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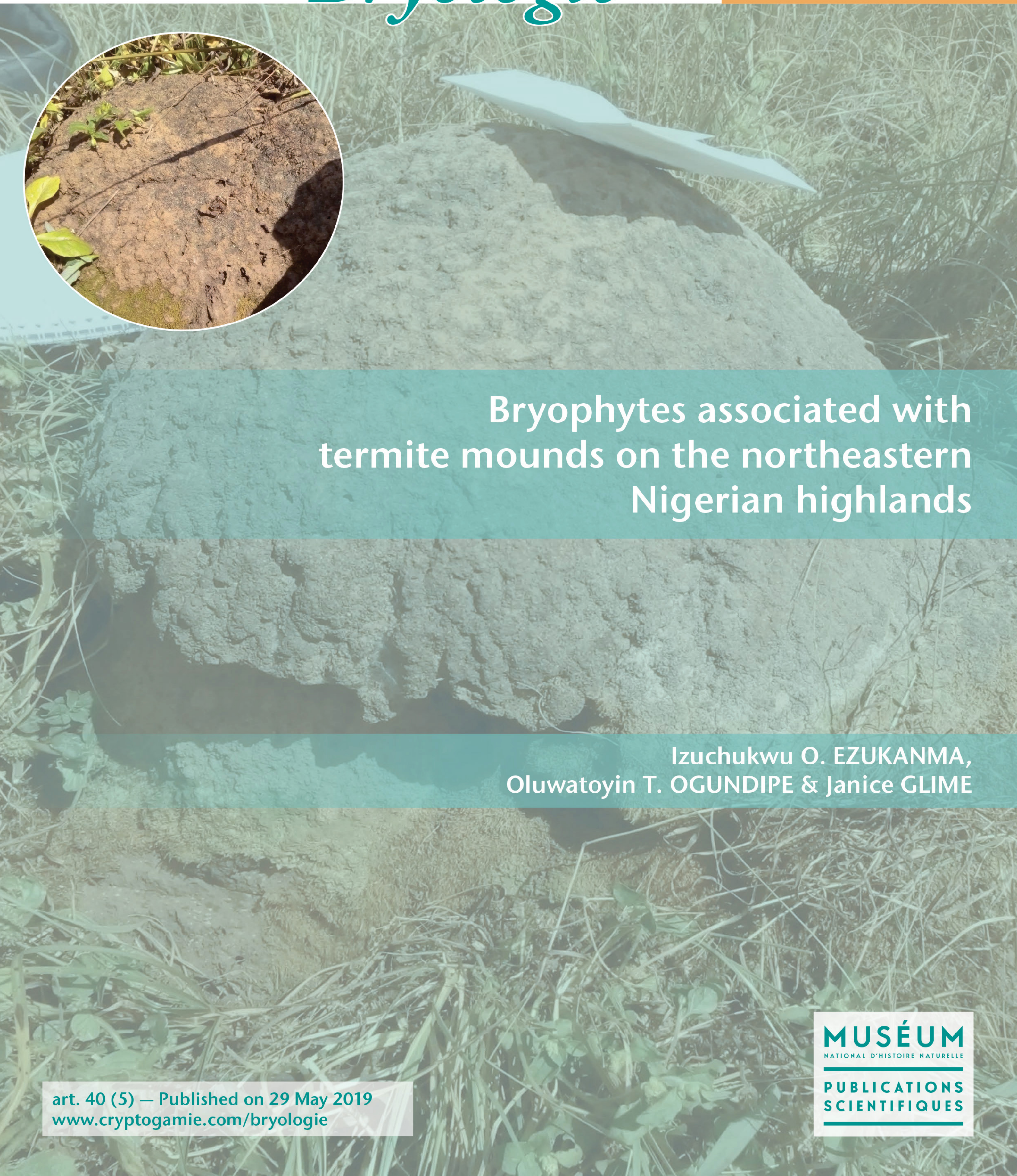

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ABSTRACT
Eighteen termite mounds on a stretch of undulating continuously grazed and burnt grasslands on the Mambilla Plateau, Eastern Nigeria, were surveyed for bryophytes. Bryophyte mats were present on all mounds investigated except one. The bryophyte mats were located at the base of the mounds, on a depression etched by raindrops and apparently serving to keep erosion at bay. We suggest that on grasslands with frequent fire episodes, the bryophyte mats may also play a role in fireproofing the mounds. In all, eight bryophytes species across five families were collected on the termite mounds. All species were new to the region but had been collected elsewhere from different substrates in Nigeria, except *Fissidens ezukanmae* Brugg.-Nann., which is a new species collected for the first time from termite mounds on Eastern Nigerian Highlands. Two species, *Campylopus obrutus* Thér. & P. de la Varde and *Fissidens intramarginatus* (Hampe) A.Jaeger, with estimated frequency of 24% each, were the most abundant species on the termite mounds.

