Diversity and palaeoecological significance of non-pollen palynomorph assemblages in East African lake sediments

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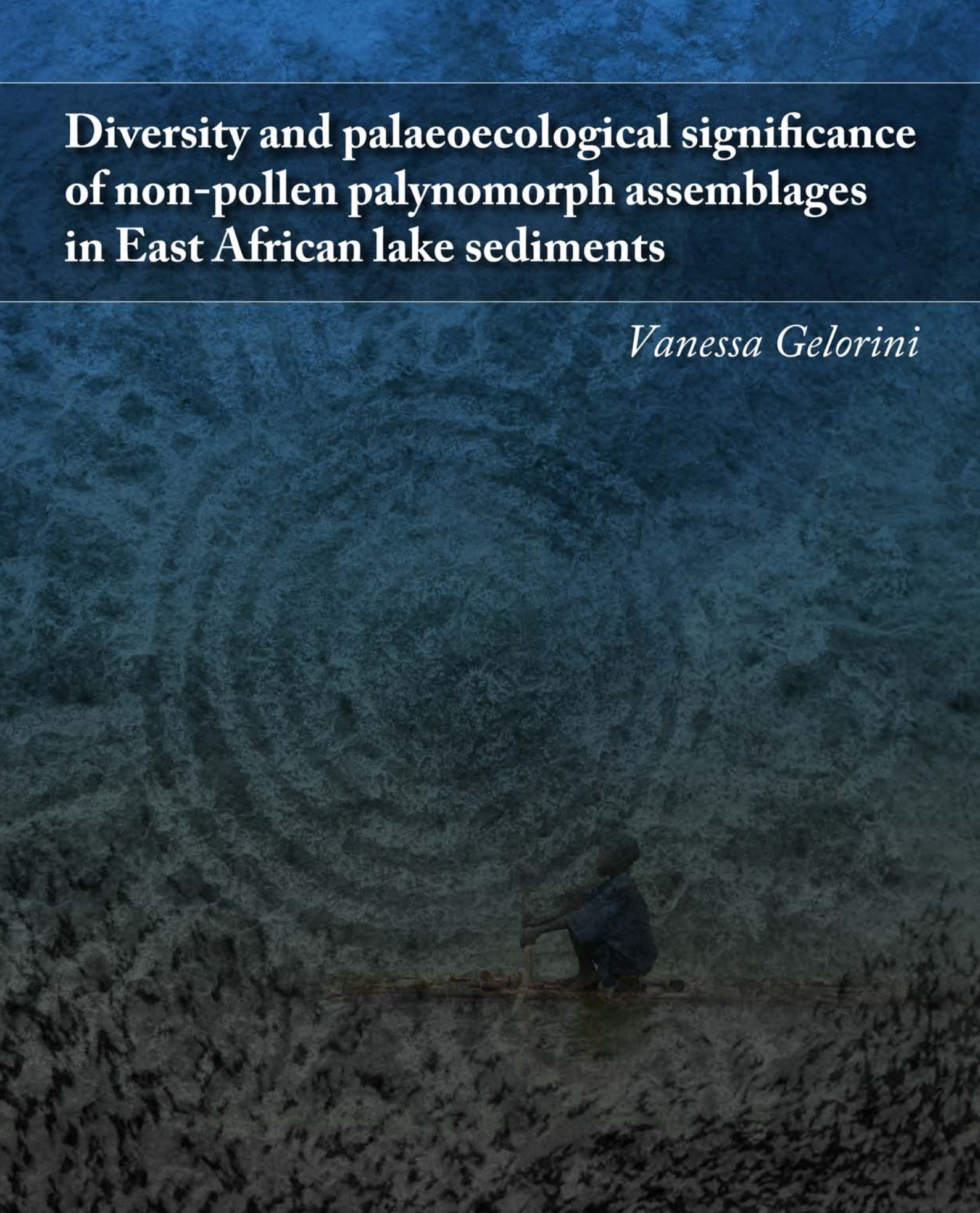

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Diversity and palaeoecological significance of non-pollen palynomorph assemblages in East African lake sediments

Diversiteit en paleoecologische betekenis van non-pollen palynomorfen assemblages in Oost-Afrikaanse meersedimenten

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Voorwoord

Aarde, water, vuur en lucht. De vier natuurelementen die me onmiskenbaar vergezeld hebben tot het volbrengen van dit werk. Tijdens mijn jeugd en universitaire studies archeologie, vormde de *aarde* reeds een essentieel onderdeel van mijn vrije tijdsbesteding. Met beide voeten 'in' de grond, was ik steeds geïntrigeerd op zoek naar sporen uit het verleden. Met de Leakey's als grote voorbeelden (en Indiana Jones als decoratief behangpapier), kreeg ik al gauw ook interesse voor exotische oorden. Mijn toenmalig iets te avontuurlijk idee om als archeologisch scriptieonderwerp de resten van de eerste Oost-Afrikaanse hominiden te onderzoeken (om Lucy te vervoegen met Anne, Roxanne en andere muzikale naaminspiraties), werd echter vanuit mijn archeologische entourage met enige argusogen aanschouwd en met wat 'prof'essioneel gemaneuvreer over een ietwat meer landelijke, floristische boeg gegooid: palynologie, toegepast op Oost-Vlaamse protohistorische waterputten. Het esoterisch onderzoeksgehalte bleef inderdaad hoog, en de biologische invalshoek hield hoe dan ook halsstarrig stand als leidraad in het verhaal. Niettemin bleek het een schot in de roos. Mijn nieuwsgierigheid werd mateloos getrakteerd op kunstzinnige micro-ontdekkingen. Met het doorbreken van de schoenmaker-blijf-bij-uw-leest-wetmatigheid en honkvast-discipline-gedrag ontpopte ik me als voorstaander van interdisciplinariteit, gericht op het ontrafelen van historische mens-milieu interacties. Mijn hunker naar een meer omvattende, wetenschappelijke houding, resulteerde dan ook in een 7-jarig bohême-bestaan, met palynologische projecten in de archeologie, geschiedenis en geografie, waarbij ik kon proeven van verschillende methodologische benaderingen. De drang naar wetenschappelijk inzicht kreeg echter pas goed vorm, toen ik in juli 2007 de kans kreeg aan een langdurig project binnen de biologie - de limnologie - mee te werken. *Water* werd bijgevolg een tweede bondgenoot. Wat aanvankelijk voor mij een nieuwe beproeving en evenwichtstest bleek te zijn, groeide uit tot een introductie in de haute-cuisine van multi-proxy gericht lacustrien onderzoek, en met de nodige vakkundige ondersteuning van rasechte limnologen baande ik me een weg in de Oost-Afrikaanse paleolimnologie. Gedreven door mijn onvoorwaardelijke passie *(vuur)* voor wetenschappelijk onderzoek, en af en toe happend naar *lucht* om niet te verdrinken in de biologerende materie, werd mijn wetenschappelijke doelstelling om een doctoraatsverhandeling te schrijven, vooralsnog ingelost.

Dankwoord / Acknowledgements

"I can no other answer make, but, thanks, and thanks"
(Twelfth Night, William Shakespeare, 1599-1601)

Tijdens deze bijna 4 jaar durende Oost-Afrikaanse queeste stond ik onder het wakend oog van Dirk; van alle mentors, die me de afgelopen jaren vergezeld hebben, heeft hij me ongetwijfeld het meest bewogen en geïnspireerd, in die mate zelfs dat ik me momenteel al meer biologe voel dan de archeologe die ik was aan het begin van het project. Zijn uitzonderlijke, wetenschappelijke kennis en inzichten hebben mede bijgedragen tot de realisatie van dit werk.

Een introductie in de wonderlijke (sprookjes)wereld van de zwammen heb ik hoofdzakelijk aan co-promotor Mieke te danken. Haar nimmer aflatend enthousiasme en positieve vibes waren een welkomsgeschenk in momenten, waarin de vele sporen me hooikoorts deden bezorgen. Samen met Lynda, Christine en Hilde behoorde ze tot het vrouwelijke team van vier charmante senior biologen, die me met de nodige flair (en soms koffie en zelfgemaakte koekjes) geregeld een duwtje in de juiste richting gaven.

Ook met de, in dit geval, warme noorderwind zijn er de afgelopen jaren heel wat wetenschappelijke en menselijke verrijkingen komen aanwaaien: Bas, ik vond het een privilege de grondlegger van het non-pollen palynomorfen (NPP) onderzoek aan mijn zij te hebben; je verdienste voor de palynologie, en het NPP onderzoek in het bijzonder, zal ongetwijfeld door toekomstige generaties ten volle in ere gehouden worden.

Every collaboration helps me grow wiser, and improves my research skills: Immaculate, Stephen, Julius and Johnson, thanks to you all I enclosed East Africa and African palaeoecology in my heart. Bob, Christine, Pierre-Denis and Julie, it was a pleasure to join the CLANIMAE team and to share my first African fieldwork experiences with you all. Rob, I am grateful for your hospitality and fruitful discussions during my stay at the KITE Environment Department in York, and during your short visits in Ghent. I also thank you and Paul for valuable comments on my PhD draft. Hilde, Luc and Bent, thanks for helping me through the statistics, and for introducing me into the "alien" world of ecological modelling.

During my PhD research, I had the opportunity to consult some of most wanted experts in the taxonomic field of tiny, little organisms, who enthusiastically joined me on my African NPP journey. Jiri Komárek, Vlasta Jankovská, Christine Cocquyt, Jean Nicolas Haas, Henri Dumont, Lynda Beladjal, S.S.S. Sarma, Jacqueline van Leeuwen, Elke Bellefroid, Ronnie Viane, Fabienne Marret, André Aptroot, Bernard Declercq and Anne-Marie Lezine: thank you very much for checking some of my fascinating microfossils.

I further gratefully acknowledge the members of the examination committee for constructive reviews on the draft version.

Historisch besef vormt een vast onderdeel van het paleo-onderzoek. Dankzij herhaaldelijke sampling- en/of onderzoeksefforts van de gehele limno-staff (1999-2010) en het voltallige CLANIMAE team (2007-2010) is een stukje Afrikaans (en ook minder Afrikaans) natuurlijk erfgoed in Gent (en omstreken) verzeild geraakt, waarvan ik uitgebreid heb kunnen gebruikmaken om de eerste NPP-puzzelstukjes in het multi-proxy geheel een voorlopige bestemming te geven.

Van de limno-collega's koester ik hoofdzakelijk de kleine, hartelijke momenten: de ontelbare socio-mailtjes (met cartoons incluis) van Leen tijdens de laatste loodjes; het broederlijk delen-gehalte van Thijs met zijn voorraad aan te grote wafels-, te veel koekjes- en kauwgom-om-op-te-krijgen tijdens mijn verdoken werkmomenten achter de kast; de small-talks (lees: platte praat) met Bob tijdens onze verdienstelijke poging om het 160 m diepe Lake Rukwanzi te bemonsteren (misschien waren we gewoon vanilla-high?); de happy hours (lett.) met Angelica in en ook buiten het labo; de lekkere taartenbak van Hilde en Els voor mijn achterstallig limno-verjaardagsfeestje; de down-to-earth, maar ludieke bemonstering- en preparatiesessies met Yoeri in het labo; het overweldigend verrrassingspakket, geleverd

door Kay tijdens de ijskoude, maar met-heldere-hemel, nachtelijke stage op de Blaarmeersen; de filosofisch-getinte middagpauzes met Générose; en de 20 m sprint met Maureen op de gang van de 10de verdieping (in een onbewaakt moment). Ook de 2de verdieping (Mycologie en Pteridologie) behoorde deels tot mijn wetenschappelijke uitvalsbasis, waar ik steeds terecht kon voor het gebruik van de ultragesofisticeerde microscoop, de noodzakelijke myco-literatuur en de nodige tussendoor-babbels. Van de terrestrische collega's blijven onherroepelijk de carnavaleske amusements- en ontspanningsmomenten doorspekt met humor me bij tijdens de middag- en koffiepauzes op de 9de verdieping; een 'Comedy Casino' van wereldformaat.

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Asante sana to all.

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Abstract

In tropical Africa the palaeoecological visibility of (pre)historical human impact on natural ecosystems is strongly impeded by a dominant signature of climate change at decade-to-century and millennial scales. Better knowledge of the relative magnitude of past human impact is, however, instrumental to properly assess the resilience, and recovery potential, of Africa's natural ecosystems. In this study, we combined taxonomic, ecological and palaeoecological approaches to validate fossil non-pollen palynomorphs (NPPs), i.e. non-pollen micro-remains from fungi and selected groups of algae, vascular plants and invertebrates, as palaeoenvironmental indicators for climate change and human impact on East African ecosystems.

We first studied fossil NPP assemblages from the sediment record of Lake Challa, a deep crater lake located near Mt. Kilimanjaro, with the aim to assess the taxonomic diversity of well-defined East African NPPs over the past 25,000 years, and to exploit their stratigraphic turnover during major climate and environmental changes as a guide to their potential as palaeoecological indicators. By comparing 61 fungal spore types with selected pollen curves of common African trees and herbs, and with independent proxies of regional climate (temperature and rainfall) history, we revealed specific habitat requirements of individual NPP taxa. Particularly, changing habitat conditions at the Glacial-to-Holocene transition (ca. 11,500 cal. yr BP) stand out as the most important event in the distribution of fungal spore types such as *Curvularia*, *Coniochaeta* cf. *ligniaria*, *Acrodyctis*, *Tetraploa aristata*, cf. *Byssothecium* and de types HdV-1032 and HdV-1033.

To expand our knowledge of NPP taxonomic richness in East African lake sediments, we then explored modern NPP assemblages in recently deposited surface sediments of 20 small crater lakes in western Uganda, located along environmental gradients of vegetation (moist evergreen and semi-deciduous forest, wooded and open grass savannah), land use (pastoralism, crop agriculture, plantations) and lake characteristics (basin morphometry, water chemistry and aquatic production). This resulted in a comprehensive inventory of 265 distinct morphotypes, of which 28% could be identified at the species, genus or family level. Focus on the taxonomy of these microfossils resulted in taxonomic descriptions of 187 morphotypes, accompanied by high-resolution photographs and ecological information, when available.

By the year 2100, land-use change will probably be the principal driver of overall biodiversity loss, particularly in the tropics where agricultural conversion of natural ecosystems and the overall intensity of anthropogenic land use continues unabated. Because of poor knowledge of the taxonomic diversity of tropical fungi and their response to habitat changes, however, mycological tools to estimate the effects of various land-use practices on fungal diversity are scarce. We used a statistical mixed-model analysis based on the Akaike Information Criterion (AIC) to comprehensively evaluate the response of African fungal spore diversity (richness and evenness) to agricultural impact at the landscape scale. For this study we used fungal spore assemblages extracted from the recently deposited surface sediments of 24 western Ugandan crater lakes, assumed to reflect fungal communities presently living in (mostly) terrestrial habitats within each lake's crater basin. This analysis revealed that the richness of fungal spore types was inversely related to the percent area of agricultural land-cover types in human-impacted crater basins. The evenness of fungal spore diversity appeared to be related to size characteristics (i.e. the crater area/lake area ratio) of the pristine crater basins, tentatively suggesting higher biomass stability in small lakes with a relatively large catchment area. These results point to the possible threat of fungal species loss, when natural ecosystems are progressively exposed to anthropogenic land use.

Finally, two paired 200-yr NPP records from relatively small, shallow crater lakes (the presently undisturbed Lake Chibwera and the human-disturbed Lake Kanyamukali) in western Uganda were studied to distinguish signals of fungal response to site-specific historical human impact from the common impacts of regional climate variability. Both NPP records registered a strong parallel signature of fluctuations in lake level and moisture balance, mainly reflected in the abundances of the fungal spore type *Coniochaeta* spp., aquatic pollen types (*Typha*, *Nymphaea* and Cyperaceae) and algal colonies/coenobia (*Botryococcus*). Moreover, the marked presence of some obligate coprophilous ascomycetes,

Sordaria spp. and *Delitschia* spp., predominantly growing on herbivore dung, also suggested intense usage of the lakes by wild and/or domestic herbivores during severe lake lowstands in the late 18th-early 19th century. From the 19th century until the present, only at Kanyamukali coprophilous fungal taxa persisted (at low relative abundances), whereas at Chibwera their signature completely disappeared. Given the continuous presence of wild animals in the savanna landscape surrounding the lakes, we surmise that a higher population density of cattle, herded by pastoralists to watering places and productive grazing areas, was consistently present at Kanyamukali. The location of Lake Kanyamukali along an ancient cattle trail and/or trading route may underscore its historical importance for transhumant pastoralism. From the mid-20th century onwards, intensified grazing and subsistence farming started in the Kanyamukali crater basin, indicated by relatively slight increases in coprophilous taxa and *Glomus* sp., an endomycorrhizal fungus associated with soil erosion.

In conclusion, this research provided new insights into important issues related to the methodology and interpretation of fossil NPP analysis, and clearly demonstrated the palaeoenvironmental significance of non-pollen palynomorphs in lake-sediment archives from tropical Africa.

Introduction

"The best prophet of the future is the past" (George Byron, 1821) is a well-known existential quote, which surely applies to all research fields dealing with the past. It reminds us of history repeating itself when lessons from the past are not being considered in reflections on the present and future. Even though this idea is a truism, it still lack essential insight about the role of the present, which is as important as the past, particularly in the Earth Sciences, where the present is directly incorporated into the principle of uniformitarianism. Hence, we first need to evaluate Earth's current natural and human-induced processes carefully to understand the past environmental changes which underly future prospects.

The recurrent idea of *'Present and past as inseparable guides for the future'* is also strongly noticeable in the BelSPO-project '*Climatic and Anthropogenic Impact on African Ecosystems*' (CLANIMAE, 2007-2010), which forms the framework of this PhD research. CLANIMAE responds to the urgent need of a long-term perspective to today's climate-human-ecosystem interaction in tropical Africa, in order to improve local strategies for management and biodiversity conservation. Based on observations of current lake ecosystems, and reconstructions of vegetation and water-quality changes, recorded in high-quality lake-sediment archives, CLANIMAE aims to provide better insight into present and ancient climate variability and land-use changes at the regional scale (Verschuren *et al.*, 2009a). As part of the CLANIMAE project, this PhD research mainly focuses on developing a new palaeoenvironmental proxy for climate change and anthropogenic impact on East African ecosystems, based on analyses of non-pollen palynomorphs (NPPs) i.e. non-pollen micro-remains from vascular plants, algae, fungi, insects and other invertebrates, encountered on pollen slides. Its four chapters are dedicated to the exploration of NPPs preserved in ancient (Chapters 1 and 4) and modern (Chapters 2 and 3) lake sediments from East Africa.

A brief review of historical climate-human-ecosystems interaction in East Africa

Introduction

Identifying the principal drivers of environmental change is highly challenging, though prerequisite for developing integrated and community-based ecosystem management and conservation strategies (e.g., IPCC, 2001, 2007; Nelleman and Corcoran, 2010). New scientific ideas about climate-human-ecosystem interaction suggest a complex theory with the related concepts of nonlinear change, feedback and regime shifts (e.g., Scheffer *et al.*, 2001; Dent *et al.*, 2002; Folke *et al.*, 2004), instead of a simplified dichotomy between climatic determinism and human resource exploitation (e.g., Huntington, 1915, 1945; Manley, 1958) (Dearing, 2006). Ironically, these seemingly contradictory ideologies are also strongly related to one another, since our evolving understanding of complex ecosystem behaviour starts with determining the role of individual ecological variables, involved in the synergistic processes of environmental change.

African environments, in particular, are extremely vulnerable to climate change, aggravated by the interaction of multiple stresses, such as high population growth, poor infrastructure, and conflicts, resulting in low adaptive capacity (Thomas and Twyman, 2005; Boko *et al.*, 2007). Agricultural production, food security and water-resource availibility are strongly compromised by rainfall variability (Mendelsohn *et al.*, 2000; Conway *et al.*, 2005; Goulden, 2005). This, in turn, interacts with human drivers, such as land-use change (e.g., deforestation, slash-and-burn practices, overexploitation of rangelands…) and the introduction of exotic species, which severely undermine the biodiversity and natural functioning of African terrestrial and aquatic ecosystems (Boko *et al.*, 2007). Soil erosion has severely increased as a result of intensified land use (crop-rotation, over-grazing, logging), land fragmentation (loss of buffer strips) and

inadequate application of fertilisers, which is detrimental for both natural resources and food production potential (Boko *et al.*, 2007). Unfortunately, the ecological ramifications of increasing human impact, in addition to natural climate variability, also threathen human health and well-being, leading to poverty, malnutrition and infectious diseases (Kochtcheeva and Singh, 2000; Millennium Ecosystem Assessment, 2005; Patz and Confalonieri, 2005; Thornton *et al.*, 2008). As such, increasing our knowledge of the causal mechanisms underlying present and past ecosystem responses to environmental change is essential to 1) tackle the complex and changing dynamics between natural forcings, human society and ecosystem domains (Fig. i), and 2) restore and sustain ecosystem services and goods for current and future generations (e.g., Dearing, 2006; Willis and Bhagwat, 2010). A proper reconstruction of historical agricultural impacts in tropical Africa, separate from substantial climate-driven environmental change (e.g., Lamb *et al.*, 2003; Verschuren, 2004; Stump, 2010), will offer the necessary reference frame to evaluate the severity of current agricultural impacts, resulting from accumulation of land use through time.

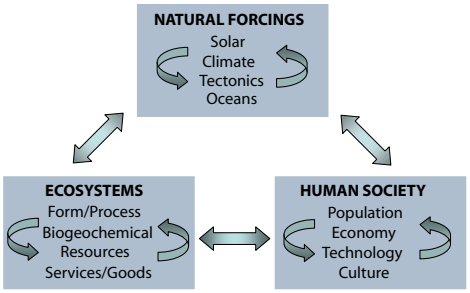

Fig. i. A cognitive template to understand environmental change: the potential interconnections between natural forcings, human society and ecosystems. Bi-directional arrows between the three state systems describe potential flows of energy, matter and information, which may define externally-driven causality and feedback; circular arrows within each state system represent internal dynamic processes (from Dearing, 2006).

Climate variability

Climate variability in East Africa is determined by strong regional variations in rainfall regime (Nicholson, 1996). At the macroscale, four related climatic phenomena are pivotal to the East African climate system: the Intertropical Convergence Zone (ITCZ), the Congo Air Boundary (CAB), the El Niño-Southern Oscillation (ENSO) and the East African Monsoon (i.e. southeast (SE) and northeast (NE) monsoons). Interannual and intraseasonal variability of rainfall is mainly governed by complex interactions between these large-scale atmospheric circulation processes, mediated by maritime influences such as Indian Ocean sea surface temperature (SST), and a rich regional topography of mountain ranges, rift valleys and large lakes (Nicholson, 1996; Mutai and Ward, 2000; Hastenrath, 2007).

