Fossil tree hollows from a Late Permian forest of the Matinde Formation (Tete, Mozambique)

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ABSTRACT

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 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 to 3.5 cm in diameter. Although thirty-one trees were densely sampled 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: tree hollows, Late Permian, Mozambique, fossil forest, Tete

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 and Wilkes 1989, Lindenmayer et al. 2000a, Gibbons and 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 centimeters to nearly a meter in diameter (Gibbons and Lindenmayer 2002), however, tree hollow analyses in modern forests reveals 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 (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 is a nearly complete snapshot in time of the tree hollows from ancient Carboniferous environments (Grey & Finkel 2011). However, despite this remarkable example, tree hollows are only sporadically reported in the paleontological literature (e.g., Grey & Finkel 2011). 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 thought to correspond to the Late Permian, probably between the Wuchiapingian and Changhsingian (GTK Consortium 2006, Pereira et al. 2016). Although Mozambican fossil tree records from the Tete Province date back to more than a century ago (Lapierre 1883, Potonié 1900), clear references to the Mágoè Fossil Forest only occurred later, starting in the 1940s (Teixeira 1946, 1947, Silva et al. 1967). This fossil forest extends for more than 75km (Ferrara 2004), indicating this is the largest fossil forest in Africa found to date. Other fossil forests in Africa can be found in Zambia, Zimbabwe (Barbolini et al. 2016) and Namibia (Schneider 2008).

The Mágoè Fossil Forest is a unique site for studying the flora and ecosystems preceding the Permo-Triassic Mass Extinction, however, despite its vast extension and abundance of fossil trees, this fossil forest remains mostly unexplored. Tree hollows are important to understand various aspects of forest ecology and plant-environment interactions but are seldom found in the fossil record. In this study, we report a fossil stump preserving tree hollows from the Mágoè Fossil Forest, thereby opening the way for future research into the paleoecology of the Permian.

<<Figure 1 here>>

MATERIALS AND METHODS

We sampled two distinct locations at the Mágoè Fossil Forest totaling 31 fossil trees. The fossil trees from the two different areas were sampled exhaustively, meaning that from that particular area no tree was left unmeasured. The stump diameters were only measurable for 27 logs (n=27). For each of the trees we registered precise geographic coordinates (precision $\pm 1\text{m}$) using a GPS, orientation of the fallen tree stem using a field compass, maximal diameter of the tree stumps at the base, photographic evidence and a sample of each specimen was

collected. Linear measurements were taken with a measuring tape (precision of 0.5cm) and angular measurements (i.e., orientation were registered using a field compass; 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 '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), it is known that this species is currently a *nomen dubium* (Merlotti & Kurzawe 2006). The species *Dadoxylon nicoli* is currently attributed to the genus *Australoxylon teixeirae* (Marguerier 1973, Merlotti & Kurzawe 2006, Bamford 2016). However, the fossilized wood anatomy of the Permian trees from the Mágoè Fossil Forest are currently being revised and is in need of a deep reinterpretation and taxonomic update.

RESULTS

<<Figure 2 here>>

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 the equations from Niklas (1993, 1994a,b) an estimated height of 35.8 m ($H_{est}=27.8D^{0.430}$).

The sample of tree trunks normally distributed (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). Average tree base diameter is 92.96 cm ($\sigma = 48.74$ cm), with a minimum diameter of 20cm (PPM2017-10) and a maximum diameter of 190cm (PPM2017-1), see Table 1. In the boxplot PPM2017-31 is in the last quartile of the dataset (Figure 2), which means that the specimen possessing the tree holes was an old tree based on the collected data sample.

<<Table 1 around here>>

There are six tree hollows visible only in one side of the stump (Figure 3). All the hollows are occurring at approximately the same level to 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 (Figure 1, 3). The smallest tree hollow is 2.1cm in diameter (1.15 cm^2) and the largest 3.6 cm in diameter (10.75 cm^2), see table 2. The Pearson correlation coefficient between area and diameter is very high (0.993), which is a consequence of the low number of present tree hollows and an indication that indeed the tree hollows are subcircular.

<<Figure 3 around here>>

<<Table 2 around here>>

DISCUSSION

Tree hollows in the main stem account for up to 47% of all hollows in eucalyptus forests (Lindenmayer et al. 2000c), however, in woodland species approximately 91% of hollows occur in the tree crown (Gibbons and Lindenmayer 2002, Newton-John 1992) as a result of broken branches (Gibbons and Lindenmayer 2002). As most specimens in the Mágoè Fossil Forest have not preserved the canopy, only the stem accounts for statistical purposes, which has inevitably skewed our statistical analyses. Nevertheless, among the 31 tree stumps analyzed

only one exhibited tree hollows, representing ~3% of the sample. This result suggests that this fossil site was a locality with low tree density, as woodlands typically have low abundance of tree hollows, when compared with forests. It is important to note that the trees from the Permian were fundamentally different from those living today, and therefore these results are merely indicative. In fact, 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 in 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 and Lindenmayer 2000). This type of hollow represents approximately 2 to 16% of tree hollows (Lindenmayer et al. 2000c), however, they have 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 tree's old age (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 and Lindenmayer 2000). Furthermore, tree growth decelerates as trees age, which decreases their capacity to repair wounds (Jacobs 1955). Indeed, the large size of PPM2017-3 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 forest, where occasional fungal/bacterial activity could affect particularly older trees. Thin-sections or polished sections through one of the hollows would help to clarify their cause, however, giving the fact that this was the only tree found possessing hollows we did not section it for curational reasons.

This study describes a rare example of fossil tree hollows from the Permian. Tree hollows can have multiple origins with predictable morphologies (Gibbons and 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.

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FIGURES AND FIGURE CAPTIONS

Figure 1. On the side of the PPM2017-31 tree trunk there are six subcircular tree hollows (A) as indicated by the arrows, an oblique view of the tree stump (B) and an orthogonal photograph of the same specimen in cross-section (C). Scale bar 10 cm.

Figure 2. (A) The histogram shows the distribution of the sampled fossil trees trunk diameters and the typical left-skewed distribution of diameters in a forest. (B) The boxplot shows the maximum (190cm) and minimum (20cm) sized tree stump, with the average being ~92cm.

Figure 3. Box-plots showing the tree hollow diameter (A) and area (B) distributions in PPM2017-31

Tables

	Diameter
Specimen	(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

Table 1 – Sampled tree trunk diameters in centimeters from the Mágoè fossil forest.

Hollow #	Diameter (cm)	Area (cm ²)
1	1,119	1,151
2	1,872	3,739
3	1,163	1,46
4	3,526	9,313
5	1,366	2,822
6	3,607	10,753

Table 2 – PPM2017-31 tree hollow diameter (cm) and areas (cm²).