KEY WORDS
Africa,
Archidium,
grassland,
Mambilla Plateau,
mosses,
Nigeria.

RÉSUMÉ
Bryophytes associés aux termitières dans les hauts plateaux du nord-est du Nigéria.
La présence de bryophytes a été étudiée sur dix-huit termitières sur une étendue de prairies continuellement broutées et brûlées sur le plateau Mambilla, dans l'est du Nigéria. Des tapis de bryophytes étaient présents sur toutes sauf une. Les tapis de bryophytes se situent à la base des termitières, dans une dépression formée par les gouttes de pluie, et servant apparemment à en préserver l'érosion. Les auteurs suggèrent que sur les prairies fréquemment brûlées les tapis de bryophytes peuvent jouer un rôle dans l'ignifugation des monticules. Dans tous, 8 espèces de bryophytes appartenant à cinq familles ont été récoltées sur les termitières. Toutes les espèces sont nouvelles pour la région, mais ont été observées ailleurs sur différents substrats sauf au Nigéria. *Fissidens ezukanmae* Brugg.-Nann. est une nouvelle espèce collectée sur les termitières des Hauts Plateaux de l'Est du Nigéria. Deux espèces, *Campylopus obrutus* Thér. & P. de la Varde et *Fissidens intramarginatus* (Hampe) A.Jaeger, avec une fréquence estimées de 24% chacune, sont les plus abondantes sur les termitières.

MOTS CLÉS
Afrique,
Archidium,
prairies,
Plateau Mambilla,
mousses,
Nigéria.

INTRODUCTION

In the tropics, naked undisturbed soil is a seldom-used substrate for bryophytes (Richards 1984), apparently due to the absence of a well-developed humic layer on the forest floor as a result of the high rate of decomposition, which renders the soil almost bare of bryophytes (Gradstein 1992; Frahm 2003). Conversely, disturbed soil has a unique bryoflora dominated mostly by species of *Fissidens* Hedw. (Pócs 1982; Richards 1984). Termite structures may have the appearance of bare soil but they are not entirely equivalent to naked soil. The termite structures present a durable surface with an elevated nutrient profile due to the enriched organic substances from termites, like saliva and faeces used during the construction of these structures (Harris 1956; Ackerman *et al.* 2009).

Termite mounds are known to have remarkable impact on their surroundings (Yamashina 2010). In Kenya and Australia, several species of plants are known to thrive on termite mounds and support the herbivore populations which prefer to feed on plants growing on the mounds (John & Stein 2004; Ragnhild *et al.* 2005). The rich nutrient contents of the soil on the mounds enhance its use as fertilizer for field cultivation in South Africa (Coaton 1950) and Amazonia (Batalha *et al.* 1995). In Kenya and Zambia, the soil of termite mounds is a rare delicacy, especially for pregnant women, and is eaten and exchanged as a precious and expensive food because of its rich mineral content (Yamashina 2010).

In most cases, the termite mound is not a fortuitous heap of earth but a construction mediated by an intricate interplay of species behavior, available material, climate and elevation (Harris 1956). The soil that is available at any particular location determines the shape of the mound. Tall, thin mounds have a sand to clay ratio of 1:1 to 3:1, while larger dome-shaped mounds range from 2:1 to 18:1 (Hesse 1955). Coaton (1947) observed an inverse proportion of mound size of the termite *Macrotermes bellicosus* Smeathman with increasing elevation. At the upper limits of its range in the Highlands of East Africa at approx. 1800 m above sea level, the mounds are low, rounded domes with a gradual increase in size as one descends to lower elevations. The most profound effect of climate on termite mounds is caused by rainfall (Harris 1956). Falling rain erodes away turrets and pinnacles, which are constructed mostly during the rains, thereby producing a dome-shaped mound. Harris (1956) suggested that the intensity of precipitation is more important than overall annual rainfall.