Since the ITCZ and CAB migrate annually through the equator from south to north, and vice versa, rainfall over much of East Africa displays a bimodal regime with long rains during boreal spring (March-May) and short rains during boreal autumn (September/October-December) (Nicholson, 1996; Conway, 2002; Mutai and Ward, 2000). These two rainy seasons are strongly driven by monsoonal wind systems from the Indian Ocean, which transfer moisture to the East African Plateau through northeastern trades (i.e. northeast monsoon) and southeastern trades (i.e. southeast monsoon) (Fig. ii). Although both monsoons are thermally stable and relatively dry, interference with the humid and unstable CAB (separating easterlies and westerlies), regional topography and coastal friction causes highest rainfall during the transition seasons (Nicholson, 1996). The western part of the East African Plateau receives additional rain from the

Atlantic Ocean during the dry season in July-August, when the CAB moves eastwards over the Plateau (Fig. ii) (McGregor and Nieuwolt, 1998). Whereas the long rains are more abundant, the short rains are particularly variable (Conway, 2002; Hastenrath, 2007). Moreover, circulation anomalies evoked by a powerful zonal–vertical circulation cell along the Indian Ocean equator, may severely affect the magnitude of equatorial surface westerlies during the short rains, leading to disastrous regional floods or droughts (Han *et al.*, 2010; Hastenrath *et al.*, 2010). The strong relationship between monthly and seasonal rainfall patterns in East Africa and phases of ENSO also amplifies interannual rainfall variability, in which ENSO warm events tend to be associated with above-average rainfall (i.e. El Niño years, e.g., 1997-1998) and ENSO cold events with below-average rainfall (i.e. La Niña years, e.g., 1999-2000) during the short rainy season (Nicholson, 1996; Nicholson and Kim, 1997; Indeje *et al.*, 2000; Mutai and Ward, 2000). Mean annual rainfall varies from ~200-400 $mmyr^{-1}$ in the most arid regions (e.g., northeastern Kenya), and exceeds 1200 $mmyr^{-1}$ in the most humid regions (e.g., Uganda). However, seasonal inter-annual rainfall patterns may differ distinctly within short distances (on the order of tens of kilometers) depending on local topography (Nicholson, 1996); for instance, mountainous areas such as Mont Elgon in Uganda, and large lake areas such as Lake Victoria experience highest rainfall, i.e. ~2500 $mmyr^{-1}$. Because of its rich topography (e.g., mountains, valleys and lakes) and land cover, mean annual temperature in East Africa varies from 10-15 °C (T_{min}) to 21-26 °C (T_{max}). Although there seems to be a general warming trend since the 1940s, temperature close to the coast and major inland lakes are gradually decreasing (King'uyu *et al.*, 2000). Recently, evidence of accelerating T_{min} rise has also pinpointed significant human land development, possibly creating locally produced aerosols, as an important temperature driver in East Africa (Christy *et al.*, 2009).

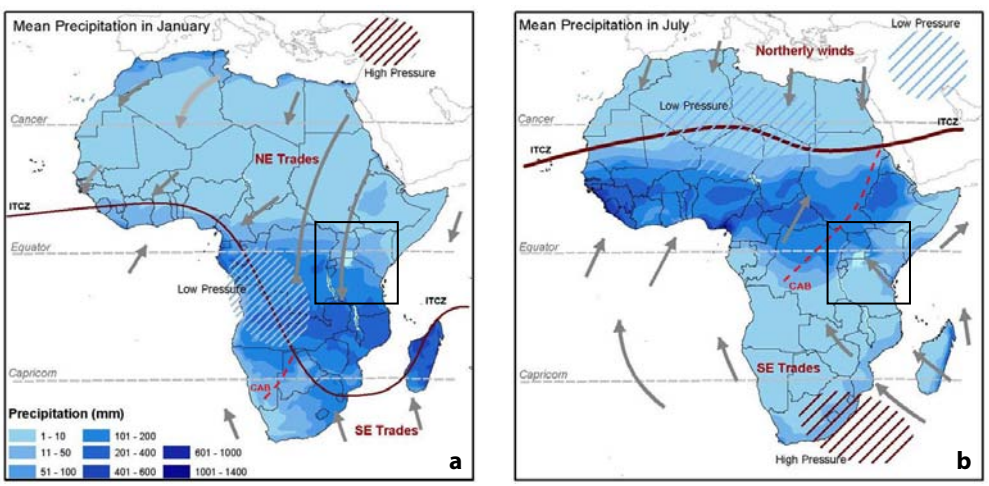

Fig. ii. General patterns of precipitation, trade winds, pressure and convergence over Africa during (a) boreal winter (northeast monsoon) and (b) boreal winter (southeast monsoon), with special reference to the East African region (CAB positions based on Nicholson, 1996; map modified from United Nations Environment Programme (UNEP), 2007. (*http://gridnairobi.unep.org/chm/EAFDocuments/Maps_and_Data/maps_thumbnails/*).

Vegetation, land use and rural livelihoods

The rainfall and temperature variability, in relation to the rapid rate of population growth in East Africa (~7.1% per annum), significantly determines the livelihood strategies of indigenous food producers (e.g., cultivators, livestock keepers and fishers) who exploit the country's natural resources (Conway *et al.*, 2005; Thornton *et al.*, 2008) (Fig. iii). In total, about 70 to 80% of the East African workforce is employed in the agricultural sector (FAOSTAT, 2009), involving many distinct crop-livestock systems exploiting a wide range of agro-products (e.g., banana, maize, sorghum, millet, potatoes, meat, milk). Over 75% of total agricultural output is provided by smallholder farmers, with farm sizes of about 2.5 ha on average, mainly producing for home-consumption, and to a lesser degree for (semi-)commercial sale of goods. The farming activities are completely organised and directed within the family, operating within a network of relations at the community level and using limited technological innovations (Salami *et al.*, 2010). Intensive small-scale subsistence farming is the most widespread permanent agricultural system (Widgren and Sutton, 2004) found in areas with high population density (Okigbo, 1990), such as the Naya in northwestern Tanzania (Maruo, 2002), the Chagga in north Tanzania (Fernandes *et al.*, 1984) and the Ankole in southwestern Uganda (Kasfir, 1993). In sparsely populated semi-arid regions, such as the Ngorongoro district in north Tanzania and the Narok district in southwestern Kenya, cattle breeding forms an essential part of the rural livelihoods (Dixon *et al.*, 2001). To optimise the use of rangeland resources for meat and milk production, transhumant pastoralists, such as the Maasai, move their herds throughout the year, maintaining semi-permanent home bases. In times of drought and during the night, livestock enclosures protect the herds from predators and from raiding by other humans (Marshall, 2000; Butt, 2010).

In the last few decades, many of East Africa's life-support have experienced dynamic changes induced by environmental, socioeconomic and political impacts (Maruo, 2002). Climate variability, however, is likely to have the most severe impact on resource-poor agriculturalists, leading to changes in productivity of rainfed crops and forage, reduced water availibility and severity of crop, livestock and human diseases (Goulden, 2005; Thornton *et al.*, 2008). Moreover, soil erosion has severely increased as a result of land-use intensification (over-cultivation, over-grazing, logging), land fragmentation (loss of buffer zones) and the lack of fertilisers (Pomeroy *et al.*, 2003; Ngecu *et al.*, 2004), and is detrimental for soil nutrients and food production potential (Toy *et al.*, 2002). Land degradation and the accelerating conversion of natural lands for agricultural purposes also causes a substantial loss of plant, mammal and bird diversity (Pomeroy *et al.*, 2003). The threat of extinction may be particularly acute for the more than a million estimated species of fungi living in direct association with plants (e.g., Hawksworth, 1991, 1993; Hyde and Hawksworth, 1997). For example, based on limited data in Uganda the rate of overall biodiversity loss is estimated to have reached 10% per decade, with even higher values in savanna systems (~20%) and agro-ecosystems (~50%) (Pomeroy and Mwima, 2002). Also surface water resources, such as lakes and wetlands, become progressively depleted by eutrophication and/or siltation due to the combined impact of human activities and climate variability (e.g., Verschuren *et al.*, 2002; Ngaira, 2009; Stager *et al.*, 2009). Anomalies in the nutrient cycling of large water bodies, such as L. Tanganyika, severely affect fish abundance and fishery (O'Reilly *et al.*, 2003). A recent more qualitative and quantitative assessment of the biogeochemical cycle in L. Tanganyika revealed that anthropogenic global warming may possibly be the main driver of decreasing lake productivity over the past 90 years (Tierney *et al.*, 2010). Thus, by studying current and past ecosystem responses to human impact and climate change, strategies necessary for successful community-based natural resource management can be developed to retain resilience of the ecosystems, which support them (e.g., Willis and Bhagwat, 2010).

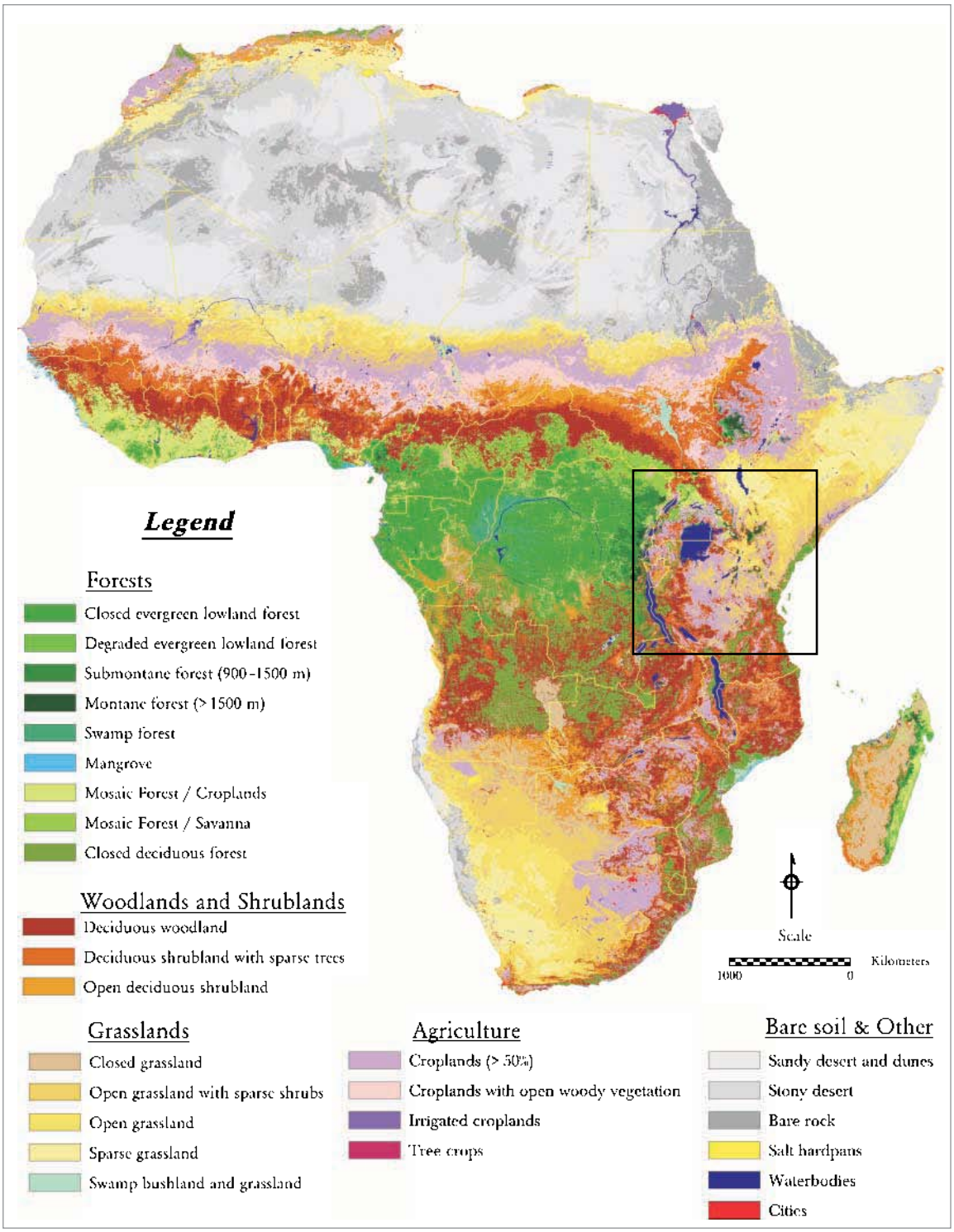

Fig. iii. Vegetation map of Africa, with special reference to the East african region, which is mainly characterised by cropland, mosaic forest, deciduous woodland/shrubland and open grassland (Mayaux *et al.*, 2004).

A glimpse into East Africa's environmental history: the last 2500 years

Climate history

Currently available proxy data indicate that the past 2500 years of tropical African climate history was much less stable and uneventful than previously assumed (Verschuren, 2004; Verschuren and Charman, 2008). Based on proxy water-balance records from East African lakes (e.g., Verschuren *et al.*, 2000; Alin and Cohen, 2003; Russell and Johnson, 2005, 2007; Bessems *et al.*, 2008) and wetlands (e.g., Stager *et al.*, 2003, 2005; Ashley *et al.*, 2004; Driese *et al.*, 2004), several decade-to-century-scale drought events have been documented over the East African Plateau. More specifically, in eastern equatorial Africa severe drought was more or less widespread during four main periods: ~50 BC-200 AD, ~900-1250 AD (broadly coeval with the Medieval Warm Period (MWP) in north-temperate regions), ~1780-1830 AD and ~1920-1960 AD (Fig. iv). However, some regional variation in rainfall between western Uganda and central Kenya was already apparent in ~900-1250 AD (Verschuren and Charman, 2008; Ryves *et al.*, 2011). These regional hydrological variations were particularly pronounced during the African Little Ice Age (LIA, ~1250-1850 AD), which consisted of two climatic episodes. In the early LIA (~1250-1550 AD) relatively moist conditions existed in most parts of East Africa, whereas the main LIA (~1550-1825 AD) generated a strong west-east moisture gradient. At that time, westernmost East Africa (western Uganda and Tanzania) - besides parts of Central and South Africa - switched to a distinctly dryer climate regime, whereas wetter conditions persisted in the eastern regions of East Africa (eastern Uganda, Kenya and Ethiopia). However, two short decade-scale drought episodes (ca. 1380-1420 and 1560-1620 AD) may also have interrupted the relatively wet conditions in central Kenya (Verschuren *et al.*, 2000). Notwithstanding this west-east moisture gradient during the main LIA, the ending of the African LIA in equatorial East Africa was marked by a severe late 18th to early 19th century drought, possibly affecting the entire tropical African region (Verschuren, 2004; Verschuren and Charman, 2008). As a result of the spatio-temporal complexity of rainfall regimes across eastern equatorial Africa (Nicholson, 1998), regionally contrasting trends were also noticeable over the past 200 years (Verschuren, 2004). In many areas of Uganda, Kenya, Tanzania and Ethiopia relatively wetter conditions occurred from the mid- to late 19th century, followed by increased aridity in the first half of the 20th century. During the 1960s and late 1970s, above-average moisture conditions progressed rapidly, shortly interrupted by a dry episode from 1968 to 1974 (Nicholson, 1996, 1998).

Decadal-to-centennial rainfall anomalies have strongly affected regional vegetation and ecosystems. Late Holocene pollen records from lake sediments (Lamb, 2001; Verschuren *et al.*, 2000; Lamb *et al.*, 2003; Vincens *et al.*, 2003; Ssemmanda *et al.*, 2005; Ryner *et al.*, 2008; Russell *et al.*, 2009; Rucina *et al.*, in prep.) and wetlands (e.g., Marchant and Taylor, 1997, 1998; Lejju *et al.*, 2005; Rucina *et al.*, 2010) show prominent vegetation changes, often concurrent with the dry/wet episodes recorded by water-balance proxies. Given the spatial distribution of the sediment records, the signals of rainfall variation observed in the pollen assemblages are rather diverse, but changes are mostly indicated by pollen fluctuations of moisture-sensitive trees and shrubs (*Acacia*, *Celtis*, *Diospyros*, *Olea*, *Phoenix*, *Podocarpus*, and Sapotaceae) and herbaceous taxa (Amaranthaceae-Chenopodiaceae and Poaceae).

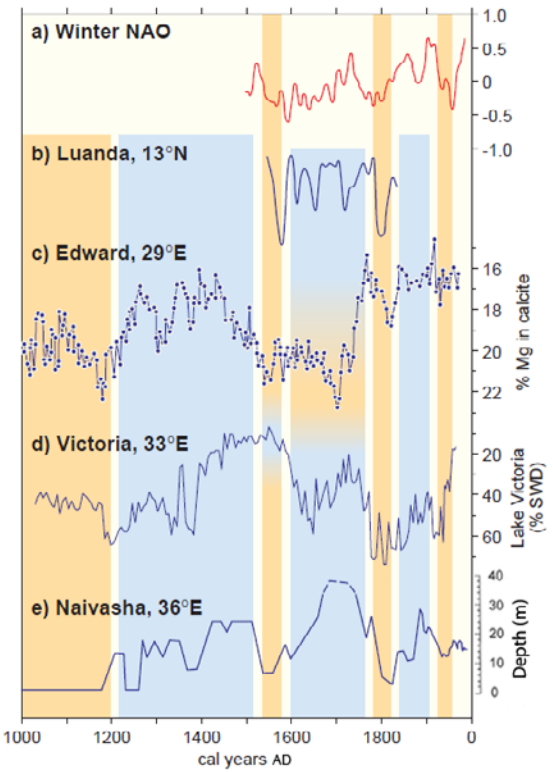

Fig. iv. Rainfall variation in eastern equatorial Africa over the past 1000 years (west-to-east transect), inferred from lake-based water-balance proxy records, and compared with shorter reconstructions of the North Atlantic Oscillation and drought along the Atlantic coast of equatorial Africa. (a) 30-year running mean of NAO/AO index (Luterbacher *et al.*, 2002), (b) Luanda drought index based on Portuguese trader data, summed per decade (Miller, 1982), (c) Percent Mg in authigenic calcite of Lake Edward, (d) Percent shallow-water species in fossil diatom assemblages from Lake Victoria, and (e) Lithology-inferred water depth of Lake Naivasha. Orange and blue bars highlight the geographic distribution of main dry (orange) and wet (blue) episodes, respectively (from Verschuren and Charman, 2008; based on Verschuren *et al.*, 2000; Stager *et al.*, 2005 and Russell and Johnson, 2007). In all records, proxy axes are oriented such that upward trends reflect wetter conditions, and vice versa.

Human-impact history

The problem of distinguishing climate-driven from human-induced tropical vegetation dynamics is one of the most urgent palaeoecological challenges, and has been the subject of enduring debate (e.g., Perrott, 1987; Vincens *et al.*, 2003; Ssemmanda *et al.*, 2005; Kiage and Liu, 2006). Global studies on historical land use have assumed that human impact on natural ecosystems in East Africa prior to 300 years ago was almost non-existent due to very low mean population density (~3% of today's population in 1700 AD) (Ramankutty and Foley, 1998, 1999; Klein Goldewijk, 2001). In contrast, palaeoecological (e.g., Vincens *et al.*, 1989; Taylor, 1990; Schoenbrun, 1993; Jolly *et al.*, 1997) and archaeological (e.g., Robertshaw and Taylor, 2000; Killick, 2009) evidence has been interpreted to indicate significant anthropogenic deforestation from at least 3000 years ago, concomitant with the spread of farming and iron metallurgy. The discrepancy between both hypotheses reflects the lack of solid evidence regarding the exact timing and relative magnitude of human-modified land clearances and the severity of past land-use impacts. This is because the idea of human-induced land clearance beginning ~3000 years ago is strongly embedded into the East African scientific community, partly

resulting from inappropriate extrapolation of Eurocentric indicators of human impact, and partly from poor appreciation of the very significant climate changes in the relatively recent past (Verschuren, 2004; Verschuren and Charman, 2008).

The fact remains that tropical ecosystems, which are exposed to climate change and/or anthropogenic disturbance, register similar environmental signatures, complicating the interpretation process. Transition from a woodland- to grassland-dominated environment can be attributed to either i) climate variability (increasing aridity, linked to natural fire frequency), ii) disturbance by large wild herbivores, iii) human interference (e.g., cultivation, pastoralism, logging, slash-and-burn practices), or iv) a complex interaction of these causal factors (e.g., Lamb *et al.*, 2003; Vincens *et al.*, 2003; Gillson, 2004; Ssemmanda *et al.*, 2005; Rucina *et al.*, 2010). Herbaceous pollen taxa such as Poaceae, Chenopodiaceae-Amaranthaceae and Urticaceae, may not only indicate pastoral activities (Taylor *et al.*, 2005; Kiage and Liu, 2006), but are also common herbs in natural grasslands visited by large wild herbivores. Furthermore, evidence for agricultural activities is mainly supported by pollen records of ambiguously human-related plants, such as the oil palm and caster oil plant (e.g., Lamb *et al.*, 2003; Darbyshire *et al.*, 2003; Vincens *et al.*, 2003; Rucina *et al.*, 2010), which are also naturally abundant in East African vegetation as a pioneer tree and ruderal plant, respectively (Radcliffe-Smith, 1987; Maley and Chepstow-Lusty, 2001).

Further compounding the problem, taxonomic identification of pollen types from crop plants cultivated in East Africa (i.e. sorghum, millet, banana, cotton, potatoes and rice) is impeded by morphological similarities between cultivated and wild species. The ~40 µm lower limit of the long axis diameter of European Cerealia pollen types (e.g., Andersen, 1979; Küster, 1988; Tweddle *et al.*, 2005) is unfortunately not applicable to the tropics, since the pollen size ranges of tropical cereals, such as sorghum and teff may significantly overlap with those from tropical wild grasses (Bonnefille, 1972). At best, only maize pollen can be unambiguously distinguished from other Poaceae species (including wild grasses and cereals) mainly by their large size, although the diameter of fossil maize pollen (~60-85 µm) often falls below that of their modern counterparts (~85-125 µm) (Tsukada and Rowley, 1964). For example, in Uganda and Kenya maize is generally introduced as a crop by the late 19th century (Sprague, 1987; McCann, 2005), however maize pollen in sediment records is dated to the last 300 years (e.g., Lamb *et al.*, 2003; Lejju *et al.*, 2005; Taylor *et al.*, 2005; Kiage and Liu, 2009). Due to the similar pollen morphology of many wild and cultivated species, cereals and other crops such as legumes, cassava/manioc and cultivated banana, are unidentifiable in pollen records (e.g., Msaky *et al.*, 2005; Kiage and Liu, 2006).

Another major problem is related to the low pollen dispersal and production of many crop plants, being mostly insect-pollinated or self-pollinated (maize excluded), limiting their abundance in pollen records. Pollen from exotic plantation trees, such as eucalyptus, cypress and pine are exclusively present in sediment records dated posterior to the early 20th century (e.g., Ssemmanda, unpublished CLANIMAE data; Kiage and Liu, 2009), when plantation forestry was stimulated to meet the growing demands of fuelwood and timber (Mclean, 1971). Phytolith records may capture anthropogenic signals as well, although evidence claiming to support a very early introduction of banana as a food crop in East Africa (Lejju *et al.*, 2005; Lejju, 2006) has been strongly debated (e.g., Mbida *et al.*, 2004; Vansina, 2004; Neumann and Hildebrand, 2009). As concerns East African charcoal records, high counts of macro- and microscopic charcoal concurrent with forest clearance are interpreted as human-induced (e.g. Thevenon *et al.*, 2003; Lejju *et al.*, 2005). However, drought episodes in savannah ecosystems may register a similar palaeoenvironmental signal (e.g., Duffin *et al.*, 2008; Gillson and Ekblom, 2009). Thus, in summary, the visibility of anthropogenic activity in tropical African palaeoecological records is generally low, or biased.

