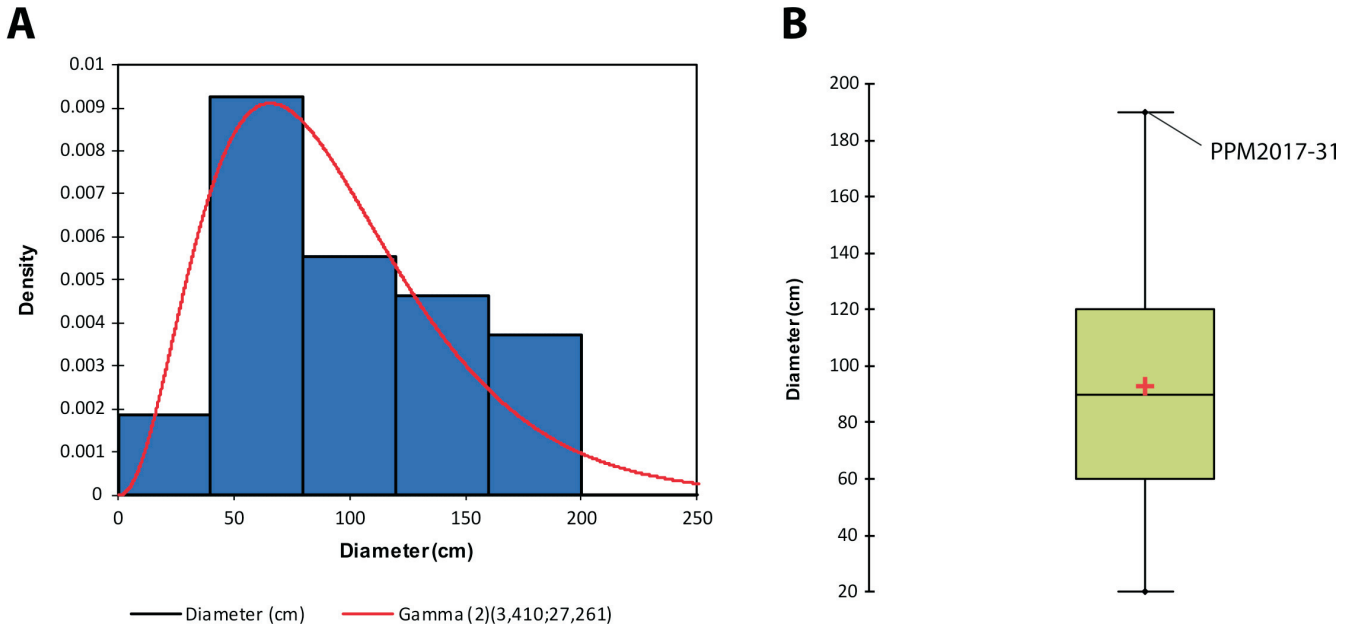


Figure 3. Statistics of the diameters of the sampled fossil trees. **A**, Histogram showing the distribution of the sampled fossil tree trunk diameters and the typical left-skewed distribution of diameters in a forest; **B**, boxplot showing the maximum (190 cm) and minimum (20 cm) sized tree stump, with the average being ~92 cm. PPM2017-31 is in the upper quartile of the whiskers plot. Red cross indicates the arithmetic mean.