Some bryophyte species are associated with the termite mounds which serve as surrogate substrate for species that preferentially dwell on disturbed soil (Reese & Pursell 2002). The shingling effect provided by the flattened, overlapping fronds of the tiny moss plants and the soil-binding effect of the moss rhizoids facilitate drainage of the raindrops. In addition, the springy stems of the moss plants attenuate the impact of raindrops, depleting their energy and dissipating their impact. These add to the long-term stability of the termite structure (Reese & Pursell 2002). Species of the genus *Fissidens* are the most common associates with termite mounds in tropical America (Churchill 1998), but Reese (2001) and Lisboa (1993) listed several species of Calymperaceae and Pilotrichaceae associated with termite mounds in Amazonia. Likewise, in parts of Africa, various *Fissidens* species have been collected from termite mounds (Potier de la Varde 1928, 1936; Bizot & Pócs 1979; Bizot *et al.* 1990; Bruggeman-Nannenga 1993). However, we are not aware of any account of bryophyte species associated with termite mounds in Nigeria. This study therefore aims to determine which bryophyte species are associated with termite mounds and the influence of the species on the stability of the structures.

MATERIAL AND METHODS

Study site

The study area is a stretch of grassland on the outskirts of Yelwa village on the path to Ngel Nyaki Forest Reserve, Mambilla Plateau, Taraba State, Nigeria. The Mambilla Plateau as described by Chapman & Chapman (2001) is a mid-altitude, submontane region ca. 1500 m above sea level located in the southeast corner of Taraba State, between 11°00' and 11°30'E, and 6°30' and 7°15'N. The plateau is a mainly open grassland of approximately 3100 km^2. Only fragments of forest limited to the stream valley remain (Akinsoji 2013; Ihuma *et al.* 2011b). The plateau is drained by numerous water courses which unite to form the main rivers to discharge eventually into River Benue, Nigeria's second biggest river. The plateau is delineated on its northern and western sides by a steep escarpment rising to 1070 m above the surrounding lowlands. To the east Mambilla is connected with the Cameroon highlands, which extend southwest towards Bamenda and northeast to the Massif de L'Adamaoua.

Geologically, the largest portion of the Plateau is basement rock (2630 km^2), whereas lava occupies 570 km^2 (Chapman & Chapman 2001). The part of Mambilla Plateau underlain by volcanic rocks is characterized by rolling grassland, becoming more hilly towards the western border where columnar jointing of the basalt gives rise locally to low cliffs and crags. Generally, the landscape is undulating with numerous dome-shaped hills and steep valleys which rarely exceed 1680 m. The soils of the grassland section of the plateau as described by Chapman & Chapman (2001) are humic ferrisols, slightly acidic (pH 5.6-6) and mainly silty loamy in texture. Mean annual precipitation exceeds 1780 mm, spread across 250 rainy days from April to October (Ihuma *et al.* 2011a) with June/July and September as the rainiest months (Chapman & Chapman 2001). The dry season is from November to March; during this period, less than 80 mm+ of rain may be recorded. Daily mean temperature usually does not exceed 30°C and frost has been recorded in the past at Mayo Ndaga in February (Chapman & Chapman 2001).

The Mambilla plateau is a high grassy upland with palatable grasses dominated by *Hyparrhenia* Andersson ex E. Fourn. sp. (Richard 2014), high rainfall, and low veterinary disease challenge that present the plateau as an ideal grazing terrain attracting large pastoralists and large herds of cattle (Blench 2013). Overgrazing and annual burning, perhaps to induce regrowth, is common on the plateau. Low dome-shaped termite mounds dot the grassland landscape and are readily visible, especially during the dry season.