Patterns of human occupation

Over the past 2500 years, eastern Africa has experienced an eventful history, with innovations in food production and

metallurgy mainly due to the emergence of trade networks, though foraging and traditional stone-tool technologies continued to prevail (Stahl, 2004). For decades, the spread of early farming and knowledge of iron working across sub-Saharan Africa (~500 BC-500 AD) has been regarded as having been conterminous with the expansion of Bantu-speaking farmers (e.g., Posnansky, 1968; Schoenbrun, 1993; Robertshaw and Taylor, 2000). However, it becomes increasingly clear that these processes of demographic, linguistic, economic and technological change may have developed independently of one another, probably through complex multi-cultural interactions at different time scales (Lane *et al.*, 2007). At present, the debate about the origin and timing of first iron metallurgy in the Great Lakes region prior to the Bantu migration is ongoing (e.g., Alpern, 2005; Killick, 2009), however the idee fixe of an exclusively Bantu-related iron work introduction between ~800-400 BC remains hinted through the discussions. This example of begging the question is possible because of the limited multi-proxy archaeological data and poorly constrained radiometric dating, together with palaeoenvironmental hints of increasing agricultural activity from that period on (e.g., Schoenbrun, 1993; Sutton, 1995; Jolly *et al.*, 1997; Taylor *et al.*, 2000; Killick, 2009), as if by evidence of human activity fairly completing the historical picture. Nothing is farther from the truth: methodological deficiencies can unfortunately not be ignored and need to be regarded from a proper perspective, totally unrestrained from apriorisms. It can surely be argued that in tropical Africa the distinction between natural and cultural landscapes is not evident, because of significant climate-driven vegetation dynamics at both short and longer time scales, and relative mobility of indigenous people in response to the impacts of this climate change on land and water resources.

How indigenous African people have interacted with climate-driven environmental changes and have modified landscapes to their food demands, has been dealt with in many reviews on the political, social, economic and cultural dimensions of East African pre-colonial and colonial societies (e.g., Smith, 1992; Connah, 1997; Schmidt, 1997; Robertshaw and Taylor, 2000; Taylor *et al.*, 2000; Robertshaw *et al.*, 2004; Stahl, 2004). Archaeological surveys have indicated that substantial occupation of the Interlacustrine area began from the ninth century AD, coeval with a pre-Medieval Warm Period of elevated rainfall (Robertshaw and Taylor, 2000). In the following centuries of region-wide drought, distinct subsistence patterns such as agro- and transhumant pastoralism developed, facilitating the occupation of dry (marginal) grasslands. Livestock keeping and crop cultivation were initially practiced in the same households, but soon became subject to class divergence (Stahl, 2004). Due to the emergence of long-distance trade networks (e.g., ivory, salt, iron, shell beads) elites started to consolidate power, leading to small chiefdoms (e.g., Ntusi and Munsa) (Robertshaw and Taylor, 2000). Wetter conditions after ~1250 AD resulted in increasing agricultural success (e.g., Engaruka; Holmgren and Öberg, 2006) and political stability (e.g., Bigo, Kibengo, Kibiro and Munsa). Around 1700 AD, however, major political economic changes occurred across the region, including the fall of the capital at Munsa (Robertshaw and Taylor, 2000). Nucleated villages were replaced by dispersed homesteads, and stratification between pastoral nobility and agricultural peasantry became more apparent in the Great Lakes region (Reid, 1996; Stahl, 2004; Robertshaw, 2010), a pattern that has mainly persisted into colonial and recent times.

Unfortunately, much of East African history is mainly reconstructed from scarce archaeological remains and historical sources affiliated to elite groups during pre-colonial and colonial times. Archaeological records from pre-colonial periods (prior ~1880 AD) remain lacking, partly due to low archaeological visibility of the temporary settlements occupied by pastoralists, leaving few materials behind once the open-air site is abandoned (Robertshaw, 1978; Banning and Kohler-Rollefson, 1992). Also the difficulty of distinguishing between hunter-gatherer and pastoral archaeological sites causes a major interpretive problem in studies of prehistoric Africa (Shahack-Gross *et al.*, 2003; Mutundu, 2010). Besides, most archaeological sites are located away from palaeoecological reconstruction sites, making it difficult to relate observed changes in habitat directly to human patterns of resource use (Lane, 2010). Historical written sources from pre-colonial times are rare, making historiographical support of current culture-historical hypotheses inadequate. The few extant written sources, which frequently served the interests of the colonial state and European settler colonies,

have undoubtedly depicted a distorted view on historical reality (Neumann, 1998; Beinart, 2000; Lane, 2009, 2010).

At present only few scholars have confronted the challenge to link historical, linguistic and/or archaeological data to adequate palaeoenvironmental evidence (e.g., Taylor *et al.*, 2000, 2005; Verschuren *et al.*, 2000; Robertshaw *et al.*, 2004; Lane, 2010). Some parallels between oral traditions and multi-proxy lake-sediment records seem strikingly consistent (Fig. v) (e.g., Verschuren *et al.*, 2000a; Lamb *et al.*, 2003). All these studies are unanimous that the complexity of past climate-human-ecosystem interactions can only be tackled by an integrated and quantitative multi-proxy approach (Dearing, 2006; Dearing *et al.*, 2006; Caseldine and Turney, 2010).

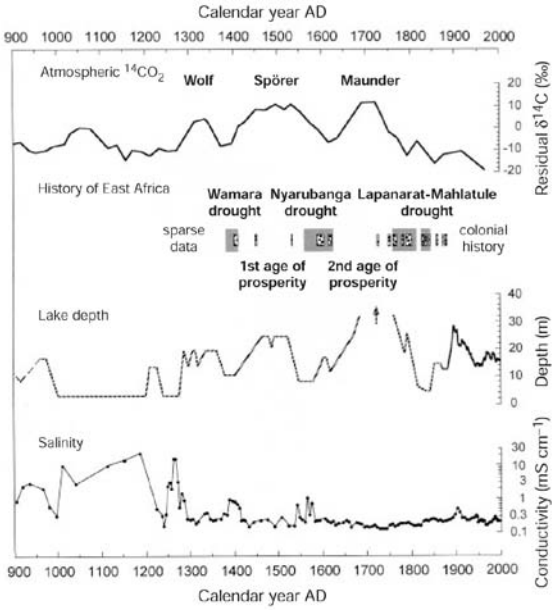

Fig. v. Reconstruction of lake-level and salinity fluctuations of Crescent Island crater basin (Lake Naivasha, Kenya) during the last 1100 years, compared with the decadal record of atmospheric CO_2 production as a proxy for solar radiation, and the pre-colonial history of East Africa. Grey bars indicate severe drought periods recorded in oral tradition; stippled bars compile the evidence of severe drought events from various archival records including the (incomplete) record of Nile River discharge (from Verschuren *et al.*, 2000).

The role of non-pollen palynomorphs in palaeoecological research

On pollen slides a wide range of non-pollen microfossils occur, which are traditionally categorised as non-pollen palynomorphs (NPPs; van Geel, 2001). These microfossils mainly capture decay-resistant microfossils consisting of sporopollenine or chitine, from biotic groups of which the organic-walled macro-remains are not preserved due to natural decay processes and harsh chemical preparation techniques. Among these biotic groups are included the fungal spores (van Geel, 1978; van Geel and Aptroot, 2006), selected algae (Jankovská and Komárek, 2000; Komárek and Jankovská, 2001), eggs produced by aquatic flatworms (Haas, 1996), eggs of Tardigrada (Jankovská, 1991) and Bacteria (Nilsson and Renberg, 1990). In palynological investigations, these microfossils form a counterpart to pollen and fern and moss spores, and provide complementary insights into climate and/or human-driven soil and hydrological processes (e.g., moisture balance, erosion, etc.), and vegetation shifts (e.g., crop cultivation, pasture, fire frequency etc.). As such,

analysis of fossil NPPs produces a unique palaeoecological archive, adjacent to pollen and other proxy indicators (such as phytoliths, diatoms, dinoflagellates etc.) to provide insights into past environmental changes.

The majority of NPPs are the ascospores, conidia and chlamydospores of fungi, mainly derived from (i) pathogenic fungi (*Fusarium* and *Puccinia*), (ii) mycorrhizal fungi (e.g., *Glomus*), and (iii) saprotrophic fungi (decomposers), of which some may be coprophilous i.e. obligately growing on herbivore dung (e.g., *Sordaria* and *Podospora*). It is suggested that most fungal spores deposited in and recovered from lake sediments, are fossilised at, or near, their source area where sporulation occurred (van Geel, 2001; van Geel and Aptroot, 2006).

Coprophilous spores as anthropogenic indicators

In European palaeoecological studies (e.g., Willemsen *et al.*, 1996; van Geel *et al.*, 2003; Mazier *et al.*, 2009), there is a long tradition to link fossil spores of saprotrophic Ascomycota (= ascomycetes) to past livestock keeping, because these fungi may be associated with the excrements of large herbivores, including soil contaminated with herbivore dung. However, the term 'coprophilous' is not always properly used, making the relationship with wild and/or domestic herbivores more ambiguous. In fact, most of the saprotrophic genera (e.g., *Cercophora* (as part of *Lasiosphaeria*), *Coniochaeta*, *Apiosordaria* and *Chaetomium*) which are classified as 'coprophilous' have representatives that are hosted on other substrates such as dead wood and plant debris (Hanlin, 1990; Romero *et al.*, 1999; Asgari *et al.*, 2007; Mukerji, 2010). Only a few genera (e.g., *Sordaria*, *Podospora, Delitschia* and *Sporormiella*) inhabit dung obligately, i.e. exclusively (Ahmed and Cain, 1972; Bell, 1983; Krug *et al.*, 2004). Because of their association with different substrates, the ecological indicator value of most saprotrophs is thus more complex and ambiguous than suggested by their (non-obligate) affinity with dung. Furthermore, proper identification of these fungi, particularly when based on the spores only, is strongly impeded by the difficulty of taxonomic discrimination. For instance, some saprotrophic fungi such as the obligate coprophilous genus *Podospora* and the occasionally dung-inhabiting genera *Cercophora*, *Schizothecium* and *Zopfiella* produce morphologically similar ascospores (Bell, 1983) and are grouped in a single morphotype, which weakens its dung indicator value. Therefore, it is rather the abundance changes of obligate coprophilous spores (e.g., *Sporormiella* type) recorded in sediment records which may indicate changes in population density of herbivores through time (Davis and Shafer, 2006).

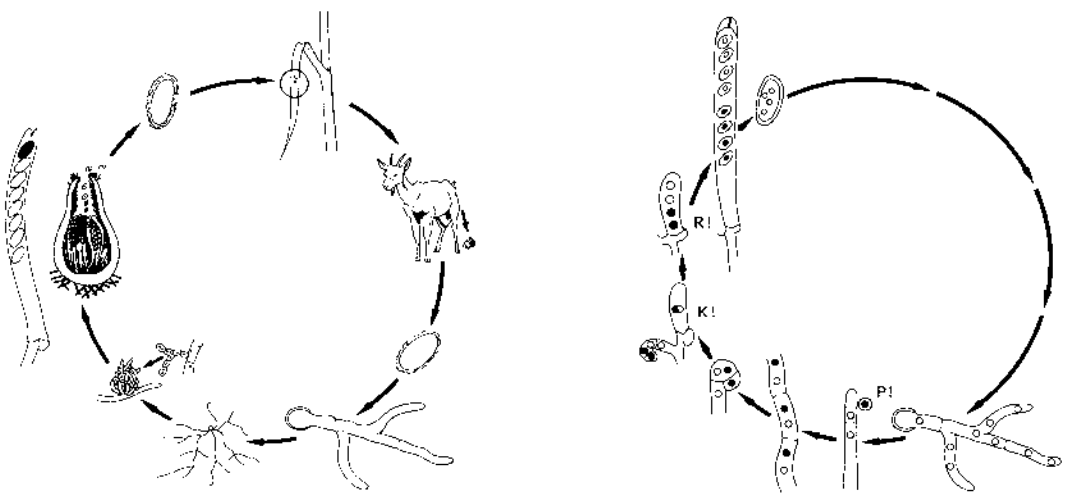

Fig. vi. Life cycle of the coprophilous ascomycete *Sordaria humicola* (from Jennings and Lysek, 1996).

The life cycle of coprophilous Ascomycota is illustrated in Fig. vi. During sporulation, spores of coprophilous fungi are forcefully discharged into the air and shot onto a grass leaf, where they remain dormant until the leaf is eaten by a grazing animal (Jennings and Lysek, 1996). Most spores germinate only after passage through the digestive tract of the mammal. When the spores are excreted with fresh dung, germination can readily take place (Krug *et al.*, 2004). Coprophilous ascomycetes, such as *Sordaria*, generally need an incubation period of 2-4 weeks to reach maturity (Bell, 1983). The resulting mycelium grows through the dung, eventually forming perithecial initials which possess receptive hyphae, which can be absorb/be dikaryotizised by nuclei of other mycelia, spermatia or conidia. This leads to plasmogamy (P! in Fig. vi) followed by the formation of the hook. The formed dikaryotic or ascogenous hyphae start to produce asci, in which karyogamy (K!) and meiosis (R!) occur. In most cases, eight ascospores now develop in each ascus (Jennings and Lysek, 1996) and are dispersed during sporulation. It is, however, a prerequisite that the ascospores of the species reach new plant material to continue the life cycle of the coprophilous fungus.

Aims and objectives

In the past decade, reconstructions of East Africa's climate history focusing on the complexity of climate dynamics at temporal and spatial scales, have significantly improved by methodological advances in palaeolimnology (Verschuren and Russell, 2009). Particularly, in-lake biological proxies have substantially been developed (e.g., Rumes *et al.*, 2005; Eggermont *et al.*, 2006, 2010); and other new temperature and hydrological proxies, such as organic biomarkers (e.g., Sinninghe Damsté *et al.*, 2009; Tierney *et al.*, 2010) are now increasingly applied to African lake-sediment archives. Yet, the way in which past human societies have contributed to landscape modifications remains highly controversial, as it needs to be disentangled from these climate patterns on both short and longer time scales. This is mainly because the responses of vegetation proxies (pollen, charcoal and phytoliths) to land-use change are significantly mediated by basin-specific factors (e.g., hydrology, lake morphometry, catchment size) (Ryves *et al.*, 2011) and proxy-specific characteristics (see above). Traditional landscape-related palaeoenvironmental proxies, such as pollen, plant macrofossils, phytoliths and charcoal, all need to be refined through calibration exercises; and novel proxies may help separate the effects of past climate variability from human impact on East African ecosystems.

The value of non-pollen palynomorphs as palaeoecological indicators has been demonstrated in the palynological study of peat deposits, archaeological features and lake sediments in Europe and South America (van Geel, 2006; Haas, 2010), but so far it has never been explored for palaeoecological archives in tropical East Africa. Within the scope of tracing climate change and human impact on the East African landscape through time, we aim to

(i) produce a reliable dataset of tropical African NPP types for palaeoecological reconstruction in a tropical African context. Most previous studies on fossil African NPPs (e.g., Lejju *et al.*, 2005; Mumbi *et al.*, 2008) near exclusively referred to European studies, with their specifically European ecological and contextual properties. Notwithstanding fern and moss spores are traditionally studied as part of pollen analysis, we included this biotic group into our dataset of 'non-pollen' microfossils, because of the lack of taxonomic knowledge on African spore taxa.

(ii) create a comprehensive scientific framework, in which methodological, interpretive and taphonomic issues on modern and fossil tropical African NPPs are confronted to each other, using a multiple-proxy approach.

(iii) validate non-pollen palynomorphs preserved in lake sediments as proxy indicators for past ecological conditions.

(iv) illuminate the indicator value of particularly coprophilous fungal spores, which may be the most valuable group of NPPs to trace past human impact in East Africa.

Our 24 calibration lakes in western Uganda were selected to cover the main landscape gradients from moist evergreen forest to grass savannah, and from relatively undisturbed to severely impacted by human activity. Also taken into account are limnological characteristics such as basin morphometry, water chemistry and aquatic production (Fig. vii). This research strategy allowed us to capture a large portion of the overall NPP richness in East African lake sediments.

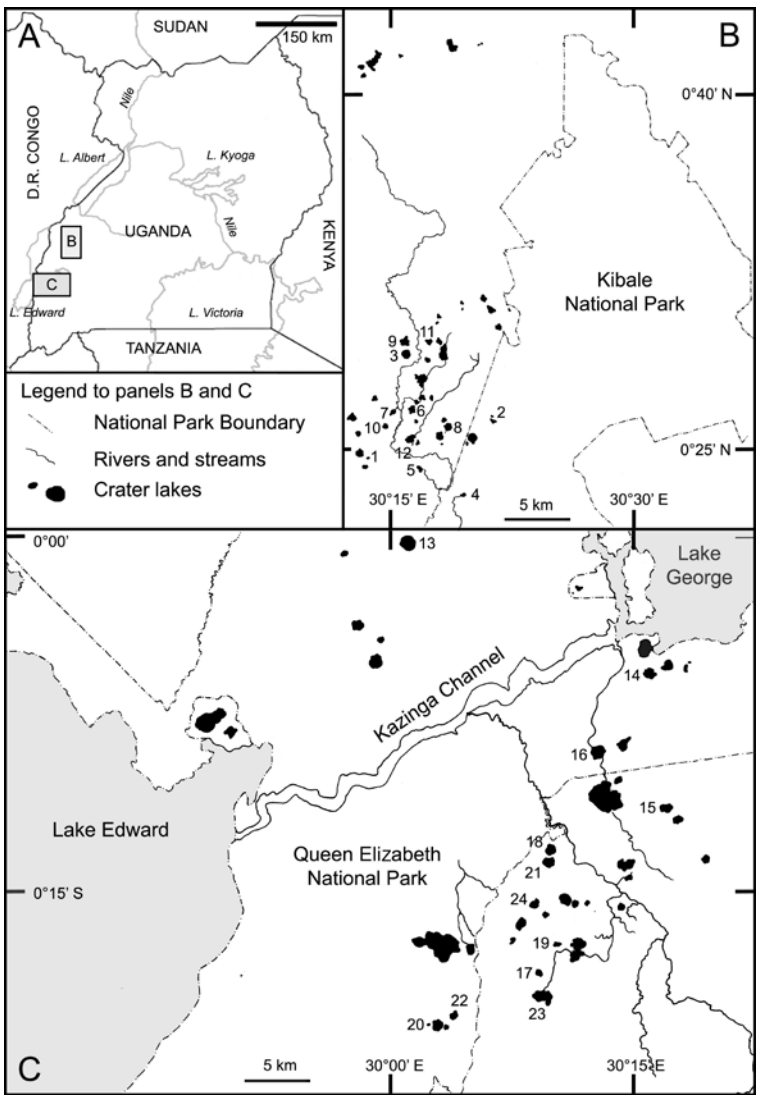

Fig. vii. Location of the 24 study sites in western Uganda (study regions B and C); modified from Rumes *et al.* (submitted). Lake basins in the Kasenda-cluster: 1. Kanyamukali, 2. Kanyanchu, 3. Katanda, 4. Kisibendi, 5. Kitere, 6. Mahuhura, 7. Mubiro, 8. Murusi, 9. Mwengenyi, 10. Nyarayabana, 11. Nyantonde, 12. Wankenzi. Katwe-Kikorongo-cluster: 13. Kikorongo. Bunyaruguru-cluster: 14. Bagusa, 15. Bugwagi, 16. Chibwera, 17. Kako, 18. Katinda, 19. Kigezi, 20. Kyogo, 21. Mirambi, 22. Murabyo, 23. Nkugute, 24. Nyungu.

Thesis outline

In developing this PhD thesis, two key concepts have been essential to assess the value of NPPs as palaeoenvironmental proxy indicators in tropical Africa: (i) insights into modern ecology and current environmental processes as a starting point to interpret past environmental changes, and (ii) multiple-proxy analysis as a comprehensive research approach to obtain better understanding of climate-human-ecosystem relationships.

This thesis covers 4 research topics, which are imperative to explore the potential value of NPPs in disentangling the role of human impact and natural climate variability on tropical African ecosystems.

In *Chapter 1* we study fossil NPP assemblages from the 25,000 year sediment record of Lake Challa, a steep-sided crater lake on the lower East slope of Mt. Kilimanjaro (southeastern Kenya), to explore NPP diversity in a tropical African context. Using the Challa pollen record and two independent proxies of past temperature and rainfall, we also assess the relationship between individual fungal taxa and particular species and biomes of tropical African vegetation, and the history of regional climate change.

To capture a significant portion of the overall NPP richness in East African lake sediments, we then analyse modern NPPs from recently deposited surface sediment in 20 small crater lakes in western Uganda, located along environmental gradients of vegetation, land use and lake characteristics *(Chapter 2)*. Using primary taxonomic literature on tropical fungi, we recovered 265 distinct morphotypes, of which 187 tropical African NPPs are presented in an illustrated guide, accompanied by high-resolution photographs and ecological information, when available.

Based on an interdisciplinary approach combining fungal spore analysis, vegetation mapping and stastistical modelling, *Chapter 3* discusses the effects of land use, habitat diversity and lake properties on modern fungal spore richness and evenness of 24 small crater-lake basins in western Uganda.

In *Chapter 4* fossil NPP data of high-resolution ~200 year sediment records, contrasting presently undisturbed (L. Chibwera) and human-disturbed (L. Kanyamukali) crater basins, are compared to assess and validate the role of NPPs as palaeoenvironmental indicators for discerning the specific fingerprints of past climatic and human impacts on tropical African lake ecosystems.

Finally, a more integrated statement on the outcome of this PhD research, with reference to the main objectives, is provided in the *General discussion and conclusion*. The strengths and weaknesses of NPPs as new palaeoenvironmental proxy are discussed in a broader scientific and conceptual framework, and some preliminary future-oriented reflections on the application of NPP analysis in African palaeoecological research are cautiously presented.

Since this PhD research has strongly benefited from the exploratory study of van Geel *et al.* (2011), to which I contributed with data processing and NPP identification, this paper in co-auteurship is integrated into this PhD thesis as *Chapter 1*, with permission of the lead author Dr. Bas van Geel.

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Diversity and ecology of tropical African fungal spores from a 25,000-year palaeoenvironmental record in southeastern Kenya

Modified from van Geel, B., Gelorini, V., Lyaruu, A., Aptroot, A., Rucina, S., Marchant, R., Sinninghe Damsté, J.S., Verschuren, D., 2011. Review of Palaeobotany and Palynology 164, 174-190.

Abstract

Fossil fungal spores and other non-pollen palynomorphs (NPPs) are powerful environmental proxies in European palaeoecological and archaeological contexts. However, their application on other continents, and particularly in the tropics, is hampered by uncertain equivalence with morphologically similar taxa in Europe, and incomplete knowledge of their ecology in the new local contexts. Here we use fossil NPP assemblages in a 25,000 year sediment record from Lake Challa, a steep-sided crater lake near Mt. Kilimanjaro in southeastern Kenya, to assess NPP diversity in a tropical-African context and the equivalence of African taxa with their European counterparts. We recovered a total of 65 well-defined NPP types, of which 61 are fungal spores, and 42 could be linked to known taxa. We provide diagnoses and illustrations of 61 recovered taxa, 58 of which have not been documented before.