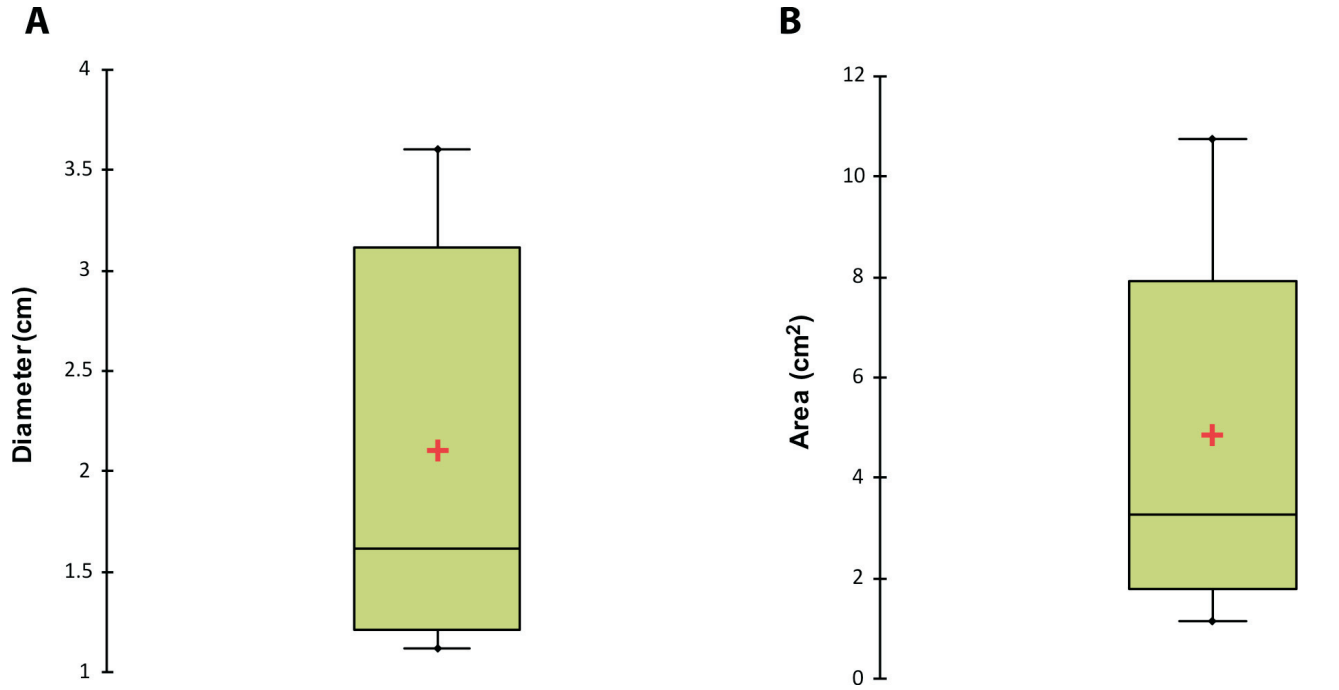


Figure 4. Box-plots showing the tree hollow parameter distributions in PPM2017-31. **A**, Diameters; **B**, areas. The red cross depicts the arithmetic mean.

Table 2. PPM2017-31 tree hollows diameter (cm) and area (cm^2).

Hollow #*	Diameter (cm)	Area (cm2)	Radius	
1	1.119	1.151	0.5595	min
2	1.872	3.739	0.936	
3	1.163	1.46	0.5815	
4	3.526	9.313	1.763	
5	1.366	2.822	0.683	
6	3.607	10.753	1.8035	max

*Hollow # from left to right.

(Gibbons & Lindenmayer 2002). In this case, an elevated Pearson correlation coefficient between the variables indicates high levels of circularity.

DISCUSSION

Tree hollows in the main stem account for up to 47% of all hollows in modern eucalyptus forests (i.e. both at the base and upwards on the stem; Lindenmayer *et al.* 2000c) but unfortunately there are no equivalent statistics for gymnosperm forests. By contrast, in woodland eucalyptus species approximately 91% of tree hollows occur in the tree crown (Gibbons & Lindenmayer 2002; Newton-John 1992) as a result of broken branches (Gibbons & Lindenmayer 2002). As most specimens in the Mágoè Fossil Forest have not preserved the canopy, only measurements of the main stems are used for statistical purposes, inevitably skewing our analyses because tree hollows can happen anywhere on the tree. Nevertheless, among the 31 tree stumps analysed only one exhibited tree hollows, representing ~3% of the sample. Provided that modern ecological dynamics apply, this result suggests that the fossil site was a locality with low tree density, as woodlands typically have low abundance of tree hollows in the main stem when compared with forests (Gibbons & Lindenmayer 2002). Nevertheless, locally elevated tree density can also occur in woodlands, therefore, additional statistical support from various sampled areas is required to affirm this statement. However, little is known from Permian tree hollow distribution between species, and it is possible that PPM2017-31 could have belonged to a species less prone to tree hollow formation. Future research on the precise geographical distribution of the fossil trees would provide complementary information concerning tree density at the Mágoè Fossil Forest site.

The tree hollows formed at the base of PPM2017-31 could have resulted from a fire. Hollows at the base of the main stem, called basal hollows, are typically fire scars (Gibbons & Lindenmayer 2000). This type of hollow represents approximately 2 to 16% of tree hollows (Lindenmayer *et al.* 2000c), but these hollows that resulted from fire tend to possess a typical subtriangular entrance extending towards the crown, whereas the tree hollows in PPM2017-31 are subcircular. Thus, it appears more likely that the PPM2017-31 basal hollows resulted from fungal/bacterial action due to the mature age of the tree (Richards *et al.* 1990; Woodgate *et al.* 1994; Stoneman *et al.* 1997). As trees grow, they are more likely to experience trunk decay and subsequent hollow formation (Gibbons & Lindenmayer 2000). Furthermore, tree growth decelerates as trees age, which decreases their capacity to repair wounds (Jacobs 1955). Indeed, the large size of PPM2017-31 suggests this specimen was an old tree. Furthermore, the occurrence of several large stumps (11 with diameter >1 m) in the Mágoè Fossil Forest, indicates it was an established woodland, where occasional fungal/bacterial activity could affect particularly older trees. Older trees have greater probability of having hollows, but this does not require them to have hollows. In our sample, it is likely chance that explains why only one specimen was found with hollows. Thin-sections or polished sections

through one of the hollows would help to assess their cause, but because this was the only tree found possessing hollows we did not section it for curational reasons. A thin section would have helped because bacterial-fungal activity leaves a typical trace in the wood (Creber & Ash 1990).

CONCLUSION

This study describes a rare example of Permian fossil tree hollows. Tree hollows can have multiple origins with predictable morphologies (Gibbons & Lindenmayer 2002) and can be indicative of fungal/bacterial activity and types of forests. Our findings highlight the importance of these structures for understanding various paleoecological aspects of ancient ecosystems.

We are grateful to Isabel L. Torres for editing the manuscript, to Joaquim Chaoma and Neva Djimo for providing field assistance, and to the Director Provincial dos Recursos Minerais de Tete, Grácio Cune, for logistical support. We are grateful to Anne-Laure Decombiex who made important suggestions in an earlier version of the manuscript. We are much indebted to Issaia Macaneta who assisted in the field and to Maria José Cerdeira for bibliographic assistance in finding rare articles and papers. Financial support was provided by the Museu Nacional de Geologia and by the Fundação para a Ciência e a Tecnologia (R.A. postdoctoral fellowship SFRH/BPD/96205/2013), FCT - AGA KHAN Development Network grant number 333206718, National Geographic Society grant number CP-109R-17. We also thank Estela Cuambe, Marcelino Moiana and Lino José from Museu Nacional de Geologia (Mozambique). We also thank Mike de Wit and Natasha Barbolini for their useful reviews.

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