Sampling

Field work was carried out in November 2015. Starting with the nearest mound about 60 m outside the fence of the Ngel Nyaki Forest Reserve and heading towards Yelwa village (*approx*. 5 km away), eighteen termite mounds were selected along a transect (Fig. 1; Table 1). After inspecting a mound, the next visible mound from the thicket at least 20 m apart was approached while walking towards the village. We mostly kept off the road to the village during the selection and inspection of the mounds for the presence of bryophytes, but the road was crisscrossed at various points. The height and diameter of each mound were recorded and distribution of mounds plotted using a GPS unit (Yamashina 2010). Bryophyte species occurring on the mounds were collected and processed following the method of Vanderpoorten *et al.* (2010). Estimated frequency of species was calculated and scored according to Frahm (2003) and Andersson & Gradstein (2005):

I	=	0-5%
II	=	6-20%
III	=	21-40%
IV	=	41-60%
V	=	61-80%
VI	=	>80%

Species distribution range analysis

The distributional range of each species was determined from O'Shea (2006) and TROPICOS (2018) to generate a species-countries/territories distribution matrices and scored for presence or recorded (1) and absence or not recorded (0). The generated matrices were used to conduct a neighbour joining clustering with similarity index and root set at Kimura and Final branch respectively for the countries/territories. The matrices were transposed for hierarchical clustering with Algorithm and Similarity index set as pair group (UPGMA) and Simpson for the species using the Palaeontological Statistics (PAST) software version 3.12 (Hammer *et al.* 2001).

Nomenclature follows O'Shea (2006) and TROPICOS (2018). Voucher specimens were prepared and deposited at Lagos University Herbarium, Lagos (LUH), Herbarium of the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków (KRAM), and the National Herbarium of the Netherlands, Leiden (L).

RESULTS

The mean diameter and height of the termite mounds were 175.61 ± 32.14 cm and 39.83 ± 10.46 cm, respectively (Table 2). Bryophytes usually occurred at the base of the mound and tended to align with a shallow depression etched by cascades of rain and flood water (Fig. 2;3). Bryophytes were found on all sampled termite mounds except one (Table 1). Unlike the other mounds that gave a thud sound when struck, the mound without bryophytes emitted a hollow sound when struck, suggesting the structure may have been abandoned by termites.

Table 1. — Termite mounds surveyed for bryophytes on Mambilla Plateau, Nigeria.

Termite	Diameter (m)	Height (m)	Bryo Presence	°N	°E	Elevation (m)
1	1.7	0.42	+	7.08514	11.06972	1691
2	1.57	0.32	+	7.08543	11.07065	1692
3	1.80	0.34	–	7.08508	11.07080	1684
4	1.95	0.50	+	7.08475	11.07095	1675
5	1.85	0.55	+	7.08468	11.07096	1675
6	1.70	0.55	+	7.08462	11.07114	1671
7	1.47	0.32	+	7.08507	11.07247	1655
8	2.40	0.43	+	7.08507	11.07254	1654
9	2.40	0.32	+	7.08504	11.07264	1653
10	1.30	0.28	+	7.08488	11.07333	1652
11	1.52	0.36	+	7.08497	11.07858	1655
12	1.60	0.42	+	7.08530	11.07548	1648
13	1.77	0.31	+	7.08544	11.07576	1646
14	1.72	0.60	+	7.08547	11.07621	1635
15	1.36	0.20	+	7,08547	11.07627	1611
16	2.25	0.45	+	7.08614	11.07618	1611
17	1.50	0.40	+	7.08605	11.07852	1604
18	1.75	0.40	+	7.08599	11.07853	1604

Table 2. — Site features of termite mounds on Mambilla Plateau.

Geographical coordinates	7.08514°N, 11.06972°E
Mean elevation ± SD (m)	1650 ± 28
Total number of mounds investigated	18
Mean diameter of mounds ± SD (cm)	175.61 ± 32.14
Mean height of mounds ± SD (cm)	39.83 ± 10.46
Number of mounds with bryophytes	17
Number of bryophyte species recorded	8

Eight bryophyte species in five families were recorded (Table 3). A new species *Fissidens ezukanmae* Brugg.-Nann. (Bruggeman-Nannenga 2019) was collected for the first time from these termite mounds on the Eastern Nigerian Highlands. *Campylopus obrutus* Thér. & P. de la Varde and *Fissidens intramarginatus* (Hampe) A.Jaeger, each with an estimated frequency of 23.5%, were the most abundant species on the termite mounds, followed by *Splachnobryum obtusum* (Brid.) Müll.Hal. and *Fissidens inflatus* (Müll.Hal.) Paris with estimated frequency of 17.6%. The other species have estimated frequencies around 10% except *Fissidens ezukanmae* (< 6% estimated frequency).