Using the Challa pollen record of past regional vegetation dynamics and two independent proxies of past temperature and rainfall, we also assessed the association of individual fungal taxa with particular species and biomes of tropical-African vegetation, and with the history of regional climate change. We often found strong correspondence between the stratigraphic distribution of individual fungal spore taxa and the occurrence of specific vegetation types. Changing climate conditions appear to have had a strong impact on the ability of fungi to play a role in the decomposition of dead plants. For fungal spore assemblages, the most prominent change in regional palaeoenvironments over the past 25,000 years occurred at the start of the wet early Holocene, following Younger Dryas drought. *Epicoccum purpurascens* is common in the Glacial and Late-Glacial parts of the sequence, but shows a strong decline during the early Holocene. *Coniochaeta* cf. *ligniaria* occurs throughout the record but shows dramatic fluctuations that appear to relate to major changes in humidity. Correlation between fungal abundance and humidity is also observed in taxa for which the Challa region provided suitable habitat from ca. 16,500 cal. yr BP (e.g., *Curvularia*) or from the Late-Glacial to Holocene transition (e.g., *Tetraploa aristata*, *Dictyoarthrinium* cf. *sacchari*, cf. *Byssothecium*, Types HdV-1032 and HdV-1033, cf. *Alternaria*, cf. *Brachysporium*, cf. *Helminthosporium*, *Spegazzinia tessarthra* and cf. *Lasiodiplodia theobromae*). Many of these taxa did not occur, or were rare, during both wet and dry phases of the Glacial period, suggesting an additional temperature effect on their occurrence in tropical African environments. A possibly dominant role of temperature is revealed in the stratigraphic distribution of *Acrodictys*, which appears at the onset of deglacial climate warming ca. 17,500 cal. yr BP and remains common throughout both wet and dry phases of the Holocene. Spores of the dung-inhabiting fungus *Sporormiella* occur throughout the 25,000-year record without notable fluctuations, suggesting little changes in the overall population density of large herbivores in the region.

Key words: Non-pollen palynomorphs, fungal spores, Lake Challa, Kenya, Late-Glacial, Holocene.

1.1. Introduction

The palaeoecological potential of fungal remains is not yet fully explored. Many palynologists do not present or discuss the remains of fungi and other non-pollen palynomorphs (NPPs) that are commonly found in pollen preparations. However, palaeomycological information can be very useful, especially in studies of peat, lake and soil deposits (van

Geel, 1978, 1986, 2001; van Geel *et al.*, 1981, 1989; Gill *et al.*, 2009; Feeser and O'Connell, 2010; Kramer *et al.*, 2010; Montoya *et al.*, 2010; Mudie *et al.*, 2010) and in archaeological contexts (van Geel *et al.*, 2003; Zong *et al.*, 2007; Cugny *et al.*, 2010; Gauthier *et al.*, 2010; McAndrews and Turton, 2010). Agricultural societies and domesticated animals have created a range of new habitats for fungi. Consequently the mycoflora of settlement sites and the surrounding cropland, pastures and hay meadows reflects these land-use and land-cover changes with different fungal assemblages relative to the original, undisturbed natural ecosystems. Up to now, the large majority of fungal and other NPP 'Types' have been recorded in European peat and lake deposits (for an overview of the palaeomycological literature see van Geel and Aptroot, 2006). In general the remains of fossil fungi in Quaternary deposits are almost exclusively ascospores, conidia and chlamydospores produced by Ascomycetes (including their anamorphs). Most of them are thick-walled and highly melanised (dark-pigmented). Many thin-walled spores, which disperse better and commonly occur in samples of atmospheric dust, either do not preserve in lake and peat sediments or are not recognizable after the chemical treatment used to prepare pollen samples for microscopic analysis.

The use of fossil fungal spores to enhance palaeoenvironmental studies has been particularly limited in equatorial Africa, where an initial attempt to analyse fungal spores in lake sediments was conducted by Wolf (1966, 1967). Jarzen and Elsik (1986) studied fungal palynomorphs from recently deposited river sediments in Zambia. They described, illustrated and classified fungal palynomorphs with form-generic names according to the system proposed by Elsik (1976), and could refer some of the fungal palynomorphs to extant taxa. The only actuo-mycological studies in Kenya were conducted by Caretta *et al.* (1998, 1999). One recent application of fungal spore palaeoecology has been carried out at the Munsa archaeological site in Uganda (Lejju *et al.*, 2006). Spores of *Kretzschmaria* (syn. *Ustulina*), a mild parasite causing soft-rot of wood on several tree species (van Geel and Andersen, 1988) indicated that the mid-Holocene landscape at Munsa was relatively forested. Presence of ascospores of the obligatory dung fungus *Sporormiella*, together with the less stenotopic dung fungi *Cercophora* and *Sordaria* type suggested that large herbivores inhabited the Munsa area at that time (Lejju *et al.*, 2005). Given the age of the sediments and the absence of archaeological evidence for pastoralism in western Uganda prior to ca. 3000 BP, this dung was probably produced by wild herbivores such as elephants. Fungal spores from later periods at Munsa were attributed to domesticated livestock (Lejju *et al.*, 2005).

To stimulate more widespread application of NPP palaeoecology in tropical African contexts, we studied fungal spores and selected other NPPs in the 25,000-year sediment record of Lake Challa in southeastern Kenya. Our primary objectives are to 1) assess the overall taxonomic diversity of East African NPPs, and 2) to use the stratigraphic turnover of fungal taxa during the major climate and environmental changes marking the Glacial-to-Holocene transition as a guide to their potential as ecological indicators. We compare the NPP record with selected pollen curves of common African trees and herbs, and with independent proxies of regional climate (temperature and rainfall) history to study relationships that might elucidate habitat requirements of individual NPP taxa. This paper does not concern the ecosystem shifts and climatic interpretation of the pollen record itself, as this will be presented in a separate publication. Instead we focus on documenting and describing the main types of fungal spores and some other NPPs, and on evaluating the potential of fossil NPP assemblages to contribute to multi-proxy reconstructions of past environmental change in tropical Africa.

1.2. Material and Methods

1.2.1. Study site and material

Lake Challa (3° 19′ S, 37° 42′ E) is a 4.2 km^2, ca. 94 m deep crater lake, filling a steep-sided volcanic caldera at 840 m elevation immediately southeast of Mt. Kilimanjaro (Fig. 1.1a-b). In this equatorial location, twice-yearly passage of the Intertropical Convergence Zone over the adjacent western Indian Ocean creates a bimodal rainfall pattern, with southeasterly monsoon winds bringing 'long rains' from March to mid-May and northeasterly monsoon winds bringing

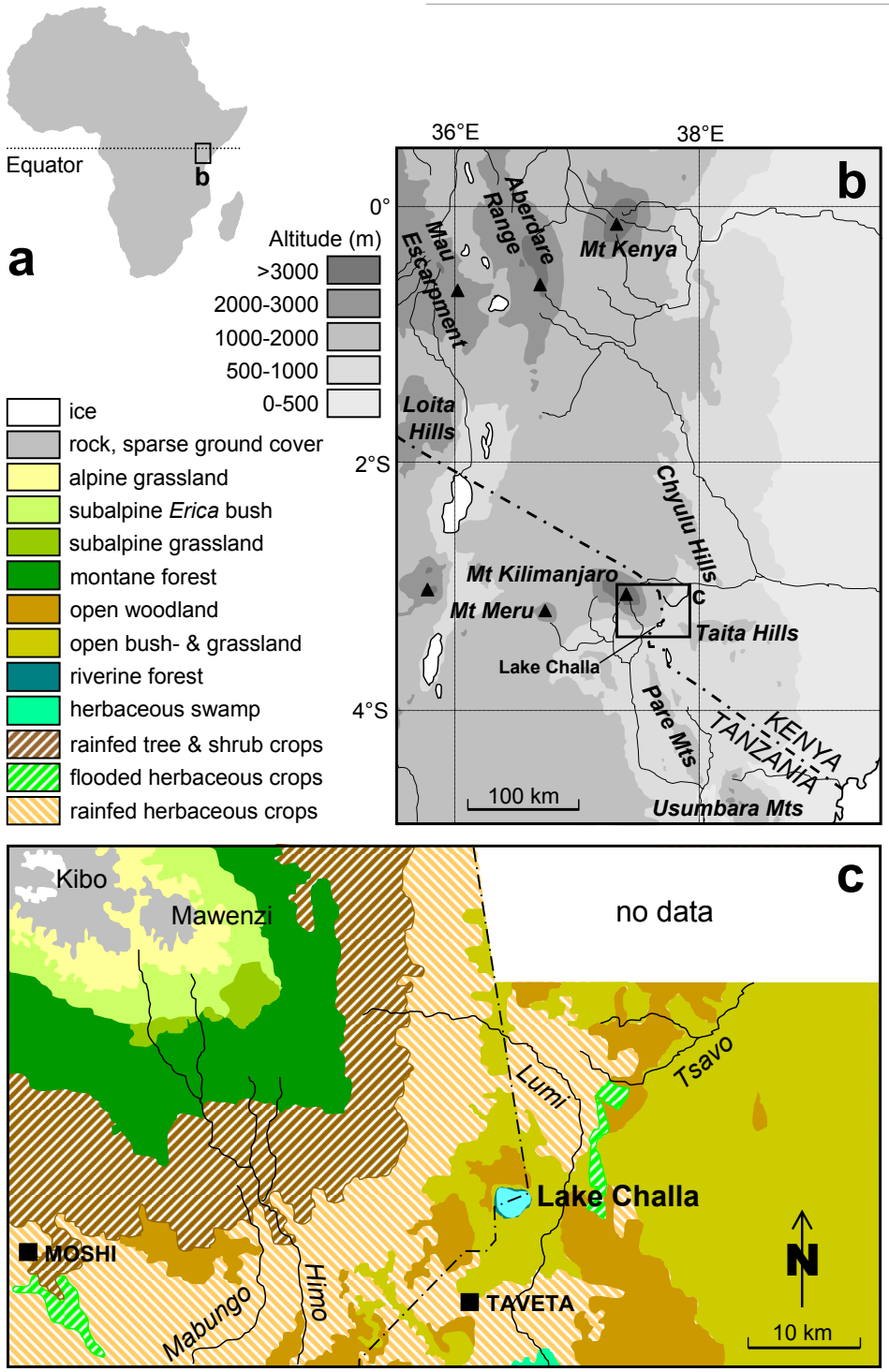

Fig. 1.1. Situation maps of Lake Challa in equatorial East Africa (a), regional topography (b) and vegetation (c). Natural vegetation at elevations below ~2000 m is deciduous wooded grassland and bushland with 15-40% crown cover (White, 1983), adapted to a tropical monsoonal climate with pronounced seasonal drought. Near Mt. Kilimanjaro most closed woodland and a substantial portion of the open woodland has been converted to cropland (hatched areas indicate that >50% of the land is under agriculture). Open bush- and grasslands with patches of open woodland in the vicinity of the Challa caldera are relatively undisturbed. Topography (b, elevations in meter a.s.l.) from Oyaya (2005); the vegetation distribution is derived from Landsat TM images taken in 1995 (Di Gregorio, 2002).

'short rains' from late October through December. The local climate is tropical semi-arid, with monthly mean daytime temperatures ranging from 26 °C in July-August to 30 °C in February-March. Total annual rainfall is ca. 565 mm yr^{-1} and surface evaporation ca. 1735 mm yr^{-1}, resulting in a negative water balance for Lake Challa (Payne, 1990). The lake is maintained by shallow groundwater originating from rainfall falling higher up the slope of Mt. Kilimanjaro. Rainfall in East Africa is spatially modified by the dissected topography of the plateau, and inter-annually by cyclic fluctuations in sea surface temperature linked to the Indian Ocean Dipole and the El Niño Southern Oscillation (Marchant *et al.*, 2006). Today Lake Challa is surrounded by a landscape of mostly open bush and grass savanna with scattered woodland trees and shrubs, and strips of moist riverine forest in (seasonally dry) stream gullies (White, 1983); the northern and western outer slopes of the Challa caldera are covered with dry colline savanna forest of *Acalypha fruticosa* and *Acacia* species (Hemp, 2006; Fig. 1.1c). The inner caldera slopes are covered by a narrow strip of evergreen riverine forest on rock-fall along the shoreline, a dry 'succulent' forest with *Commiphora baluensis*, *Haplocoelum foliolosum* and *Euphorbia bussei* on steep middle slopes, and open grassland with scattered trees and shrubs on gentle higher slopes below the rim.

In 2005 three parallel piston cores of 20-22 m length were recovered from a mid-lake location (3° 19.05' S, 37° 41.88' E). Following cross-correlation of overlapping core sections these together form a 21.65-m long composite sequence of mostly finely laminated organic muds. Excision of five turbidite horizons yielded a single 20.82-m long sequence of continuous deepwater sedimentation (Verschuren *et al.*, 2009). Lake Challa's spatially uniform sedimentation and relatively stable physical limnology over the past 25,000 years (Moernaut *et al.*, 2010) accumulated a climate archive with high temporal resolution and virtually unprecedented radiometric (^{210}Pb, ^{14}C) age control (see the supplementary online information of Verschuren *et al.*, 2009). Age indications in the present paper are given in calendar years BP (Before Present), with Present being 1950 AD.

1.2.2. Laboratory procedures

Sediment samples of 1 ml volume extracted for microfossil analysis were boiled in 10 % Na-pyrophosphate, dehydrated with 96% acetic acid and treated with an acetolysis mixture of one part H_2SO_4 to nine parts acetic anhydride. The samples were heated in this mixture to 100 °C for ca. 10 min in a water bath. Sample tubes were then cooled, centrifuged and washed with distilled water, and centrifuged again in 96 % ethanol. The separation of organic material from sand and clay was accomplished in a heavy liquid (bromoform-ethanol mixture, specific gravity 2). The samples were finally washed in 96 % alcohol, centrifuged, put in glycerine and stored overnight in an oven at 40 °C before being mounted on microscope slides for identification and counting. Following the methodology initiated by van Geel (1972, 1978), 'Type' numbers were assigned to each type of non-pollen microfossil with characteristic morphology. Their coded designation of origin HdV stands for Hugo de Vries-Laboratory, University of Amsterdam. Using mycological literature, in many cases these Types, or fossil morphotaxa, could be positively identified as extant fungal taxa at the genus or species level. The word 'Type' *sensu* van Geel (1978) has no further taxonomic significance. In most cases it represents a more or less homogeneous morphological entity and can be considered as a provisionally named form-species. However, since morphologically similar European and African types can differ substantially in size and, given the enormous diversity of tropical fungi, may be subject to taxonomic variation at the genus or species level, we used new type numbers for related African types.

We analysed fossil NPP assemblages in a total of 93 sediment samples spaced evenly at 32 cm (~400 years) intervals along the 25,000-year sediment sequence, and spaced at 8 cm (~100 years) intervals over the last 2000 years (Fig. 1.2). The abundances of individual NPP taxa are expressed as percentages relative to a non-local pollen sum. The non-local pollen sum excludes aquatic plants, here mostly Cyperaceae and *Typha*. NPPs in each sample were counted until ca. 200 pollen grains (mean 206; range 100-245) had been encountered. Given this combination of time resolution and absolute counts, we interpret trends in the NPP curves at the millennial time scale. Stratigraphic zonation with CONISS (Grimm, 1987) was based on the distributions of 37 fungal spore taxa found in at least 10 sediment samples.

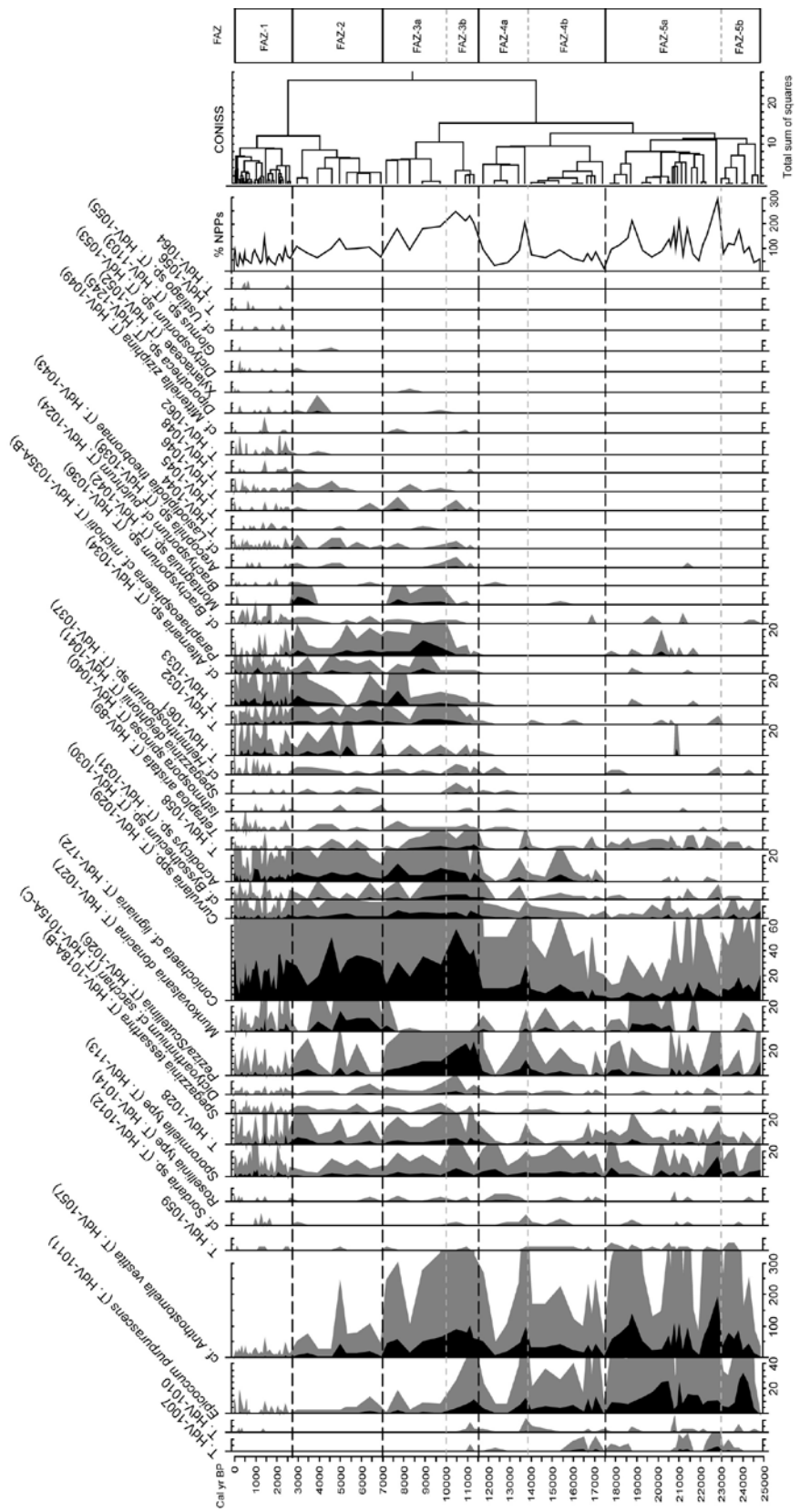

Fig. 1.2. Stratigraphic distribution and zonation of fossil fungi and some other NPPs in sediments of Lake Challa covering the last 25,000 years; taxon abundances expressed as percentages of the sum of non-local pollen.

1.2.3. Palaeoenvironmental reconstructions

Using two independent moisture-balance proxies extracted from the Challa sediment record, Verschuren *et al.* (2009) reconstructed past changes in lake level and rainfall over the past 25,000 years, i.e. from before the Last Glacial Maximum (LGM) to the present. This showed that in this equatorial region with bimodal seasonal rainfall regime, the intensity of monsoon rainfall varied at half-precessional (~11,500-year) intervals in phase with orbital insolation forcing. On sub-millennial time scales, hydrological change in equatorial East Africa shows clear signatures of northern high-latitude climate variability, such as an episode of pronounced aridity during the period 13,000-11,700 cal. yr BP, i.e. broadly coeval with the Younger Dryas (YD). Here we compare the stratigraphic record of fossil NPPs in Lake Challa sediments with that of the Branched and Isoprenoid Tetraether (BIT) index (Hopmans *et al.*, 2004), which describes the relative abundance of glycerol dialkyl glycerol tetraether (GDGT) membrane lipids derived from terrestrial soil bacteria versus those derived from aquatic archaea. The BIT record of Lake Challa is interpreted as a moisture-balance proxy mainly reflecting the amount of soil run-off to the lake, which is taken to be influenced primarily by the amount and intensity of monsoon rainfall (Verschuren *et al.*, 2009). On orbital and millennial time scales this inference is supported by the history of Challa lake-level changes, reconstructed from seismic-reflection data (Moernaut *et al.*, 2010). The history of regional temperature change is represented by the TEX_{86}-inferred palaeo-temperature reconstruction from Lake Tanganyika in central equatorial Africa (Tierney *et al.*, 2008). The TEX_{86} proxy is based on the relative degree of cyclization of isoprenoidal GDGT lipids in the cell membrane of aquatic archaea (Schouten *et al.*, 2002), which is linearly related to temperature (Powers *et al.*, 2004). The evolution of terrestrial vegetation is represented by pollen curves of a selection of common plant taxa (Fig. 1.3), expressed as percentages of the non-local pollen sum and based on total pollen counts between 130 and 2300 grains (on average 694) per sample (Rucina *et al.*, unpublished data). The processing of sediment samples for pollen analysis was identical to that for NPP analysis.

1.3. Results

Analysis of 93 depth intervals in the Challa sediment record produced a total of 16,403 distinct NPP specimens, which based on a variety of diagnostic character states could be assigned to 65 different, and well-defined, NPP Types. Sixty-one of these NPPs are fungal spore types, and 42 of these could be linked to known fungal taxa. However, genus and species attribution is not always certain, because many morphological features necessary for proper identification (fruit bodies, asci, conidiophores) were not found. Most of the recovered fungal remains are spores of Ascomycetes and Dematiaceae, taxa known to occur on a variety of substrates.

In the following overview, taxonomic descriptions of 61 Types follow the sequence of assigned Type numbers. We include the descriptions and illustrations of 16 Types which are rare in the Challa record and are not included in the stratigraphic diagram (Fig. 1.2) due to their erratic distribution. Little descriptive information about the spores is provided, as the morphological details illustrated in plates I-III can hardly be improved with text. Newly described taxa start with Type number 1001, because most numbers below 1000 have been assigned in earlier studies. The arrangement of Type numbers in this paper is simply sequential and does not infer any relationship between the fossils, unless otherwise indicated.

1.3.1. Descriptions and illustrations of African fungal spore types

Type HdV-89: *Tetraploa aristata* Berk. & Broome (van Geel, 1978) (Plate I; Fig. 1.2)

Conidia verrucose, muriform, 4 columns of cells terminating in septate setiform appendages. *Tetraploa aristata* is known from many locations worldwide, mainly in subtropical and tropical regions but also in the temperate climatic zone. It is found on a variety of host plants, usually on leaf bases and stems just above the soil (Ellis, 1971; Farr and Rossman, 2009).

Type HdV-113: *Sporormiella* type (van Geel *et al.*, 2003) (Plate I; Fig. 1.2)

Ascospores of modern-day *Sporormiella* species are three- to multi-septate. Each ascospore cell shows an oblique to diagonal germ slit, extending over the entire length of the cell. The ascospores easily split up in separate cells, consequently in the fossil state usually no complete ascospores are found. Identification of *Sporormiella* and similar genera to the species level is not possible because fruit-bodies, asci and complete ascospores are not available (Ahmed and Cain, 1972). Representatives of the related genus *Sporormia* lack germ slits, but as the descriptions of Ahmed and Cain (1972) are based on non-germinated spores, a slit may appear after germination, and thus we cannot exclude that our fossil assemblages also include *Sporormia* (van Geel and Aptroot, 2006). Both *Sporormia* and *Sporormiella* are coprophilous fungi, often associated with the dung of large herbivores (Comandini and Rinaldi, 2004). Fossil *Sporormiella*-like part-spores were distinguished by Davis *et al.* (1977), Davis and Turner (1986), Davis (1987), Burney *et al.* (2003), and van Geel *et al.* (2003). The spores are considered to be a reliable proxy for large herbivore populations occurring near the site of recovery (Burney *et al.*, 2003). *Sporormiella* type spore cells of variable size (10-16 µm) are common throughout the Lake Challa record.

Type HdV-172: *Coniochaeta* cf. *ligniaria* (Greville) Massee (van Geel *et al.*, 1983a) (Plate I; Fig. 1.2)

Ascospores circular to ellipsoid in outline, 14-20 x 11-15 μm, one-celled, bilaterally flattened, the two flattened dark brown sides have a light brown zone encircling the spore. A germ slit is present along the narrow side in the light brown zone. Jarzen and Elsik (1986) described and illustrated similar spores from river deposits in Zambia as *Exesisporites*. According to Munk (1957), *C. ligniaria* is common on dung and wood (see also Farr and Rossman, 2009). Ascospores of this species were found in soil surface samples from a Roman Period settlement site with strong evidence for a high density of domesticated animals (van Geel *et al.*, 2003; van Geel and Aptroot, 2006). This Type is common throughout the Challa record, particularly during the Holocene.

Type HdV-1001: *Caryospora* sp. (Plate I)

Ascospores 3-septate, apiculate, bigger cells dark brown, smaller cells light brown, ca. 50 x 28 μm. *Caryospora* species occur on dead plant material (Barr, 1979). Only one specimen was found in the Challa record (in the full-Glacial section).

Type HdV-1004 (Plate I)

Fungal spores (conidia?) cylindrical with rounded end cells, 3-5 septate, ca. 24-31 x 10 μm. Small pore in end cells. Rare in the Challa record; all 4 specimens were found in the full-Glacial section.

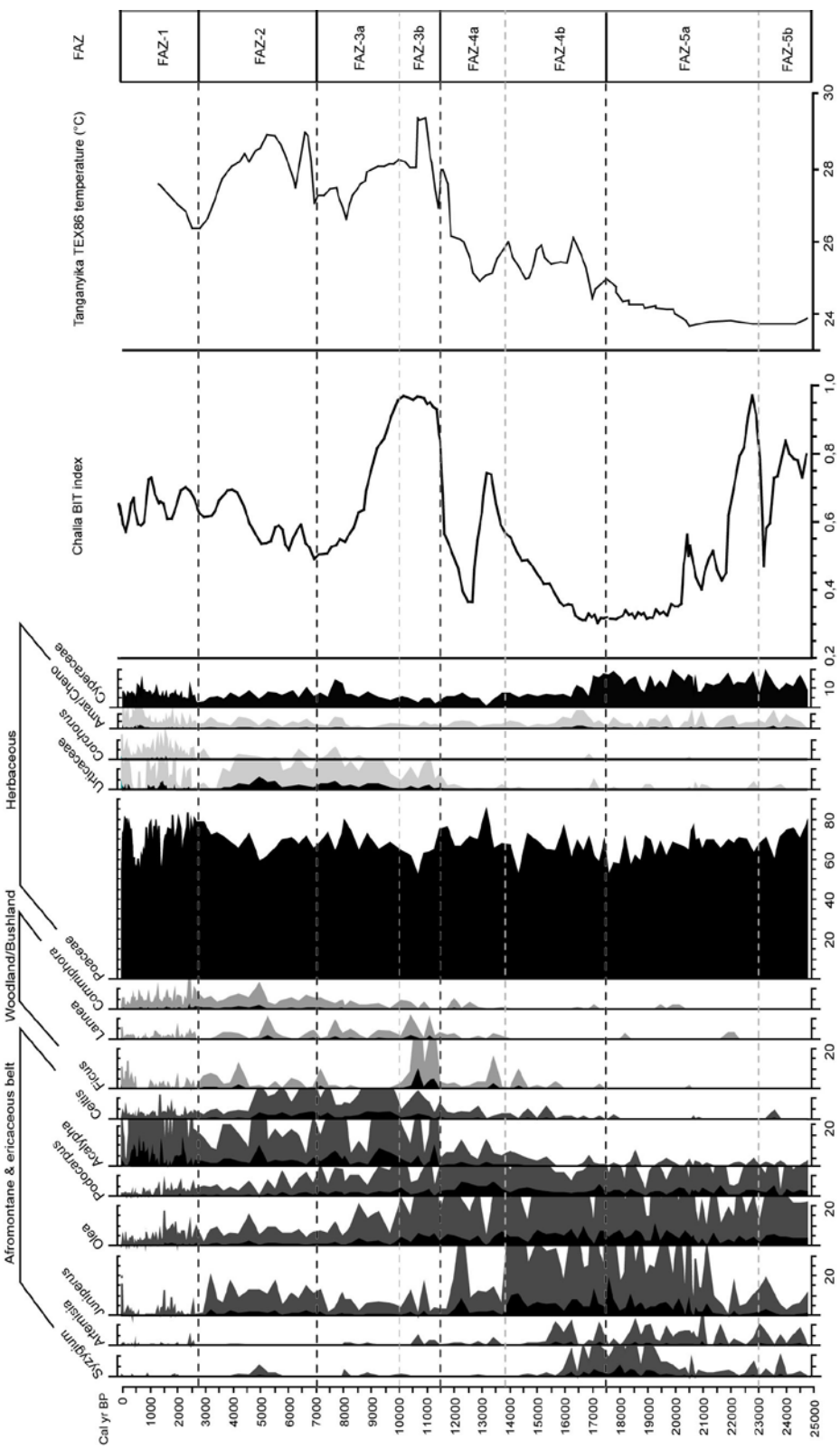

Fig. 1.3. Selected pollen curves and long-term trends in monsoon rainfall intensity (biomarker BIT index; Verschuren *et al.*, 2009) recorded in the sediments of Lake Challa over the last 25,000 years, and the TEX86 biomarker record of Lake Tanganyika surface-water temperature (in °C; Tierney *et al.*, 2008, in press) as proxy for the temperature evolution of central and eastern equatorial Africa. Both curves are 3-pt running averages, to highlight long term trends. FAZ boundaries are based on the fungal record (Fig. 2) and given for reference. Amar/Cheno refers to the combined pollen taxon derived from either Amaranthaceae or Chenopodiaceae.

Type HdV-1005: *Brachydesmiella* sp. (Plate I)

Conidia lemon-shaped, 2-septate, ca. 28-36 x 20 *µ*m, the central cell large, the end cells small with thinner walls than central cell. The extant taxon *B. biseptata* was found on wood of deciduous trees in N-America and Europe (Ellis, 1971). Very rare in the Challa record; all 3 specimens occurred in two adjacent intervals about 20,500 cal. yr BP.

Type HdV-1006 (Plate I)

Fungal spores one-septate, ca. 25 x 10 *µ*m, elliptic-cylindrical, one cell slightly broader than the other one. Apices have thicker walls, darker than central part. Rare in the Challa record (5 specimens total); present only in Glacial-period deposits.

Type HdV-1007 (Plate I; Fig. 1.2)

Fungal spores (conidia?) 3-septate, ca. 24-30 x 8-10 *µ*m, constriction at central septum well developed, the other two septa not closed, with less constriction. Apical cells showing hilum. Type HdV-1007 spores were only recorded in the Glacial and Late-Glacial sections of the Challa record, disappearing from ca. 11,000 cal. yr BP.

Type HdV-1008: cf. *Valsaria* sp. (Plate I)

Ascospores uniseptate, ca. 30 x 20 *µ*m, thick verrucose wall, septum very pronounced and slightly protruding. Fossil *Valsaria* type ascospores were recorded by van Geel *et al.* (2003) in soil samples from a Roman Period settlement site in the Netherlands. In the Challa record Type 1008 spores are relatively rare, but with a distinct Glacial and Late-Glacial distribution: 14 specimens were found in 7 intervals older than 11,100 cal. yr BP.

Type HdV-1009: *Chaetomium* sp. (Plate I)

Ascospores lemon-shaped, ca. 8-10 x 7-8 µm, bilaterally flattened with apical pores. *Chaetomium* species are cellulose-decomposing fungi occurring on plant remains and dung. Apart from the occurrence of their fossil ascospores in deposits from natural habitats (Type HdV-7A; van Geel, 1978; van Geel *et al.*, 1989), fossil *Chaetomium* spores also appeared to be linked to archaeological sites (Buurman *et al.*, 1995; van Geel *et al.*, 2003). In the Challa record *Chaetomium* spores are very rare; we recovered 5 specimens in sediments dated between 18,200 and 7,700 cal. yr BP.

Type HdV-1010 (Plate I; Fig. 1.2)

Fungal spores uniseptate, fusiform, ca. 32 x 11 *µ*m, with a pore at one end.
Type HdV-1010 spores regularly occur in the Glacial and Late-Glacial sections of the Challa record but are largely absent in the Holocene, with the exception of a few finds at ca. 1300 and 400-300 cal. yr BP.

Type HdV-1011: *Epicoccum purpurascens* Ehrenb. (Plate I; Fig. 1.2)

The conidia of *Epicoccum purpurascens* are globose, 15-28 µm in diameter, verrucose, with multiple transverse and vertical septa and a funnel-shaped smooth base with attachment scar. *E. purpurascens* is a ubiquitous saprophytic fungus found on a variety of substrates. It is an extremely common cosmopolitan invader of dead plant material (Ellis, 1971), but is also known from soil, litter, wheat, potato, sugar beet, hay, bird nests, pulp, paper, cotton and wood (Domsch *et al.*,

1980). Spores of *Epicoccum* are common in the Glacial, Late-Glacial and earliest Holocene sections of the Challa record, but become less frequent after 10,000 cal. yr BP.

Type HdV-1012: cf. *Sordaria* sp. (Plate I; Fig. 1.2)

Ascospores ellipsoidal, 17-24 x 10-12 µm, with one pronounced apical pore and a much smaller pore at the other end. Type HdV-1012 spores are similar to *Sordaria*-like ascospores recorded in samples from European archaeological sites (Bakker and van Smeerdijk, 1982; Buurman *et al.*, 1995; van Geel *et al.*, 1981, 1983a, b, 2003), often in combination with ascospores of other coprophilous Ascomycetes. *Sordaria* species are not obligatory coprophilous (Munk, 1957). These spores are uncommon in the Challa record but found more or less throughout the sequence.

Type HdV-1013: *Cercophora* type (Plate I)

Ascospores with truncate base (in some cases the hyaline pedicel is partly preserved) and conical apex with pore; spores ca. 20-25 x 12 µm (excl. pedicel). Jarzen and Elsik (1986) recorded similar spores as *Basidiosporites* in river deposits in Zambia. *Cercophora* species are Ascomycetes known from woody substrates, herbaceous stems and leaves and dung (Lundqvist, 1972). The fossil record of similar ascospores (Type HdV-112) in European sites in relation to independent archaeological information (Buurman *et al.*, 1995; van Geel *et al.*, 1981, 1983a, 2003) indicates that *Cercophora* type spores often can be used as an indication for animal dung in the vicinity of the sample site. Based on variation in ascospore size and morphology, several different species are probably present in the Challa collection. A total of 10 specimens were recovered, distributed throughout the record.

Type HdV-1014: *Rosellinia* type (Plate I; Fig. 1.2)

Ascospores fusiform, ca. 28 x 10 *µ*m, with a long, oblique germ split. The species is reported to grow either on herbaceous or woody substrates, in alpine and subalpine regions of Europe and North America (Petrini and Petrini, 1989). Uncommon in the Challa record but found more or less throughout the sequence.

Types HdV-1015A-C: *Dictyoarthrinium* cf. *sacchari* (J.A. Stev.) Damon (Plate II; Fig. 1.2)

Conidia square, cruciately septate, flattened in one plane, verruculose, 10-16 *µ*m in diameter. The three Types (differing in the number of appendages, see Plate II) were in first instance recorded separately, but later grouped together and represented by one curve in Fig. 1.2. *Dictyoarthrinium sacchari* is reported from a variety of tropical plants (Ellis, 1971). In the Challa record these conidia are rare in the Glacial and Late-Glacial sections, becoming more common during the Holocene.

Type HdV-1018A-B: *Spegazzinia tessarthra* (Berk. & M.A. Curtis) Sacc. (Plate II; Fig. 1.2)

Conidia cruciately septate, 14-18 *µ*m in diameter, excluding spines which are up to 3 *µ*m long (Type HdV-1018A). Smooth conidia also occur (Type HdV-1018B). The species is known to occur on a variety of tropical plant species (Ellis, 1971). Jarzen and Elsik (1986) described and illustrated *Spegazzinia*-like spores from river deposits in Zambia. Caretta *et al.* (1999) recorded *S. tessarthra* from Kenyan grassland vegetation. In the Challa record these conidia are rare in the Glacial and Late-Glacial sections, becoming more common during the Holocene.

Type HdV-1020 (Plate II)

Fungal spore ellipsoidal, 24-28 x 16-18 *µ*m. Apices have thicker walls, darker than central part. Rare in the Challa record (9 specimens), and except for a single find dated to ca. AD 1900, occur only in Glacial and Late-Glacial sections before 13,800 cal. yr BP.

Type HdV-1022: *Clasterosporium* sp. (Plate II)

Conidia obclavate, transversally septate, ca. 53 x 12 *µ*m. Dark cells showing striae. Identification is based on Ellis (1971). Rare in the Challa record (3 specimens).

Type HdV-1023: *Spegazzinia intermedia* M.B. Ellis (Plate II)

Conidia disc-shaped, flattened, dentate at the margin, cruciately septate, ca. 28 *µ*m in diameter. This fungus has been isolated from soil and from *Hibiscus* in Tanzania and from tobacco in the USA (Ellis, 1976). Jarzen and Elsik (1986) described and illustrated *Spegazzinia*-like spores from river deposits in Zambia. These conidia are rare in the Challa record (9 specimens), being restricted to Holocene and Late-Glacial sediments younger than 14,700 cal. yr BP.

Type HdV-1024: *Brachysporium* cf. *pulchrum* M.B. Ellis (Plate II)

Conidia mostly 4-septate, 41-50 x 20-25 *µ*m, central cell very large, dark brown, other cells pale and smaller. *B. pulchrum* has been found on *Phylica* (Rhamnaceae) on Tristan da Cunha (Ellis, 1971). This type should not be confused with Type UG-1099 (Gelorini *et al.*, 2011), which as suggested by size differences includes several other *Brachysporium* species apart from *B. pulchrum*. Rare in the Challa record (11 specimens), mainly recovered from mid- and late Holocene sediments.

Type HdV-1025: *Diplocladiella* cf. *scalaroides* G. Arnaud ex M.B. Ellis (Plate II)

Conidia triangular, 2-horned, ca. 25 *µ*m wide from horn tip to horn tip, horns 2-septate. The species was observed on dead wood in Europe (Ellis, 1976). Fossil spores were recorded by Barthelmes *et al.* (2006) in a Holocene deposit in Germany. Rare in the Challa record (8 specimens), with sporadic distribution.

Type HdV-1026: *Peziza/Scutellinia* (Plate II; Fig. 1.2)

Ascospores elliptical but slightly asymmetrical, ca. 23 x 9 *µ*m, covered with fine warts. Spores of this type are common throughout the Challa record, and particularly abundant in the early Holocene section.

Type HdV-1027: *Munkovalsaria donacina* (Niessl) Aptroot (Plate II; Fig. 1.2)

Ascospores ca. 19 × 7 *µ*m, elliptical, thick-walled, 1-septate near in the middle, constricted at septum, one cell wider and pointed, the other cell longer and rounded (Aptroot, 1995). This species has been found on a variety of plants. In the Challa record it is most common in the full Glacial period (20,500-18,500 cal. yr BP) and the mid-Holocene (7000-4000 cal. yr BP), but also recorded in other periods.

Type HdV-1028 (Plate II; Fig. 1.2)

Rows of globose fungal cells; each cell ca. 10-12 x 8-10 μm in diameter; constrictions at the septa. The observed variability suggests that this is probably a heterogeneous Type, including different taxa. Type HdV-1028 fungal remains occur throughout the Challa record, but most commonly in the Holocene part.

Type HdV-1029A-B: *Curvularia* spp. (Plate II; Fig. 1.2)

Conidia curved, with three or more transverse septa, 29-35 x 13-18 μm. Central cells darker than end cells. Type HdV-1029A is symmetrical; Type HdV-1029B is asymmetrical. These types are identified with reference to Ellis (1971, 1976). These conidia regularly occur in the Glacial and Late-Glacial sections of the Challa record, but are most common during the early and middle Holocene.

Type HdV-1030: cf. *Byssothecium* sp. (Plate II; Fig. 1.2)
Ascospores 3-septate, constricted at the middle septum, ca. 62 x 16 μm. End cells have thinner walls (therefore lighter colour). These ascospores regularly occur in the Glacial and Late-Glacial sediments of Lake Challa but are most common during the Holocene, especially the early Holocene.

Type HdV-1031: *Acrodictys* sp. (Plate II; Fig. 1.2)

Conidia ellipsoidal, ca. 30-33 x 20 μm, muriform, basal cell truncate, ca. 3 μm wide. This type is identified with reference to Ellis (1971, 1976). These conidia are rare in full Glacial Lake Challa sediments, but become frequent from 17,000 cal. yr BP onwards and are particularly common during the Holocene.

Type HdV-1032 (Plate II; Fig. 1.2)

Fungal spores one-celled, ca. 15 x 10 μm, ellipsoidal, wall pitted. Type HdV-1032 spores are rare in sediments of the full Glacial and Late-Glacial periods but become common during the Holocene.

Type HdV-1033 (Plate II; Fig. 1.2)

Ascospores one-septate, ca. 37 x 15 μm, constricted at the septum, one cell somewhat broader than the other, spore surface finely warted. These spores are very rare in full Glacial and Late-Glacial Lake Challa sediments but become common during the Holocene.

Type HdV-1034: cf. *Alternaria* sp. (Plate II; Fig. 1.2)

Conidia 45-50 x 12-18 μm, obclavate, tapering gradually to a beak, swollen at the tip, with transverse and longitudinal septa, verrucose. Jarzen and Elsik (1986) described and illustrated *Alternaria*-like spores from river deposits in Zambia. This type is identified with reference to Ellis (1971). These conidia regularly occur in the Holocene sediments of Lake Challa.

Type HdV-1035A-B: *Paraphaeosphaeria* cf. *michotii* (Westend.) O.E. Erikss. (Plate II; Fig. 1.2)

Ascospores one-septate, 22-27 x 7-8 μm, constricted at the septum, one cell much shorter than the other. Longer cell

pinched in the middle, surface verrucose.
P. michotii has been found mostly on Poaceae, Cyperaceae and Juncaceae (Shoemaker and Babcock, 1985). In Lake Challa sediments these spores occur at low densities from 22,000 to 18,000 cal. yr BP, and then commonly in most Holocene samples with a distinct peak from 10,000 to 8,500 cal. yr BP.

Type HdV-1036: cf. *Brachysporium* sp. (Plate II; Fig. 1.2)

Conidia 2-septate, 22-28 x 11-13 μm, apical cell elongated, dark-brown, connected with a smaller pale-brown central cell, basal cell small and hyaline, originally forming the connection with the mycelium. These spores are common in Holocene Lake Challa sediments.

Type HdV-1037: cf. *Helminthosporium* sp. (Plate II; Fig. 1.2)

Conidia pseudoseptate, 70-260 μm long, with a dark narrow scar at the base. These conidia are rare in sediments of the full Glacial and early Late-Glacial periods, and occur more frequently, though always in low numbers, from 12,500 cal. yr BP and through the Holocene.

Type HdV-1038: *Arecophila* sp. (Plate II; Fig. 1.2)

Ascospores ca. 20 x 8 μm, slightly constricted at the septum, showing a number of longitudinal slits (Hyde, 1996). These spores rarely occur in the early (11,500-9,500 cal. yr BP) and late Holocene (from 5000 cal. yr BP onwards) Lake Challa sediments.

Type HdV-1040: *Isthmospora spinosa* F. Stevens (Plate II; Fig.2)

Conidia (isthmospores) complex, lobed, sarciniform, echinulate, and ca. 23 x 18 μm excluding the 1–2 μm long spines. In the tropics, *Isthmospora spinosa* is a hyperparasite on various genera and species of the fungal family Meliolaceae (Hughes, 1953; Ellis, 1971). It is known from Central and South America including the Caribbean, tropical Africa and tropical East Asia, and can be locally abundant. Its teleomorph, *Trichothyrium asterophorum* (Berk. and Br.) Höhn., is rarely found but equally restricted to the same host and distribution range. Outside the tropics fossil conidia of *Isthmospora spinosa*, together with remains of its host ascomycete *Meliola ellisii*, which itself parasitised the heath plant *Calluna vulgaris*, have been recorded and illustrated by van Geel *et al.* (2006) in a Holocene raised bog deposit from northern England. In Lake Challa sediments the spores of *I. spinosa* are rare, the few specimens being found mostly in Late-Glacial and Holocene sediments. Spores of Meliolaceae fungi, their presumed host, were not found.

Type HdV-1041: *Spegazzinia deightonii* (S. Hughes) Subram. (Plate II; Fig. 1.2)

Conidia originally 8-celled but fossils always fragmentary. Separate cells ca. 12-16 μm in diameter, excluding the up to 5 μm long spines. *S. deightonii* occurs on a variety of plants (Ellis, 1971). In Lake Challa these conidia regularly, but uncommonly, occur in the late Late-Glacial to early Holocene (~13,000-10,000 cal. yr BP) section and again in the mid-Holocene (~6000-2500 cal. yr BP).

Type HdV-1042: *Montagnula* sp. (Plate II; Fig. 1.2)

Ascospores 27-29 × 12-14 μm, thick-walled, uniseptate, constricted at septum, one cell wider and pointed, the other cell

longer and rounded. Wall 'double-layered' (Aptroot, 1995). The lower spore illustrated in Plate II seems to have fossilised remnants of the original thick gelatinous sheath, which is now secondarily contracted to form apiculae. These spores are common in the early Holocene deposits of Lake Challa (~10,500-7000 cal. yr BP), but also for a brief period around 3000 cal. yr BP.