The distributional range of the eight species were predominantly Palaeotropic and Neotropic except *Archidium ohioense* Schimp. ex Müll.Hal and *Splachnobryum obtusum*, which are also known from North America (Southern United States) and Western Europe (United Kingdom). The combined distributional range of the eight species is 66 countries/territories with New Caledonia as the farthest range of a species (*A. ohioense*) collected from the termite mounds.

The hierarchical clustering of the recorded species indicates that two pairs of species: *Fissidens intramarginatus* and *Wijkia trichocoleoides* (Müll.Hal.) H.A.Crum, and *Splachnobryum obtusum* and *Campylopus savannarum* (Mull.Hal.) Mitt. share very similar distributional patterns, > 80%, while *Fis-*

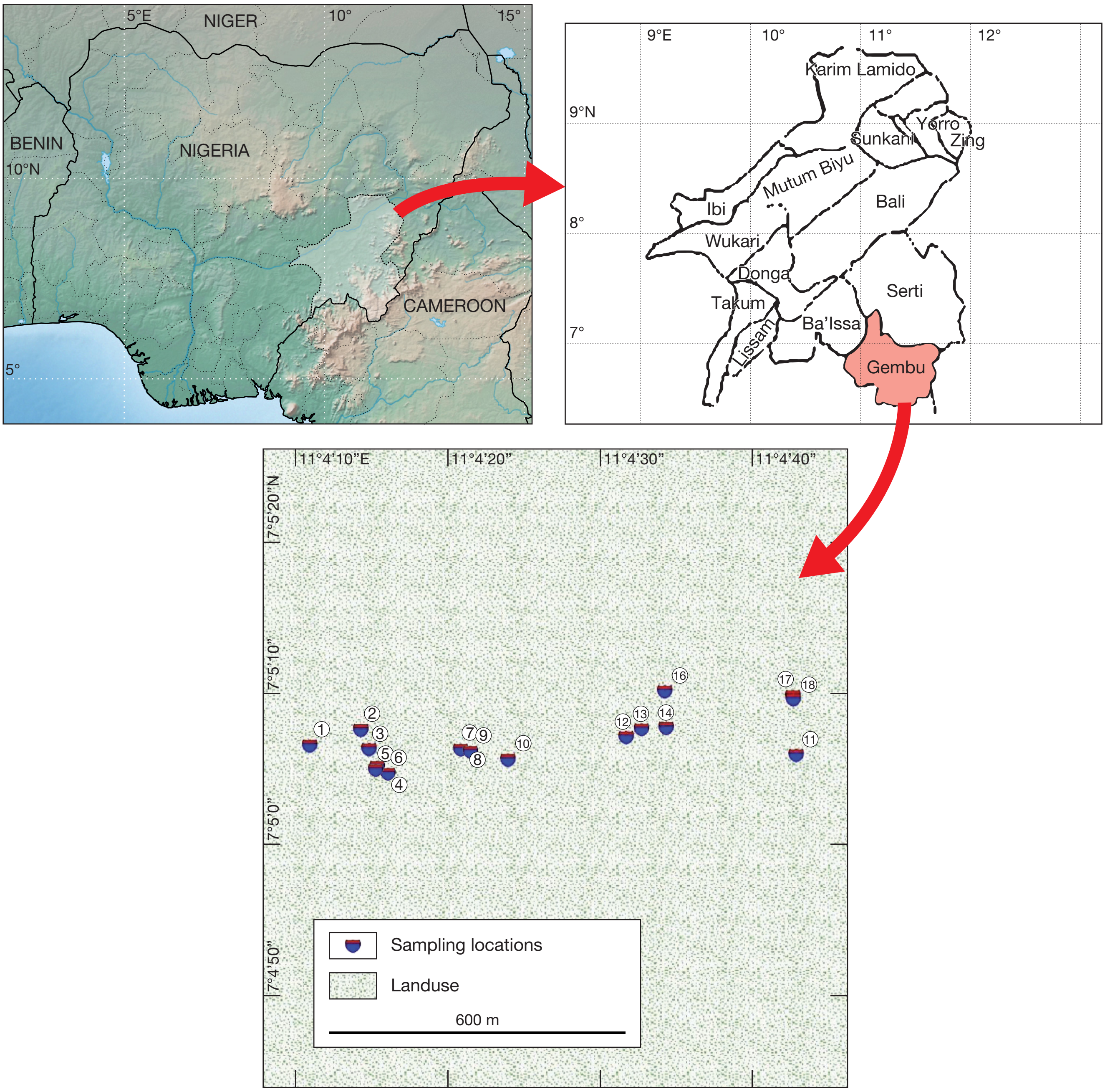

FIG. 1. — Map indicating position of termite mounds sampled on the Mambilla Plateau, Nigeria.