Type HdV-1043: cf. *Lasiodiplodia theobromae* (Pat.) Griffon & Maubl. (Plate II; Fig. 1.2)

Ascospores uniseptate, ellipsoidal, ca. 27 x 14 µm, with 3-4 longitudinal grooves in surface view (Müller and von Arx, 1962). In Lake Challa sediments, *L. theobromae* spores occur throughout the Holocene but at low counts.

Type HdV-1044 (Plate II; Fig. 1.2)

Ascospores fusiform, 32-38 x 12 µm, about eight weakly developed transverse septa; slightly constricted at central septum. Rare in Lake Challa and only recorded in the Holocene deposits.

Type HdV-1045 (Plate II; Fig. 1.2)

Fungal spores 2-septate, curved, ca. 33 x 18µm, middle part of the central cell thick-walled, dark. Rare in Lake Challa and only recorded in its Holocene deposits.

Type HdV-1046 (Plate II; Fig. 1.2)

Fungal spores 24-40 x 7-10 µm, slightly curved, with many transverse and a few longitudinal septa. Rare in Lake Challa and only recorded in its Holocene deposits.

Type HdV-1047: *Rhytidospora* cf. *tetraspora* Jeng & Cain (van Geel *et al.*, 1983a) (Plate I)

Ascospores ellipsoid, one-celled, brown, 16-20 x 18-19 µm excluding the up to 2 µm wide, undulate hyaline epispore. Two apical pores ca. 1 µm in diameter. Similar, but slightly smaller ascospores with the characteristic ornamentation probably referable to *R. tetraspora* (Jeng and Cain, 1977) were found at a Bronze Age archaeological site in the Netherlands (Buurman *et al.*, 1995). The number of ascospores per ascus, reported to be a valid species-level character in this genus, could not be assessed, leaving some doubt about the species identification. All known species of this genus inhabit dung (van Geel and Aptroot, 2006). This type is rare in the Challa record: only 3 specimens were found throughout the record.

Type HdV-1048 (Plate III; Fig. 1.2)

Ascospores ellipsoidal, 29-34 x 19-21 µm, 2-septate, with hyaline outer wall and inner dark brown wall. Rare in Lake Challa and almost exclusively recorded in late Holocene (< 4000 cal. yr BP) deposits.

Type HdV-1049: cf. *Mitteriella ziziphina* Syd. (Plate III)

Conidia fusiform, 28-34 x 14-16 µm, with large and dark central cell (too dark to see septa, if any) and shorter other cells; one end cell is pale, the other one rather dark. Identified with reference to Ellis (1971). Rare (13 specimens) in Lake Challa sediments; only present in the Holocene section.

Type HdV-1051 (Plate III)

Ascospores ellipsoidal, 24-28 x 11-13 μm, with eight short longitudinal furrows. Very rare (4 specimens) in Lake Challa; only present in Holocene deposits.

Type HdV-1052: Xylariaceae (Plate III)

Ascospores sub-fusiform, 28-43 x 12-15 μm with one flattened side with long furrow. Rare (4 specimens) in Lake Challa; only present in mid- to late-Holocene deposits.

Type HdV-1053: *Dictyosporium* cf. *heptasporum* (Garov.) Damon (Plate III)

Conidia broad ellipsoidal, 42-71 x 21-25 μm, branched, composed of ca. 7 rows of cells. *D. heptasporum* has been observed on wood and stems in Europe, India and North America (Ellis, 1971). Rare (8 specimens) in Lake Challa; only present in late Holocene deposits younger than 2,900 cal. yr BP.

Type HdV-1054: *Rosellinia* cf. *valdiviensis* Speg. (Plate III)

Ascospores cylindrical and rounded at the ends, ca. 28 x 11 μm, with a long, oblique germ split over the whole length of the spore (Petrini, 1993). Barthelmes *et al.* (2006) reported similar spores as cf. *Helicogermslita* (of which some species have *Rosellinia* as a synonym). One single specimen was found in the Lake Challa sediments, dated to ca. 2500 cal. yr BP.

Type HdV-1055: cf. *Ustilago* sp. (Plate III)

Spores globose, 16-24 μm in diameter, reticulate with verruculose meshes. For an overview of Ustilaginales spores see Vánky (1994). In Lake Challa these spores (6 specimens in total) were recorded only in late Holocene sediments younger than 2,300 cal. yr BP.

Type HdV-1056 (Plate III)

Spore elliptical, 25-30 x 19-22 μm, thick-walled with verrucae. In Lake Challa these spores (6 specimens in total) were recorded only in late Holocene sediments younger than 2,200 cal. yr BP.

Type HdV-1057: cf. *Anthostomella vestita* Speg. (Plate III; Fig. 1.2)

Ascospores ellipsoidal, ca. 10-13 x 8 μm. Possibly a heterogeneous Type. These spores were very common both in the Glacial and Late-Glacial sections of the Lake Challa record, and during the first half of the Holocene; after 7000 cal. yr BP this type declines to very low numbers through to the present.

Type HdV-1058 (Plate III; Fig. 1.2)

Spores globose, 13-17 μm in diameter including the 2-5 μm long appendages. These spores occur throughout the Lake Challa sequence except much of the Younger Dryas chronozone (13,500-12,000 cal. yr BP) and a brief episode around 7000 cal. yr BP; it is most common during the early Holocene.

Type HdV-1059 (Plate III; Fig. 1.2)

Spores globose, ca. 22 μm in diameter including the 6-7 μm long appendages. These spores are rare but found more or less throughout the Challa sediment core.

Type HdV-1061 (Plate III)

Spores globose, 13-18 μm in diameter, including the irregularly placed ca. 0.5 μm high warts. In Lake Challa, these spores are almost entirely restricted to the Holocene sediments.

Type HdV-1062 (Plate III)

Ellipsoidal microfossil, 31-40 x 22-28 μm excluding a series of irregular appendages up to about 6-12 μm long. One protruding pore of ca. 7 μm wide on the opposite side. Probably of zoological origin. These peculiar microfossils were only recorded in late Holocene Lake Challa sediments, from ~4000 cal. yr BP onwards.

Type HdV-1064 (Plate III)

Globose microfossil, ca. 43 μm in diameter and 4 μm high; reticulate with meshes 10-17 μm wide. This Type was very rare in Lake Challa (7 specimens), found only in late Holocene samples younger than 2,500 cal. yr BP.

Type HdV-1093: *Gelasinospora* cf. *cratiphora* R.S.Khan & J.C.Krug (Plate I)

Ascospores ellipsoidal, non-septate, ca. 35 x 25 μm. The dark brown surface is ornamented with 1 μm wide, hyaline pits. Based on molecular phylogeny (García *et al.*, 2004), all *Gelasinospora* species were recently included in the genus *Neurospora*. Following van Geel and Aptroot (2006) we retain the name *Gelasinospora* as their ornamentation differs considerably from the longitudinal grooves characteristic of *Neurospora* species. According to Lundqvist (1972), *Gelasinospora* mainly occur on excreta, but also occur on charred substrates and on wood. In Lake Challa sediments, spores of this type are rare (4 specimens).

Type HdV-1103: *Glomus* sp. (van Geel *et al.*, 1989) (Plate I)

Chlamydospores globose, 30-50 μm in diameter excluding the hyphal attachment. *Glomus* species are endomycorrhizal fungi living in the plant roots of a variety of host plants. Anderson *et al.* (1984) identified *G. fasciculatum* in post-glacial lake sediments in Maine (USA), where it became established with tundra vegetation on newly developing soils soon after icecap retreat. It was postulated that high soil erosion accounted for the abundance of *Glomus* in Late-Glacial sediments, and that reduced abundance in Holocene sediments was due to the establishment of trees. In the Lake Challa sediments few of these chlamydospores were found (3 specimens), and only in late-Holocene sediments up to 4,500 years old.

Type HdV-1245: *Diporotheca* sp. (van Geel *et al.*, 1986) (Plate I)

Ascospores biseptate, fusiform, 32-49 x 18-25 μm, both ends truncate with a germ pore. Surface often with dark brown anastomosing ribs. Ascospores of *Diporotheca* occur regularly in European Interglacial deposits (Holocene and Eemian) formed in eutrophic to mesotrophic conditions (van der Wiel, 1982; van Geel *et al.*, 1986, 1989). Van Geel *et al.*

(2003) recorded *D. rhizophila* ascospores and fruit-bodies in soil samples from a Roman Period settlement site in The Netherlands. We may expect host-parasite relationships for this representative of the Diporothecaceae (Gordon *et al.*, 1961). *Diporotheca* ascospores are relatively rare (17 specimens) in the Lake Challa sediments, occurring only in the Holocene interval.

Type HdV-1351: *Gelasinospora* cf. *dictyophora* R.S.Khan & J.C.Krug (Plate I)

Ascospores ellipsoidal, non-septate, ca. 32 x 22 μm. The dark brown surface is ornamented with 3-4 μm wide hyaline pits. This *Gelasinospora* species is similar to *G. retispora*. The ascospores of *G. dictyophora* differ from it in their ornamentation, with large, more rounded pits forming a network pattern in the spore wall (Khan and Krug, 1989). In Lake Challa sediments these spores are very rare (1 specimen).

1.3.2. Stratigraphy and zonation of the fungal flora

The CONISS stratigraphic zonation of NPP assemblages in the Challa record defines five major fungal assemblage zones (Fig. 1.2: FAZ-5 to FAZ-1), with FAZ-5, FAZ-4 and FAZ-3 each subdivided into two distinct sub-zones. We start the zone numbering at the top of the cored sequence (FAZ-1), considering the possibility that a much longer record will eventually be extracted from this site (Moernaut *et al.*, 2010). The abundance of NPP remains varied from 21 to 296 % (mean value: 96 %) of the sum of non-local pollen, with markedly higher mean abundances being reached in FAZ-5a and FAZ-3 than in the other zones.

FAZ-5b (ca. 25,000 - ca. 22,800 cal. yr BP)

This interval of the full Glacial period is characterised by high abundances of *Epicoccum purpurascens* and cf. *Anthostomella vestita*, and relatively high abundances of *Coniochaeta* cf. *ligniaria*, *Peziza/Scutellinia*, *Curvularia* and *Sporormiella* type. The regional climate during this period was cool (3.5-5 °C below present; Vincens *et al.*, 1993; Pinot *et al.*, 1999; Tierney *et al.*, 2008) and mostly wet (Verschuren *et al.*, 2009). Short-lived regional drought ~23,500-23,000 cal. yr BP (Fig. 1.3), i.e. coeval with the Heinrich-2 event (Hemming, 2004), is not clearly reflected in the fungal assemblage except perhaps a temporary decrease of *E. purpurascens* (Fig. 1.2). The pollen assemblage of this sub-zone is characterised by above-average percentages of grasses (mean value >70%), sedges (mean ~10%) and some herbs (Amaranthaceae/ Chenopodiaceae). It is supplemented with pollen of montane forest trees (*Juniperus*, *Olea* and *Podocarpus*) from the slopes of nearby Mt. Kilimanjaro which during the glacial period occurred at lower elevation than today (Zech, 2006) but would not have reached the immediate vicinity of the Challa caldera. We thus infer that local vegetation within and around the caldera was mostly a grass savannah.

FAZ-5a (ca. 22,800 - ca. 17,500 cal. yr BP)

This interval covering the final stages of the last Glacial period is characterised by the continued high abundances of *Epicoccum purpurascens* and cf. *Anthostomella vestita* combined with stable abundances of *Peziza/Scutellinia* and *Sporormiella* type but slightly reduced mean abundances of *Coniochaeta* cf. *ligniaria* and *Curvularia*. These are complemented by the (almost) continuously present Types HdV-1028, HdV-1058, HdV-1059 and *Parasphaeosphaeria* cf. *michotii*. Also notable is the combination of high abundance of *Munkovalsaria donacina* with absence of Type HdV-1007 and cf. *Byssothecium* from 20,500 to 18,500 cal yr BP. Regional climate during this period was initially cool and wet, but evolved to very dry after ca. 20,000 cal. yr BP (Verschuren *et al.*, 2009) more or less together with the onset of modest post-glacial warming (Fig. 1.3). In the pollen record this climatic shift is reflected in a slight reduction of grass (mean

value ca. 65%) compensated by increasing *Syzygium*. This tree is characteristic for riverine forest at lower and middle elevations on Mt. Kilimanjaro (Hemp, 2006) but may also have occurred within the crater on shorelines falling dry during lake-level decline. In the fungal assemblage this climate shift is marked by *Coniochaeta* cf. *ligniaria* being reduced to a relative abundance of about 4 %, its lowest level of the entire 25,000-year record (Fig. 1.2), and strong presence of *Munkovalsaria donacina* at broadly the same time.

FAZ-4b (ca. 17,500 - ca. 13,750 cal. yr BP)

This early Late-Glacial period is characterised by decreasing mean abundances of *Epicoccum purpurascens*, cf. *Anthostomella vestita* and Types HdV-1058, relative stability in *Sporormiella* type, *Peziza/Scutellinia*, *Curvularia* and cf. *Byssothecium*, and a notable increase in *Coniochaeta* cf. *ligniaria*. *Acrodictys* is now also consistently present, following rare and erratic occurrence in the lower section of FAZ-5a. Among the rarer fungal taxa previously mentioned, Type HdV-1007 disappears in the upper half of this zone whereas Types HdV-1059 and HdV-1010 persist albeit at very low levels. *Dictyoarthrinium* cf. *sacchari* is also more or less consistently present, up from more erratic occurrences in FAZ5a-b. Climatically this period is characterised by further warming (Tierney *et al.*, 2008) and, from 16,500 cal. yr BP onwards, more rainfall (Fig. 1.3). In the pollen record we see strong reductions in *Artemisia* and *Syzygium*, particularly from 16,000 cal. yr BP, but continued high abundances of the montane trees *Olea*, *Podocarpus* and *Juniperus*, suggesting that vegetation zones on Mt. Kilimanjaro had not yet retreated upward substantially by that time. Important are the first continuous appearances of the trees *Celtis* and *Ficus* (Fig. 1.3) as well as *Acalypha* (most probably the shrub *A. fruticosa*), indicating establishment of woodland/bushland within the Challa area, and possibly a predecessor of the present-day moist riverine forest inside Challa caldera. The mostly drought-adapted herbs of the Amaranthaceae and Chenopodiaceae also experience lower mean abundances, indicative of increasing moisture availability benefiting the local mycoflora.

FAZ-4a (ca. 13,750 - ca. 11,500 cal. yr BP)

This zone broadly covers the Younger Dryas chronozone. During this period of severe regional drought (Fig. 1.3) the Challa fungal record shows widespread, modest to drastic reductions in the previously common taxa *Epicoccum purpurascens*, cf. *Anthostomella vestita*, *Peziza/Scutellinia*, *Acrodictys* and even *Coniochaeta* cf. *ligniaria*, and a (near-) complete disappearance of the rarer Types HdV-1010, HdV-1028, HdV-1032, HdV-1058, HdV-1059 and *Spegazzinia tessarthra*. In contrast, *Curvularia* is able to maintain continuous presence through this period, and taxa such as *Tetraploa aristata*, *Spegazzinia deightonii* and cf. *Helminthosporium* record their first consistent presence in the Challa sediment sequence. Of special interest is *Rosellinia* type, an otherwise (in both previous and later periods) rare fungal type which only in FAZ-4a is consistently recovered. In the Challa pollen record the Younger Dryas is a transitional period characterised by strong reduction in the montane tree *Juniperus*, peak abundance of *Podocarpus*, and the first continuous presence of the dry woodland/bushland trees *Commiphora* and *Lannea* (Fig. 1.3). One dominant signal is the increased (mean value >70%) but variable presence of grass pollen.

FAZ-3b (ca. 11,500 - ca. 10,000 cal. yr BP)

The start of the Holocene period is characterised by an immediate increase in most of the fungal types which had reduced percentages in FAZ-4a, most notably the common taxa *Coniochaeta* cf. *ligniaria*, *Epicoccum purpurascens*, cf. *Anthostomella vestita*, *Peziza/Scutellinia* and *Acrodictys*. However, among these taxa only *Coniochaeta* cf. *lignaria* and *Acrodictys* continued to maintain high abundance throughout the Holocene. The other three reached more or less prominent peaks in subzone FAZ-3b (in the case of *Peziza/Scutellinia* its highest percent abundance of the entire record), followed by a return to more modest abundances in FAZ-3a. This pattern is also evident in the uncommon taxa

Dictyoarthrinium cf. *sacchari* and cf. *Byssothecium*. A contrasting pattern is displayed by *Munkovalsaria donacina*, which after being relatively common in glacial (~FAZ-5) and Late-Glacial (~FAZ-4) sections is largely absent from FAZ-3 before reappearing again in FAZ-2. Types HdV-1007 and HdV-1010, which were also recorded relatively frequently throughout much of FAZ-5 and FAZ-4, make a brief re-appearance at the onset of FAZ-3b but then largely disappear in more recent Challa sediments. The fungal assemblage of the earliest Holocene lived under climatic conditions of interglacial tropical temperatures combined with intense monsoon rainfall, which resumed immediately upon the end of the Younger Dryas (Fig. 1.3). The regional pollen assemblage is characterised by marked expansion of *Acalypha*, *Celtis*, *Ficus* and *Lannea*, the rather sudden and prominent appearance of Urticaceae herbs, and decreasing percentages of montane forest pollen from *Juniperus* and *Podocarpus*. Broadly matching the pattern displayed by some fungal types (Types HdV-1007 and HdV-1010, *Epicoccum purpurascens*, *Peziza/Scutellinia*, *Dictyoarthrinium* cf. *sacchari*), *Ficus* pollen reaches peak abundance in this subzone, falling back to very low levels after 10,500 cal yr BP (Fig. 1.3). In terms of fungal habitat we can infer that vegetation inside the Challa caldera started to approach its modern-day composition.

FAZ-3a (ca. 10,000 - ca. 7,000 cal. yr BP)

In FAZ-3a a sizable number of spore types, e.g. cf. *Alternaria*, *Paraphaeosphaeria* cf. *michotii*, *Montagnula* and Types HdV-1032 and HdV-1033, become regular components of the Challa fungal assemblage after at best erratic occurrences during Glacial and Late-Glacial time, and only modest appearances in FAZ-3b. The FAZ-3a assemblage also comprises a large number of fungal taxa which had not previously been recorded, e.g, cf. *Lasiodiplodia theobromae* and Type HdV-1045 (Fig. 1.2). In the course of the period covered by FAZ-3a, very wet climatic conditions characterizing the early Holocene evolved after 9000 cal. yr BP towards a markedly drier mid-Holocene (Fig. 1.3). The FAZ-3b to FAZ-3a transition in fungal assemblages around 10,000 cal yr BP coincides with notable changes in regional vegetation, such as the onset of a decrease in *Olea* pollen (~2000 years after the decrease in other montane forest taxa), and the near-complete disappearance of *Ficus*.
The high CONISS split between the two subzones of FAZ-3 reflects the distinction between locally established fungal taxa which recovered immediately at the Late-Glacial to Holocene transition (i.e., the end of the Younger Dryas at 11,700 cal. yr BP), and many newly colonizing fungal taxa which appear only around 10,000 cal. yr BP. Also contributing are the types HdV-1007 and HdV-1010, which had been characteristic for Glacial and Late-Glacial sections but disappear only after a few sampled intervals within the earliest Holocene (Fig. 1.2).

FAZ-2 (ca. 7000 – ca. 2700 cal. yr BP)

This fungal zone broadly covers the mid-Holocene period of relative aridity evolving into the wetter conditions characteristic of recent millennia (Fig. 1.3). Clear separation from FAZ-3 by CONISS (Fig. 1.3) points to the highly dynamic nature of the Challa fungal assemblages during the Holocene. Some common and uncommon fungal taxa more or less maintain the percent abundances that they had established during the early Holocene: *Coniochaeta* cf. *ligniaria*, cf. *Helminthosporium*, *Spegazzinia tessarthra*, *Acrodictys*, *Paraphaeosphaeria* cf. *michotii*, cf. *Brachysporium*, and Types HdV-1028, HdV-1032 and HdV-1033 are commonly present. A large contingent of taxa experience substantial and sustained reductions: for example, *Epicoccum purpurascens*, cf. *Anthostomella vestita*, *Rosellinia* type, *Sporormiella* type, *Dictyoarthrinium* cf. *sacchari*, *Peziza/Scutellinia*, *Curvularia*, cf. *Byssothecium* and Type HdV-1058. Only few taxa increase their presence. The most notable of these is *Munkovalsaria donacina*, which temporarily becomes the second-most common fungal type, but also notable are cf. *Lasiodiplodia theobromae* and Type HdV-1061. The dominant patterns in the pollen record of this period are the expansions of *Juniperus*, *Ficus* and *Commiphora* pollen types. *Syzygium* has a marked peak around 5000 cal. yr BP concomitant with the highest percentages of *Acalypha* within FAZ-2, evidently reflecting vegetation change inside or nearby the Challa caldera.

FAZ-1 (ca. 2700 cal. BP to the present)

The exact position of the FAZ-1/FAZ-2 transition is hard to determine, because greater time resolution in the last 2500 years of the Challa sequence increases the apparent between-sample variability and mimics a change in the distribution pattern of fungal taxa. The associated greater total sampling effort also increases the probability of recovering rare taxa, consequently the unique presence of certain fungal Types in this zone cannot be taken as proof that they were absent in older sections. Taking these caveats into account, FAZ-1 is defined on the basis of the clearly decreasing average abundance of common taxa such as cf. *Anthostomella vestita* and *Paraphaeosphaeria* cf. *michotii*, and the more consistent presence of Xylariaceae, *Dictyosporium*, cf. *Ustilago* and Types HdV-1044, HdV-1048 and HdV-1062. Climate in the Challa region was variable but generally semi-arid during this period (Fig. 1.3). FAZ-1 broadly corresponds with a pollen assemblage characterised by a decrease in *Juniperus* and *Podocarpus* mirrored by rises in *Acalypha*, *Corchorus*, sedges and Amaranthaceae/Chenopodiaceae. There is also a modest re-appearance of *Artemisia* pollen (Fig. 1.3), but this must reflect long-distance transport from high up on Mt. Kilimanjaro.

1.4. Discussion: associations of the mycoflora with climate variables and local vegetation

By covering the complete transition from the full Glacial period (25,000 cal. yr BP) to the present, the large gradient of local climatic conditions represented by the Lake Challa record and independent reconstructions of temperature, rainfall and vegetation together represent a natural experiment allowing an environmental assessment of the preferences of tropical African fungi whose ecology is as yet unknown.