sidens inflatus (and the new species *F. ezukanmae*) share the least similarity, < 1%, with other species (Fig. 4). Similarly, the neighbour joining clustering of the countries/territories indicates that Nigerian termite mound flora based on these eight species were most related to species known from DRC (Zaire), Tanzania, Ivory Coast, Central African Republic, Bioko, Cameroon, Rwanda, Gabon, Kenya, and Mexico (Fig. 5).

DISCUSSION

The absence of bryophytes on the 'abandoned' mound suggests that the bryophyte species occurring on mounds were not chance occurrences. Instead, these species may have been deliberately selected and cultivated by the termites. Although it is not so clear if all the mounds were constructed by the same termite species, it is obvious that the occupants of the mounds have an intrinsic relationship with the grasses and the grassland. It is likely that the termite species on the grassland are grass feeders, like *Trinervitermes* spp. (Nasutitermitinae) (Duponnois *et al.* 2005), rather than litter-feeders or fungus-growing termite species such as *Macrotermes* Holmgren and *Odontotermes* Holmgren spp. (Macrotermitinae) (Contour-Ansel *et al.* 2000; López-Hernández *et al.* 2005; Coaton & Sheasby 1972). Although the mounds were positioned on an incline, with an increased likelihood of being washed off by

Fig. 2. — Termite mound with bryophyte mats at the base. Mambilla Plateau, Nigeria.

the torrents, the size of the termite structures with a mean diameter and height of 175.6 and 39.8 cm, respectively, is not likely due to reduction in size caused by erosion.

The bryophytes on the mounds seem to be strategically placed to abate the accelerated floodwater as it cascades down the incline of an undulating landscape. But in a continuously grazed grassland with frequent episodes of fire outbreak, the bryophyte mats on the mounds may have additional roles like fire mitigation, due to their moisture-holding ability. It appears that the bryomass at the base is 'placed' to contend with the smoldering splinters. Perhaps there are morphological adaptations of bryophyte species on the mound to attenuate both raindrops and floodwater impact and to serve as fireproofing for the mound. However, this is beyond the scope of the present study and is worth considering in future studies that include experimental work. For the bryophytes,

Fig. 3. — Bryophyte mats at the base of termite mound. Mambilla Plateau, Nigeria.

the mounds may provide special conditions that are favorable, including shading, enhanced nutrients, favorable pH, and greater retention of moisture. These parameters need to be measured and manipulated experimentally to determine their role in bryophyte establishment.

It is not clear whether the different positions of the bryophyte mat on the mounds in the present study as compared with mounds on the Amazonian forest floor, where mosses are elevated above the forest floor, leaf litter and pooling rainfall (Reese & Pursell 2002), may reflect the local microclimatic conditions. It seems that air humidity towards the crests of the mounds in the open grassland is usually too low and unfavorable for bryophyte growth. A related trend is observed among epiphytic bryophytes on isolated trees which are often restricted to the base of the tree and are unable to grow higher up the trunk (as opposed to the more desiccation-tolerant lichens). In rain forests, however, where humidity conditions are less constrained, bryophytes may freely grow higher up the trunks. This may explain why bryophytes on termite mounds in Amazonian rain forest areas are not restricted to the base of the mound. However, we are not aware of any correlations between bryophyte