Direct correlation (across 73 joint observations) of the stratigraphic distribution of individual fungal spore types in the Challa record with the Tanganyika record of TEX_{86}-inferred temperature (Tierney *et al.*, 2008) reveals that of the 61 fungal taxa considered in this study, 29 taxa display a significant positive relationship ($r = 0.26\text{-}0.73$; $p < 0.05$) with the principal long-term trend in regional temperature change. The strongest associations ($r > 0.50$) occur for *Coniochaeta* cf. *ligniaria*, cf. *Byssothecium*, *Acrodictys*, cf. *Alternaria* and Type HdV-1032. *Coniochaeta* is the single-most abundant taxon in the Challa record overall but with highest peak abundances reached during the Holocene (FAZ-3 through FAZ-1). Cf. *Byssothecium* and *Acrodictys* display a common pattern of infrequent occurrence during Glacial time (FAZ-5ab) followed by continuous presence starting ~17,500 cal. yr BP (the base of FAZ-4b), when the post-glacial temperature rose substantially above full-Glacial conditions (Fig. 1.3). Cf. *Alternaria* and Type HdV-1032 share the distinct pattern of near-absence during Glacial and Late-Glacial time (FAZ-5 and FAZ-4) followed by continuous presence in the Holocene (FAZ-3 through FAZ-1) after the full-interglacial temperature regime had become established (Fig. 1.3). A total of seven other fungal taxa display a significant negative relationship with the principal trend in temperature. In most cases the relationship is relatively modest ($r = -0.24$ to -0.39) but it is very strong ($r = -0.63$) in *Epicoccum purpurascens*, on account of this taxon being common to abundant throughout Glacial and Late-Glacial time, and being reduced to very low numbers about 2000 years after the start of the Holocene (Fig. 1.2).

Similarly, correlation of the stratigraphic distribution of individual fungal spore types with BIT-inferred variation in local rainfall (across 34 joint observations) reveals that six fungal taxa display a significant positive relationship with rainfall. These are, in order of decreasing r value (range 0.61-0.35), *Coniochaeta* cf. *ligniaria*, *Peziza/Scutellinia*, *Rhytidospora* cf. *tetraspora,* cf. *Byssothecium*, *Curvularia* and *Gelasinospora*. *Rhytidospora* and *Gelasinospora* are rare taxa whose sporadic occurrences happen to coincide with episodes of high BIT values in FAZ-5b and FAZ-3 (Fig. 1.3). Distributions of the other four, more common taxa mimic significant portions of the BIT-index record, particularly in FAZ-4 and FAZ-3 but extending to FAZ-5 (*Coniochaeta*, *Curvularia*) or FAZ-2 (*Peziza/Scutellinia*, cf. *Byssothecium*). Without exception these four taxa display strong increases at the FAZ-4a/FAZ-3 boundary, i.e. the Younger Dryas to Holocene transition when also BIT index values strongly increase (Fig. 1.3). Three other fungal taxa display a significant negative relationship with rainfall; in

order of decreasing r value (range -0.43 to -0.49) these are *Diplocladiella*, Type HdV-1007 and *Chaetomium*. *Diplocladiella* and *Chaetomium* are rare taxa whose sporadic occurrences coincide mostly with episodes of low BIT values. The more common Type HdV-1007 is restricted to Glacial and Late-Glacial sections of the record, but with strong presence near the top of FAZ-5a and the base of FAZ-4b when BIT values are at a minimum.

Correlations of fungal taxa with the principal group taxa of higher plants in regional vegetation reveal tentative evidence of plant-fungi associations. For simplicity we limited this exercise to the 15 pollen taxa presented in Fig. 1.3, which together (except Cyperaceae, which are excluded from the pollen sum) amount to on average 85% (range 65-94%) of the non-local pollen sum. Consistent with vegetation surveys of the Mt. Kilimanjaro region (Hemp, 2006), and to optimally represent the principal long-term trend in regional vegetation dynamics, we included *Acalypha* (here most likely *A. fruticosa*, a savanna woodland shrub) and *Celtis* (here most likely *C. africana*, a shrub of riverine and colline savanna forest) with the woodland/bushland biome rather than with the high-elevation montane/ericaceous biome.

Of the 61 fungal types considered and 93 joint fungi-pollen observations, nine fungal types display a stratigraphic distribution that is significantly and positively correlated (r = 0.21-0.58) with the pollen sum of montane/ericaceous plants; the six more common taxa among them are *Epicoccum purpurascens*, cf. *Anthostomella vestita* and Types HdV-1007, HdV-1059, HdV-1058 and HdV-1010. Given that montane forest on Mt. Kilimanjaro did not move down to the elevation of Challa caldera even under peak Glacial climate conditions (Zech, 2006), these fungi can not have had a particular association with the montane/ericaceous biome. Rather these are taxa for which suitable habitat occurred inside Challa caldera mostly during the Glacial and Late-Glacial periods (FAZ-5 and FAZ-4), and that disappeared or became less common in the course of the Holocene (FAZ-3 through FAZ-1). Conversely, fungal types with distributions that are negatively correlated (r = -0.21 to -0.60) with the montane/ericaceous biome (25 in total) are taxa which found suitable habitat in Challa caldera mostly during the Holocene, and were either less common (e.g., *Coniochaeta* cf. *ligniaria*, *Acrodictys*) or largely absent (e.g., cf. *Alternaria*, Types HdV-1032, HdV-1033, HdV-1061) during Glacial and Late-Glacial periods. Stratigraphic associations of individual fungal taxa with the woodland/bushland biome (28 are positively and 6 are negatively correlated) are mostly opposite to associations with the montane/ericaceous biome, and mostly concern the same taxa. In this case the association may imply that woodland/bushland plants in the local Challa basin vegetation did indeed provide particular habitat types favouring certain species of fungi. However, the group of fungal taxa that is positively related with the woodland/bushland biome also substantially overlaps with the group that is positively correlated with temperature, and vice versa. We therefore cannot ascertain whether the past distribution of individual fungal species in this system was controlled directly by the ambient temperature regime or by vegetation shifts resulting from plant response to temperature change.

Significant correlations of individual fungal types with the herbaceous biome (grasses plus Urticaceae, *Corchorus* and Amaranthaceae/Chenopodiaceae) are recorded for 10 taxa, among which five are positive (r = 0.23-0.35) and five are negative (r = -0.21 to -0.35). The mostly rather low coefficients for these associations may be due to the lack of a distinct long-term trend in the generally abundant grass pollen (Fig. 1.3). Significant correlations with the Cyperaceae are recorded for about half (29) of all fungal taxa considered, among which 8 are positive (r = 0.24-0.46) and 21 are negative (r = -0.21 to -0.55). Fungi that are positively correlated with the Cyperaceae are often negatively correlated with the woodland/bushland biome, because Cyperaceae pollen abundance is high (on average ca. 15%) during the Glacial and early Late-Glacial periods (FAZ-5) compared to the later periods when woodland/bushland plants become established.

In all, 50 of the 61 fungal taxa recorded in this study display significant positive or negative correlation with the records of one or more of the six environmental variables that we selected for analysis. Of these taxa, 19 show the highest correlation (either positively or negatively) with the TEX_{86} temperature proxy, 6 with the BIT rainfall proxy, 13 with the montane/ericaceous biome, 7 with the woodland/bushland biome, one (Xylariaceae) with the herbaceous biome, and 7 with the Cyperaceae pollen curve.

1.5. Conclusions

The Lake Challa deposits that we studied showed a large variety of NPP taxa occurring in different quantities. The richness of the fungal spore assemblage (of mainly terrestrial origin; Gelorini *et al.*, 2011) may be a function of specific combinations of temperature and precipitation, and of crater basin morphology, the diversity of flowering plants, host relationships and how both pollen and spores are incorporated into Lake Challa sediments. The prominent fraction and obvious strength of stratigraphic associations between individual fungal taxa and selected habitat variables observed in this study indicates strong environmental control on the distribution of African fungal taxa, and hence substantial potential as ecological indicators. Truly specific palaeoenvironmental information that can be derived from fungal spore distributions and associations in the Challa record is still relatively limited. But the combined records of pollen, fungal spores and BIT index shows that species composition and frequency changes of the fungal flora are strongly linked with major changes in climate and/or vegetation. For example, when at the Glacial-to-Holocene transition the spectrum of flowering plant species changed considerably, changing moisture conditions had a strong impact on the production of biomass and the ability of fungi to play a role in the decomposition of dead biomass. Spores of *Epicoccum purpurascens* are common in the Glacial part of the core, but show a strong decline during the early Holocene. Ascospores of *Coniochaeta* cf. *ligniaria* occur throughout the core and are characterised by fluctuations, and as these are common during wet periods they are apparently related to major humidity changes during the last 25,000 years. The occurrence of some other taxa (*Acrodictys*, *Curvularia*) appears to be linked with increased humidity, with thresholds passed from ca. 16,000 cal. BP when a variety of taxa reacted to the intensifying monsoon and especially from ca. 11,500 cal. BP at the Late-Glacial to Holocene transition. Since a comparable number of fungal taxa displayed strongest associations with either a particular biome (28 in total) or a climate variable (25 in total), our data do not settle the issue whether the regional mycoflora responds most to abiotic or biotic habitat characteristics. In some cases, very obvious co-occurrence (for example, *Peziza/Scutellinia* with a pollen maximum of *Ficus*) may reflect these taxa to be host and parasite. Spores of the obligately dung-inhabiting fungus *Sporormiella* occur throughout the Challa record without major fluctuations, showing that probably no major changes in the population density of large herbivores in the region occurred before, during or after deglaciation.

It is expected that future African NPP studies will significantly increase information about the relationships of fungal populations with past vegetation changes and associated environmental conditions. Progress on ecological understanding and the consequences of land-use changes for the African mycoflora can be made with calibration studies of fungal spore assemblages in surface-sediment samples from large numbers of African lakes, and more studies of the relationship of extant African fungi with living plants and decomposing plant biomass, as pioneered by Caretta *et al.* (1998, 1999).

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Plate I. T. HdV-1093: *Gelasinospora* cf. *cratiphora*; T. HdV-1351: *Gelasinospora* cf. *dictyophora*; T. HdV-89: *Tetraploa aristata*; T. HdV-113: *Sporormiella* type; T. HdV-1245: *Diporotheca* sp.; T. HdV-1047: *Rhytidospora* cf. *tetraspora*; T. HdV-172: *Coniochaeta cf. ligniaria*; T. HdV-1103: *Glomus* sp.; T. HdV-1001: *Caryospora* sp.; T. HdV-1004; T. HdV-1005: *Brachydesmiella* sp.; T. HdV-1006; T. HdV-1007; T. HdV-1008: cf. *Valsaria* sp.; T. HdV-1009: *Chaetomium* sp.; T. HdV-1010; T. HdV-1011: *Epicoccum purpurascens*; T. HdV-1012: cf. *Sordaria* sp.; T. HdV-1013: *Cercophora* type; T. HdV-1014: *Rosellinia* type.

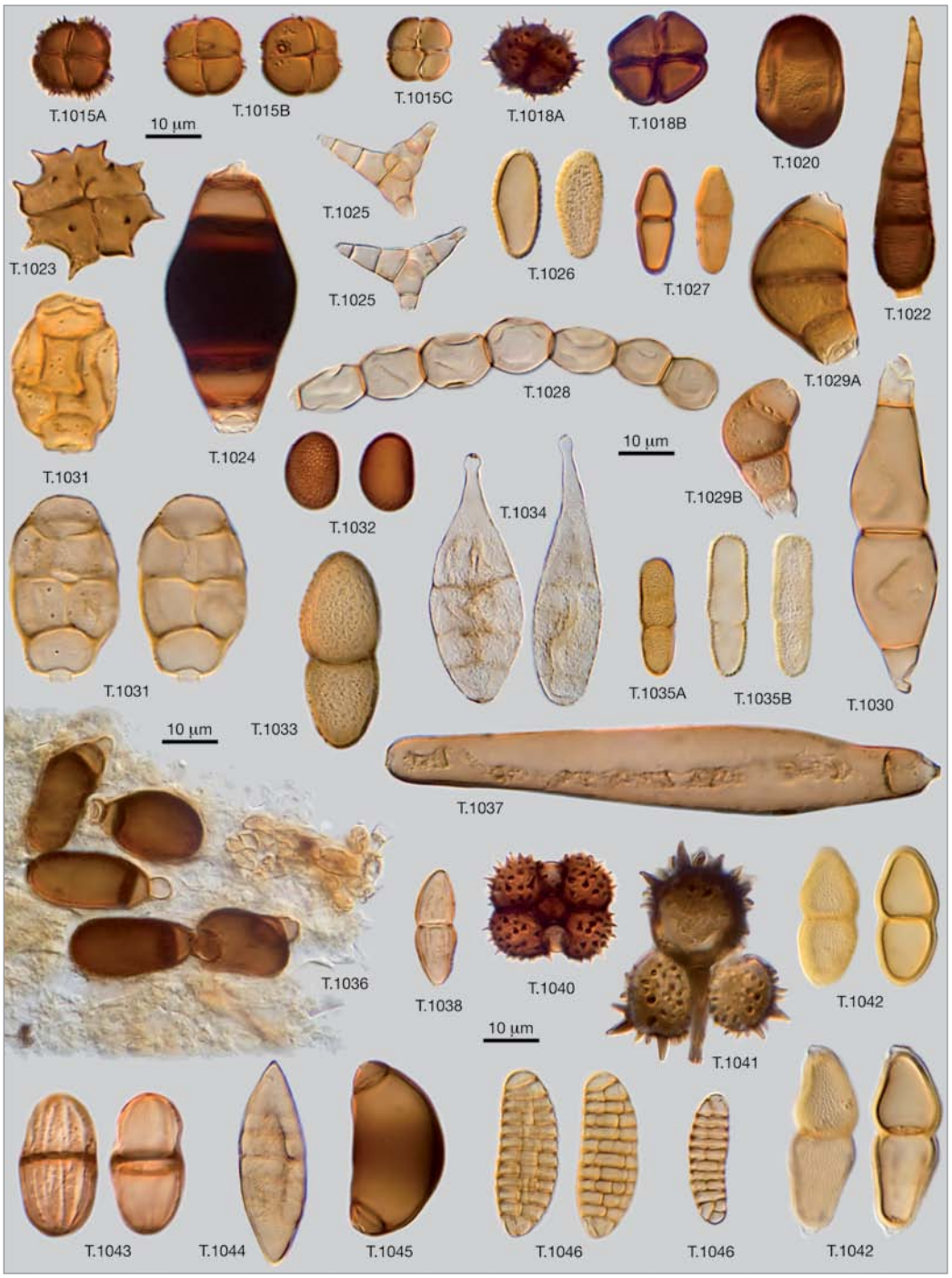

Plate II. T. HdV-1015A-C: *Dictyoarthrinium* cf. *sacchari*; T. HdV-1018A-B: *Spegazzinia tessarthra*; T. HdV-1020; T. HdV-1022: *Clasterosporium* sp.; T. HdV-1023: *Spegazzinia intermedia*; T. HdV-1024: *Brachysporium* cf. *pulchrum*; T. HdV-1025: *Diplocladiella* cf. *scalaroides*; T. HdV-1026: *Peziza/Scutellinia*; T. HdV-1027: *Munkovalsaria donacina*; T. HdV-1028; T. HdV-1029A-B: *Curvularia* spp.; T. HdV-1030: cf. *Byssothecium* sp.; T. HdV-1031: *Acrodictys* sp.; T. HdV-1032; T. HdV-1033; T. HdV-1034: cf. *Alternaria* sp.; T. HdV-1035A-B: *Paraphaeosphaeria* cf. *michotii*; T. HdV-1036: cf. *Brachysporium* sp.; T. HdV-1037: cf. *Helminthosporium* sp.; T. HdV-1038: *Arecophila* sp.; T. HdV-1040: *Isthmospora spinosa*; T. HdV-1041: *Spegazzinia deightonii*; T. HdV-1042: *Montagnula*; T. HdV-1043: cf. *Lasiodiplodia theobromae*; T. HdV-1044; T. HdV-1045; T. HdV-1046.

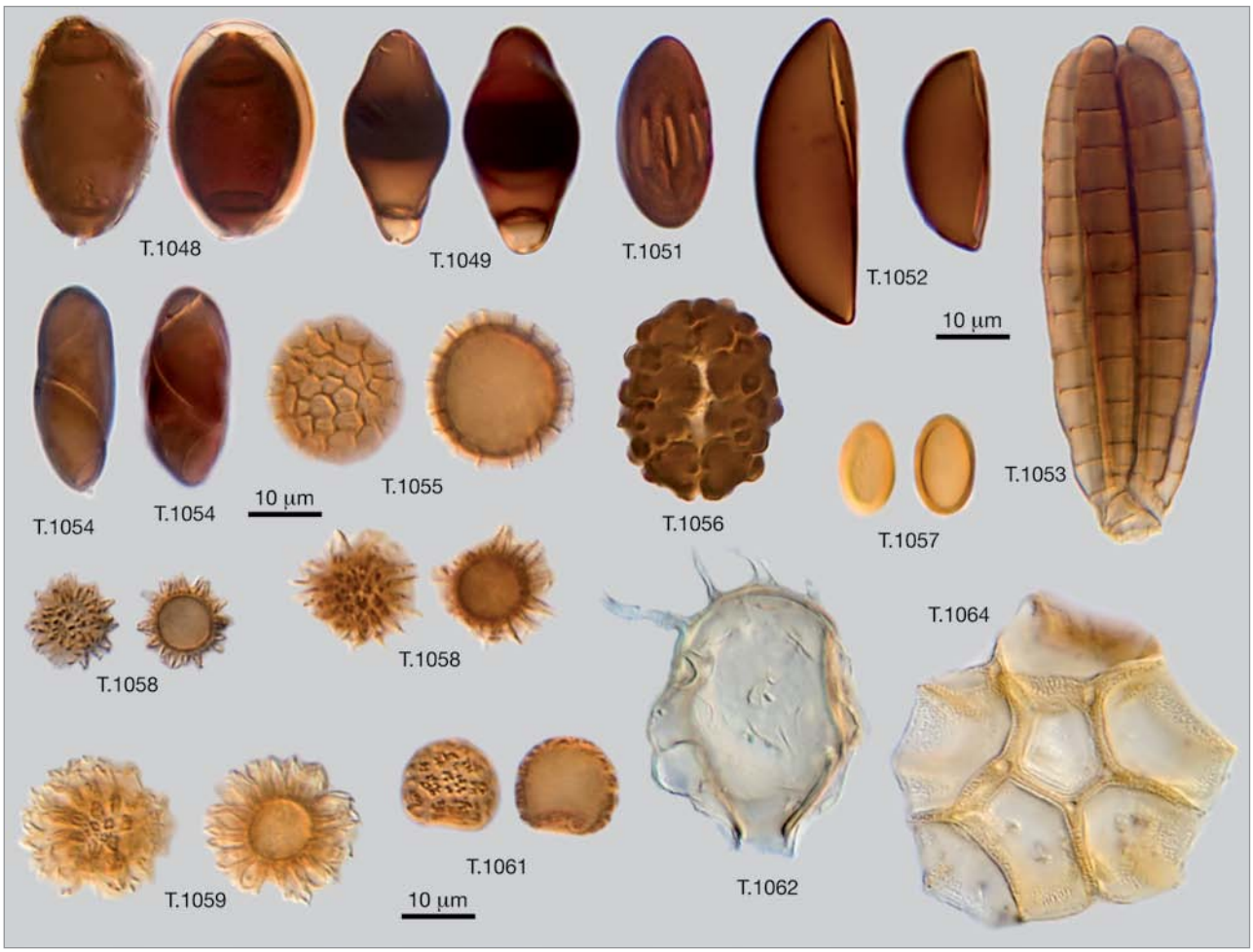

Plate III. T. HdV-1048; T. HdV-1049: cf. *Mitteriella ziziphina*; T. HdV-1051; T. HdV-1052: Xylariaceae; T. HdV-1053: *Dictyosporium* cf. *heptasporum*; T. HdV-1054: *Rosellinia* cf. *valdiviensis*; T. HdV-1055: cf. *Ustilago* sp.; T. HdV-1056; T. HdV-1057: cf. *Anthostomella vestita*; T. HdV-1058; T. HdV-1059; T. HdV-1061; T. HdV-1062; T. HdV-1064.

Modern non-pollen palynomorphs from East African lake sediments

Modified from Gelorini, V., Verbeken, A., van Geel, B., Cocquyt, C., Verschuren, D., 2011. Review of Palaeobotany and Palynology 164, 143-173.

Abstract

This paper presents an illustrated guide to the identification of non-pollen palynomorphs (NPPs) preserved in lake-sediment archives from equatorial East Africa. Modern NPPs were recovered from recently deposited surface sediment in 20 small crater lakes in western Uganda, located along environmental gradients of vegetation (moist evergreen and semi-deciduous forest, wooded and open grass savannah), land use (pastoralism, crop agriculture, plantations) and lake characteristics (basin morphometry, water chemistry and aquatic production). We analysed 9700 NPP specimens, which could be assigned to 265 distinct morphotypes, of which 239 belong to six major taxonomic groups: spores and other remains of fungi (198 morphotypes), spores of ferns and mosses (19 morphotypes), microscopic zoological remains (14 morphotypes), colonies, coenobia or zygo-/aplanospores produced by filamentous algae (7 morphotypes) and microscopic aquatic plant remains (1 morphotype). The remaining 26 morphotypes could not be assigned to a specific taxonomic category. Using primary taxonomic and molecular phylogenetic literature, 73 (28 %) of the recovered morphotypes could be identified at the species, genus or family level, thereby conferring ecological indicator value to them. This study may facilitate the use of fossil NPPs to help reconstruct past climatic and anthropogenic impacts on African ecosystems, as already broadly established in other study regions outside Africa.

Keywords: tropical Africa, non-pollen palynomorphs (NPPs), fungal spores, biodiversity, taxonomy, palaeoecology, palaeolimnology.

2.1. Introduction

The study of fossil non-pollen palynomorphs (NPPs) was introduced to the research discipline of palynology by van Geel (1978), who in the late 1970s analysed a heterogeneous group of non-pollen microfossils found in pollen preparations from Holocene peat-bog sections in Germany and the Netherlands. These microfossils included remains of vascular plants as well as a great variety of degradation-resistant remains of fungi, algae and invertebrates. Van Geel (1978) provided descriptions, identifications and/or morphotype code numbers and, when available, ecological information on the taxa concerned. Since then palynologists have exploited the palaeoenvironmental indicator value of these microfossils, resulting in the established use of NPPs as a palaeoecological tool supplementary to palynology all over Europe (Kuhry, 1985; van Smeerdijk, 1989; Ralska-Jasiewiczowa and van Geel, 1992; López Sáez *et al.*, 1998; Carrión and Navarro, 2002). During the most recent decade, NPP reference literature has expanded remarkably (including a special issue of the *Review of Palaeobotany and Palynology*: van Geel, 2006, and *Vegetation history and Archaeobotany*: Haas, 2010), and many newly described NPPs have been added to the morphotype list, which now counts in excess of 1000 types. NPP analysis recently also started to develop in other parts of the world such as North America (van Geel *et al.*, 2007), Asia (Limaye *et al.*, 2007; Zong *et al.*, 2007; van Geel *et al.*, 2008), the Subantarctic (Yeloff *et al.*, 2007), and tropical South America (Berrío *et al.*, 2006; Ledru *et al.*, 2006; Rull *et al.*, 2008).