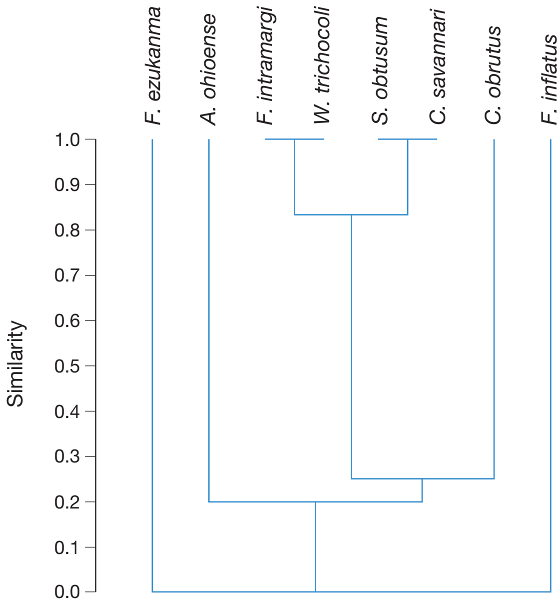

FIG. 4. — Distributional affinities of species collected from termite mounds from northeastern Nigerian Highlands.

TABLE 3. — Species occurring on termite mounds on Mambilla Plateau.

Bryophyte species	**Family**	**Estimated frequency**
Archidium ohioense Schimp. *ex* Müll. Hal.	Archidiaceae	II
Campylopus obrutus Thér. & P. de la Varde	Dicranaceae	III
Campylopus savannarum (Mull.Hal.) Mitt.	Dicranaceae	II
**Fissidens ezukanmae* Brugg.-Nann.	Fissidentaceae	I
Fissidens inflatus (Müll.Hal.) Paris	Fissidentaceae	II
Fissidens intramarginatus (Hampe) A.Jaeger	Fissidentaceae	III
Splachnobryum obtusum (Brid.) Müll. Hal.	Splachnobryaceae	II
Wijkia trichocoleoides (Müll.Hal.) H.A.Crum	Sematophyllaceae	II

composition and shape of the mounds, as described by Reese & Pursell (2002).

Just like on the Amazonian forest mounds studied by Reese & Pursell (2002), *Fissidens* species traditionally associated with termite mounds were similarly present on the mounds in this study. The genus *Fissidens* is widely distributed in Africa with about 90 species out of the estimated 450 species distributed worldwide and has a very wide altitudinal amplitude (Bruggeman-Nannenga 2013a, b). The discovery of a new species on the termite mounds from the Eastern Nigerian Highlands may suggest marked preference of this *Fissidens* for termite mounds.

All the bryophyte species in the present study are new records for the Eastern Nigerian highlands but had been collected from other substrates from different parts of Nigeria. For instance, Egunyomi (1984) reported *Archidium ohioense, Campylopus obrutus,* and *C. savannarum* on rocky substrates and exposed

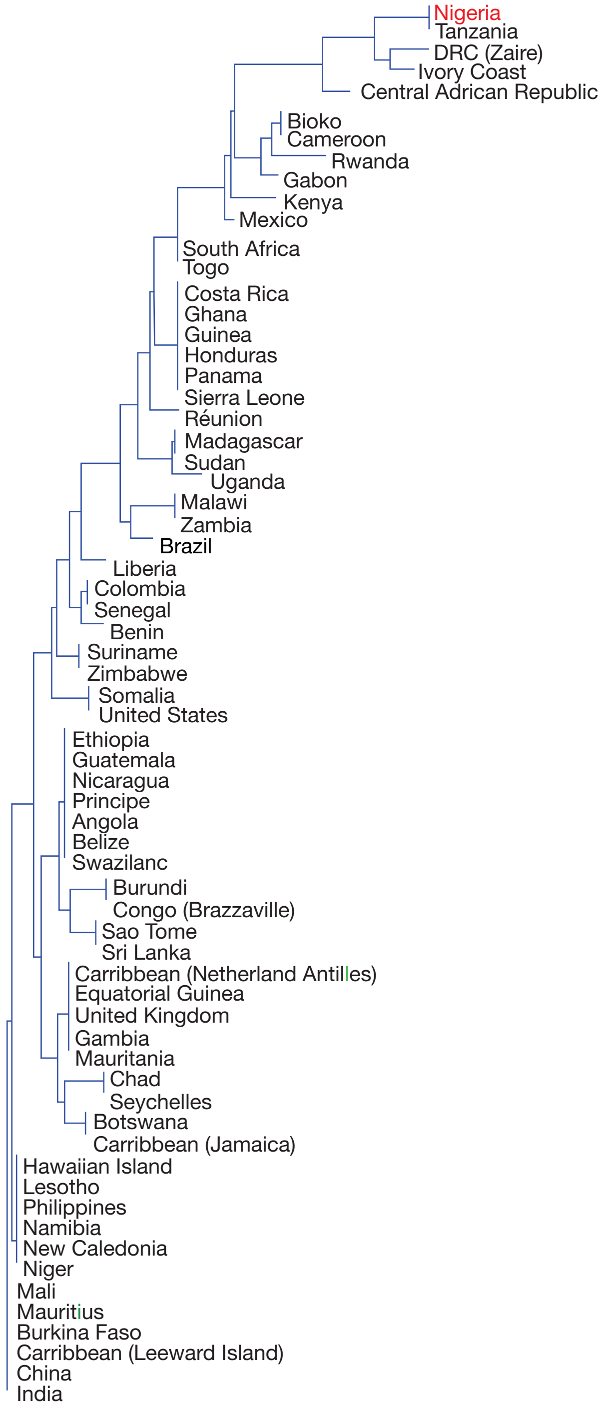

FIG. 5. — Neighbour joining clustering of countries/territories from which species collected from termite mounds on eastern Nigerian Highlands are known, indicating greatest similarity to the Nigerian mound bryophytes to the left and least similarity to the right.

inselberg in Southwest Nigeria. This suggests that these species are widely distributed in Nigeria and are common in open and exposed surfaces. The distributional patterns of the species differ markedly. Four species: *Campylopus obrutus, Fissidens ezukanmae, F. inflatus,* and *Wijkia trichocoleoides* are exclusively African in distribution, while the other species: *Archidium ohioense, Campylopus savannarum, Fissidens intramarginatus,* and *Splachnobryum obtusum* are known from various parts of Africa and are widely represented in the Neotropics and elsewhere (TROPICOS 2018).

Egunyomi (1984) attributed the Afro-American bicontinental distribution of species to remnants of the time on Gondwanaland during the Jurassic, about 135 million years ago when the continents were connected (Frahm 2003). However, recent molecular studies have shown that bryophyte species are not that old and that continental disjunctions of bryophyte species are more likely due to long-distance dispersal (Devos & Vanderpoorten 2009; Gradstein 2013; Laenen *et al.* 2014).

The hierarchical clustering of the eight species distribution ranges (Fig. 4) highlights two pairs of species with over 80% distribution similiarity: *Splachnobryum obrutus* + *Campylopus savannarum* and *Fissidens intramarginatus* + *Wijkia trichocoleoides*. These species are likely to have developed over time similar successful adaptation strategies, efficient reproduction and dispersal mechanisms to enable them to colonize diverse substrates over wide geographical range.

The Eastern Nigerian Highlands is currently a bryophyte under-collected region but preliminary records of bryophytes from the region (Ezukanma *et al.* 2017) found greater distributional affinities with flora from eastern and southern Africa and the Neotropics (Fig. 5) than that found for the neighbouring West Africa countries like Chad, Benin, Togo, Ghana, and Niger Republic. Similarly, Keay (1953) observed a related pattern in the phanerogam flora on the Jos-Bauchi Plateau, where many species were found not to occur elsewhere in West Africa but are identical with those from eastern and southern Africa. Likewise, the liverwort collection on the Jos Plateau gathered by E. A. Drew in 1962 were consistent with Keay's (1953) phanerogam distributional pattern on the Jos-Bauchi Plateau. (Harrington & Jones 2004). It might be helpful to get familiar with flora from eastern and southern Africa and the Neotropics for future studies of bryophytes of Eastern Nigerian Highlands.

In all, the bryophyte mats on termite mounds on grassland on the highland of Northeastern Nigeria may represent a unique and mutually beneficial co-evolutionary association. While the mounds avail a surrogate stable nutrient-enriched substrate for the bryophyte species 'cultivated' by the termites, the bryophyte mat may act to attenuate the impact of the falling raindrops and cascading floodwater on the mounds, thereby reducing erosion and enhancing the long-term stability of the termite structures. We also suggest that the bryophyte mats may play a role in fireproofing the termite mounds. The history and mechanisms of termite-bryophyte coevolution are still poorly understood and present opportunities for future investigation.

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