The use of NPPs to help reconstruct tropical African palaeoenvironments has, thus far, been very modest in comparison. The first African NPP studies by Wolf (1966, 1967a,b) assessed the diversity of fungal spores preserved in the

bottom sediments of some East African lakes sampled by D. A. Livingstone: Lake Naivasha in Kenya, Lake Chishi in Zambia, Lake Rukwa in Tanzania, and Lakes Kitandara and Mahoma in the Rwenzori Mountains of Uganda. Wolf identified a sizable number of fungal spores from these deposits, but their reference value remained limited due to their representation by pencil drawings with little detail, and lack of diagnostic descriptions and ecological information. Jarzen and Elsik (1986) studied fungal palynomorphs from recent river deposits in Zambia, mostly referring to the taxonomy and inferred ecology of Tertiary fossil fungi, to constrain the environmental conditions associated with certain fungal assemblages recovered from Neogene sediments. All later studies on fossil African NPPs (Carrión *et al.*, 2000; Burney *et al.*, 2003; Lejju *et al.*, 2005; Mumbi *et al.*, 2008) were fully integrated into analyses of fossil pollen and spore assemblages, and African NPP morphotypes were identified with near-exclusive reference to European NPP morphotypes. This procedure evidently cannot derive much useful ecological information from NPP morphotypes not previously encountered in European contexts. Also it carries the risk that similarly looking European and African NPP morphotypes, many of which have not been positively attributed to a particular biological taxon, may occupy distinctly different ecological niches, such that transfer of ecological information from the European to the African taxon may be invalid. A first step towards scientifically sound application of NPPs in African palaeoecology was recently made by van Geel *et al.* (2011) through analysis of NPP diversity and biostratigraphy in relation to regional climate and vegetation history in a 25,000-year lake-sediment record from Lake Challa in southeastern Kenya. These authors imaged and described 61 NPP morphotypes, and related the stratigraphic distribution of some spore types to past changes in rainfall and the regional distribution of vegetation biomes.

A key requirement of understanding past environmental dynamics is to successfully link the fossil record to the distributions, tolerances and associations of living organisms in modern-day ecosystems (Birks and Birks, 1980; Blackford and Innes, 2006); i.e., the uniformitarian principle that is the foundation of geology and paleontology. However, the ecological indicator value of individual NPP morphotypes has traditionally been derived from their stratigraphic association with certain environmental conditions inferred from other palaeoecological indicators, documented in other research or geographical contexts (Blackford and Innes, 2006). This procedure carries risk that the stratigraphic association with those other indicators is fortuitous, and hence that palaeoecological inferences based on the occurrence of those NPPs in a new context are erroneous. A regressive methodological approach, which starts from the association between modern-day NPP assemblages and actual environmental conditions and/or taphonomical processes, is only recently being explored in earnest. Nevertheless, the number of ecological studies focusing on modern NPP diversity and distribution in various substrates is rising (Pinto da Luz *et al.*, 2002; Mulder *et al.*, 2003; Prager *et al.*, 2006; Blackford and Innes, 2006; Medeanic, 2006, Cugny *et al.*, 2010) and reveals their true potential as a means to elucidate past vegetation changes and human activity in the landscape. With regard to tropical Africa, Carreta *et al.* (1998, 1999) studied the modern-day diversity of filamentous fungi on stems and leaves of grassland vegetation, and the presence of coprophilous fungi on wild animal dung (e.g., antilope, buffalo, zebra) from Marula Estate in Kenya. The significance of these studies for palaeoecological applications is unfortunately limited by the lack of diagnostic morphological descriptions.

This paper is the first of two contributions on a collection of modern NPPs recovered from recently deposited bottom sediments in western Ugandan crater lakes. Here we provide best-possible identifications, descriptions and images of all NPP morphotypes encountered, and we evaluate the observed NPPs against taphonomic processes and the species richness of the corresponding living organisms reported in tropical East Africa. The second paper will assess the effects of land-use intensity and habitat differentiation on the observed fungal spore diversity in the study lakes (Gelorini *et al.*, see Chapter 3).

2.2. Material and methods

2.2.1. Environmental setting of the study lakes

The Lake Edward-George branch of the East African Rift System in western Uganda (0°43'N-0°15'S, 29°50'-30°21'E) comprises about 80 maar-crater lakes, distributed over four lake districts identified as Fort Portal, Kasenda, Katwe-Kikorongo and Bunyaruguru (Melack, 1978). Intensifying land use, mainly based on small-scale subsistence farming, has reduced the area covered by natural forest vegetation (tropical high forests and savanna woodlands), to only 20.3% of the total land area (Andrua, 2002). Gently sloping crater walls surrounding the lakes are generally occupied by plantations (banana, coffee, *Eucalyptus*, pine and cotton), annual food crops (sorghum, millet, maize), mixed vegetable gardens (potatoes, beans, cabbage) and meadows (grazed by cows, sheeps and goats). On steeper crater slopes the natural vegetation of some succulent species (such as *Euphorbia dawii*), shrubs and light-demanding ferns has often remained more or less intact. Also a fair number of crater lakes are located in the savannah of Queen Elizabeth National Park, and in the partially undisturbed, partially secondary forest of Kibale National Park. Until a few years ago, only few of these lakes had been the subject of limnological or biological studies (e.g., Beadle, 1932; Kilham, 1971; Melack, 1978; Kizito *et al.*, 1993). More recently their great number and diversity is being exploited to develop regional calibration datasets for a range of palaeoecological proxies (Eggermont and Verschuren, 2004a,b; Rumes *et al.*, 2005; Eggermont *et al.*, 2006, 2010), and some lakes have been the site of palaeohydrological or palaeoecological reconstruction (Ssemmanda *et al.*, 2005; Russell *et al.*, 2007, 2009; Bessems *et al.*, 2008).

During two field campaigns in January-February and August-September 2008 we surveyed 41 Ugandan crater lakes to map the distribution of relatively undisturbed and disturbed vegetation, various types of human land use, patterns and intensity of human occupation, and the abundance ratio of livestock versus large wild herbivores within the crater catchments. The present inventory of NPP diversity in East African lake sediments is based on processed samples from 20 of these 41 surveyed crater lakes (Fig. 2.1), selected to cover the main landscape gradients from moist evergreen forest to grass savannah, and from relatively undisturbed to severely impacted by human activity. Also taken into account are limnological characteristics such as basin morphometry, water chemistry and aquatic production (Table 2.1). The study lakes are all small (surface area 0.01-0.92 km^2), but have a surface-water salinity ranging from 56 µS/cm (freshwater) to 61,100 µS/cm (saline); a trophic status ranging from oligothrophic to hypertrophic; and water-column mixing regimes ranging from shallow polymictic to deep and permanently stratified (Verschuren *et al.*, 2009).

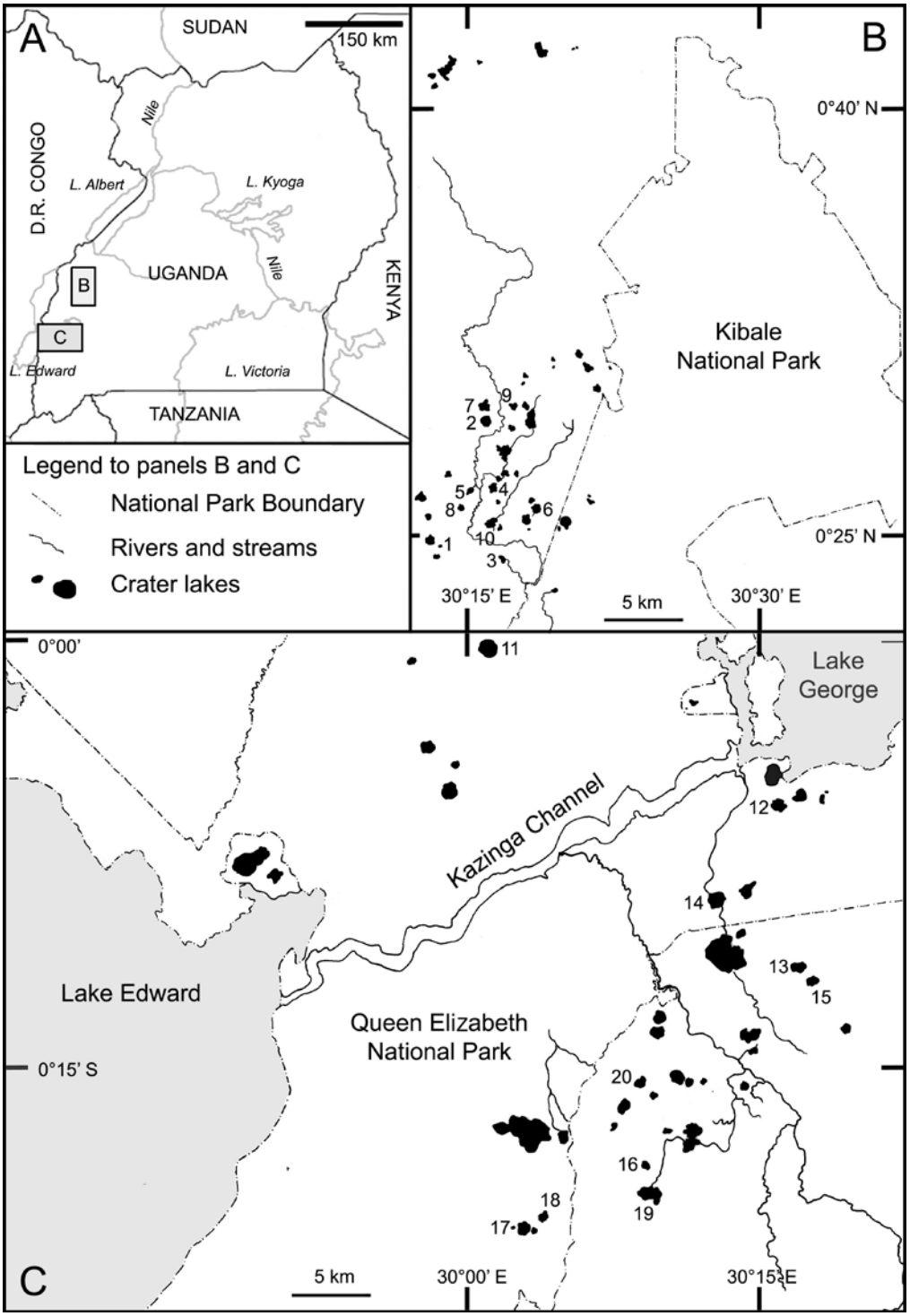

Fig. 2.1. Location of the 20 study lakes in western Uganda (modified from Rumes *et al.*, submitted). Kasenda-cluster: 1. Kanyamukali, 2. Katanda, 3. Kitere, 4. Mahuhura, 5. Mubiro, 6. Murusi, 7. Mwengenyi, 8. Nyarayabana, 9. Nyantonde, 10. Wankenzi; Katwe-Kikorongo-cluster: 11. Kikorongo; Bunyaruguru-cluster: 12. Bagusa, 13. Bugwagi, 14. Chibwera, 15. Ibamba, 16. Kako, 17. Kyogo, 18. Murabyo, 19. Nkugute, 20. Nyungu.

Table 2.1. Selected limnological and land use data of the 20 study lakes. Abbreviations: A_0 (Surface area), Elev (Elevation), Cond (Water conductivity, surface), MAT (Mean annual temperature), TOC (Total organic carbon), HI (Human index), Fo (Forest), Sa (Savannah), Pag (Perennial agriculture), Tpl (Tree plantation), Fa (Fallow land), Aag (Annual agriculture), Pa (Pasture), B (Bare land).

#	Lake/Cluster	A0 *km²*	Elev *m asl*	Cond *µS/cm*	MAT *°C*	TOC *mg/l*	pH	Chl a *µg/l*	HI	Fo *%*	Sa *%*	Pag *%*	Tpl *%*	Fa *%*	Aag *%*	Pa *%*	B *%*
Kasenda																	
1	Kanyamukali	0	1150	920	23,2	8,2	8,6	8,2	3,4	18	0	3	15	45	1	18	0
2	Katanda	0,4	1340	419	21,6	3,3	8,5	1,9	2,0	65	0	4	0	0	23	3	5
3	Kitere	0,1	1160	711	23,1	5,1	9,0	16,8	1,6	65	0	4	0	16	2	10	3
4	Mahuhura	0,2	1254	600	22,3	2,3	9,0	8,4	1,9	55	0	1	13	16	1	13	1
5	Mubiro	0,2	1208	718	22,7	4,5	9,0	1,8	2,8	40	0	2	0	20	1	37	0
6	Murusi	0,2	1226	382	22,5	8,6	8,5	1,3	3,4	25	0	6	2	34	1	30	2
7	Mwengenyi	0,3	1397	352	21,2	3,8	8,4	1,6	3,8	25	0	21	7	5	9	20	13
8	Nyarayabana	0,1	1179	857	22,9	11,2	8,8	9,2	1,7	60	0	0	0	34	5	0	1
9	Nyantonde	0,1	1387	501	21,2	2,9	8,8	2,3	4,7	18	0	9	2	0	41	0	30
10	Wankenzi	0,2	1158	496	23,1	7,6	8,7	13,7	2,4	55	0	11	5	0	14	0	15
Katwe-Kikorongo																	
11	Kikorongo	0,9	915	22400	25,1	51,3	9,6	3,5	0,0	0	100	0	0	0	0	0	0
Bunyaruguru																	
12	Bagusa	0,3	905	61100	25,1	228,4	10,6	670,6	0,0	0	100	0	0	0	0	0	0
13	Bugwagi	0,6	1048	441	24,0	3,2	9,0	3,8	3,9	25	0	45	0	5	5	10	10
14	Chibwera	0,8	971	457	24,6	1,9	8,9	6,7	0,0	0	100	0	0	0	0	0	0
15	Ibamba	0	1073	104	23,8	23,1	6,6	7,5	4,9	0	0	59	5	20	1	0	15
16	Kako	0,2	1396	89	21,2	1,5	8,2	1,2	4,9	0	0	40	6	25	24	5	0
17	Kyogo	0	1113	56	23,5	3,7	6,9	2,0	0,0	100	0	0	0	0	0	0	0
18	Murabyo	0,3	1098	141	23,6	6,3	8,4	5,9	0,0	100	0	0	0	0	0	0	0
19	Nkugute	0,9	1409	121	21,1	5,2	8,7	15,9	4,1	3	0	32	43	3	4	10	5
20	Nyungu	0,1	1172	430	23,0	6,6	9,4	47,1	4,7	0	0	64	0	35	1	0	0

2.2.2. Sampling and analytical procedures

Surface sediments were collected from the deep, central part of each lake using a UWITEC gravity corer, and extruded upright with a fixed-interval sectioning device (Verschuren, 1993) in 1-cm to 5-cm increments depending on local sedimentation conditions. Samples were prepared for NPP analysis according to standard pollen extraction techniques (Faegri *et al.*, 1989) which included sieving at mesh size 212 µm, KOH (10%) treatment, acetolysis, heavy liquid separation (density: 2.0) with sodium polytungstate, and mounting in glycerin jelly. For routine scanning and counting of NPPs an Olympus CX 31 light microscope was used at 400x and 1000x magnification. Identification of known NPP morphotypes was based on comparison with descriptions and illustrations in Wolf (1966, 1967a,b), van Geel (1978, 2001), van Geel and van der Hammen (1978), Pals *et al.* (1980), Bakker and van Smeerdijk (1982), van Geel and Aptroot (2006), Prager *et al.* (2006) and van Geel *et al.* (2011). NPP morphotypes with no apparent analogue in the European NPP literature were identified by reference to primary taxonomic literature, including Ellis (1971, 1976), Ellis and Ellis (1985), Hanlin (1990), Vánky (1994) and Bell (1983) for fungal remains; Hires (1965, 1978) and Tryon and Lugardon (1990) for fern and moss spores; Haas (1996) for microscopic zoological remains and Van Meel (1954), Batten and Grenfell (1996), Komárek and Jankovská (2001) and John *et al.* (2002) for algal remains; and specialised tropical taxonomic literature (e.g. Dennis, 1961; Goh *et al.*, 1997; Goh *et al.*, 1998; Sivichai *et al.*, 1998; Mibey and Kokwaro, 1999).

Since the taxonomy of fungi is in a state of constant flux due to increasing phylogenetic research, there is still no unique generally accepted system at the higher taxonomic level. However, multiple effort in establishing a consistent nomenclature based on molecular phylogenies is currently in progress under the auspices of the '*Assembling the Fungal Tree of Life*' (AFTOL; Celio *et al.*, 2006) project, and the Deep Hypha Research Coordination network (Hibbett *et al.*, 2007). Therefore, all identified fungal remains were classified with reference to the latest taxonomic developments, implemented in the *Index fungorum* (CABI database, Index Fungorum Partnership, 2004). Besides this, fungal species can also have multiple scientific names depending on their life cycle and mode of reproduction. Especially in tropical regions, the anamorphs (asexual states) of fungi are far better represented than teleomorphs (sexual states); often the latter are totally lacking. This frequently hampers the recognition of taxa, since anamorphs often do not contain sufficient diagnostic features to guarantee unambiguous identification (Whalley, 1993). When dealing with anamorphic states of known teleomorphs, we added the scientific name of the teleomorph to the taxonomic description.

The biotic richness and taxonomic complexity encountered in the study material necessitated rigorous application of standard taxonomic principles, to avoid mis-identification and mis-classification. Morphotypes were attributed to known species or genera only when published literature allowed a high degree of taxonomic precision (e.g., *Pediastrum angulosum*) and the taxon's biogeographical distribution in tropical regions could be confirmed. We used 'cf. (conferatur)' when a morphotype resembled a known species or genus (e.g, from the European NPP inventory) but positive association could not be made due to the fragmentary knowledge of the distribution of tropical species (e.g., *Curvularia* cf. *comoriensis*). When morphological resemblance was superficial or ambiguous, 'type' was added to the genus name (e.g., *Cercophora* type). Such morphotypes mostly represent not accurately identifiable but more or less homogeneous entities, based on conservative distinction of general morphological features of shape, size, and surface texture. Thus the word 'type' does not confer the taxonomic significance of a holotype on the described and photographed specimen, but is rather a provisional, not formally named form-species (van Geel 1978). All morphotypes were photographed with a high-resolution Nikon DMX1200 digital camera. They were assigned to an existing type number (HdV) when already described previously by van Geel and others. Due to the affiliation with van Geel *et al.* (2011), first recorded African NPP morphotypes were given a new number, following the numbering system of van Geel *et al.* (2011), preceded by our lab initials UG (*Universiteit Gent*). Each assigned morphotype was classified in a broad taxonomic group, except for spores of ferns and mosses, which were assembled in a single morphological group. This is because both ferns (Pteridophyta) and mosses (Bryophyta) can produce trilete spores, which cannot properly be discerned from each other when identification is uncertain.

To facilitate morphological classification within a broad taxonomic category, some subgroups were formed on the basis of general diagnostic character states such as the presence and number of apertures (pores), germ slits and septa, and surface sculpture (smooth or ornamented). When fungal spores could not accurately be classified into conidia or ascospores, they were simply described as spores. Fungal morphotypes of which the total number of septa or pores was unclear due to fragmentation or unfavourable orientation were classified in the category corresponding with the visible features. Also to enhance consistency in classification, every division between two cavities was defined as a septum. Size differences between the single cells of a spore are described by terms of equality, while the geometry of the spore itself is expressed by terms of symmetry. The reported mean/modal length and width of each morphospecies were based on measurements of one to three intact (if present) and straight specimens from each lake where it was recovered. All descriptive botanical and nomenclatural terms follow the glossary of the Flora of Tropical East Africa (Beentje and Cheek 2003) and some botanical (Stearn 2004) and fungal standard dictionaries (Kirk *et al.*, 2008). Abbreviations of the authorities for all botanic groups, including fungi and algae follow the Brummitt and Powell (1992) standard for botanical names.

2.3. Results

The 20 surface-sediment samples processed for this study yielded a total of 9700 NPP specimens, which could be attributed to 265 distinct morphotypes. Most of these belong to one of six major taxonomic groups: spores and other remains of fungi (198 morphotypes, 74.7%), fern and moss spores (19 morphotypes, 7.2%), microscopic zoological remains (14 morphotypes, 5.3%), colonies, coenobia or zygo-/aplanospores of algae (7 morphotypes, 2.6%) and microscopic aquatic plant remains (1 morphotype, 0.4%). The taxonomic affinity of the remaining 26 morphotypes (9.8%) is at present unknown, but many of them are nevertheless included in the analysis because of their sizable combined contribution to total NPP diversity, and their possible value as palaeoecological indicator once their distribution in relation to relevant environmental variables is established. We also illustrate and provide short diagnoses for NPP taxa (17 types) presented by van Geel *et al.* (2011), to better convey the level of morphological discrimination which we applied when NPP morphotypes are considered identical or distinct, and to allow the possibility that western Ugandan and south-eastern Kenyan populations are eventually found to be distinct. In the following overview, 78 unidentified NPP morphotypes which have only occasionally been observed (≤ 3 specimens) and lacked clear diagnostic characters are not included in the text or illustrations. Table 2.2 categorises all 187 described morphotypes into the four broad abundance classes 'abundant', 'common', 'uncommon' or 'rare', based on their representation in our collection of 9700 recent NPP specimens from western Uganda. In all, 73 of the 265 morphotypes (about 28%) recovered from this Ugandan material could be identified at the family, genus or species level.

Table 2.2. Representation of each described morphotype (in ascending order) in our collection of 9700 recent NPP specimens from western Uganda, categorised into four broad abundance classes 'abundant' (>10% of all specimens), 'common' (1-10%), 'uncommon' (0.1-1.0%) and 'rare' (<0.1%).

a. Abundant (>10%)

UG-1208: *Coniochaeta* spp.

b. Common (1-10%)

HdV-1013: *Cercophora* type, UG-1068, UG-1073, UG-1099: *Brachysporium* spp., UG-1231: *Botryococcus* cf. *neglectus*, UG-1233: *Coelastrum reticulatum*, UG-1236: *Pediastrum boryanum* var. *brevicorne* , UG-1237: *Pediastrum boryanum* cf. var. *Forcipatum*, UG-1274, UG-1315: monoletes undiff.

c. Uncommon (0.1-1%)

HdV-89: *Tetraploa aristata*, UG-1002: *Sporoschisma* spp., HdV-1005: *Brachydesmiella* sp., HdV-1029A: *Curvularia* cf. *intermedia*, HdV-1043: cf. *Lasiodiplodia theobromae*, HdV-1048, HdV-1052: Xylariaceae, HdV-1053: *Dictyosporium* cf. *heptasporum*, UG-1066: *Delitschia* spp., UG-1070: Xylariaceae, UG-1072, UG-1077: cf. Xylariaceae/Sordariaceae/Coniochaetaceae, UG-1078: *Sporidesmium* spp., UG-1080: *Sordaria* spp., UG-1084, UG-1087, UG-1091: *Bactrodesmium* type, HdV-1093: *Gelasinospora* cf. *cratophora* , UG-1098, HdV-1103: *Glomus* sp., UG-1104, UG-1106, UG-1109, UG-1110, UG-1145: cf. *Fusarium* sp., UG-1148, UG-1151, UG-1153, UG-1155, UG-1173, UG-1174: *Rosellinia* sp., UG-1176, UG-1178: *Sordaria* type, UG-1180, UG-1185, UG-1223, UG-1224, UG-1235: *Pediastrum angulosum*, UG-1241: Epidermis of *Nymphaea nouchali*, UG-1243: cf. *Asplenium* sp., UG-1245: *Diporotheca* sp., UG-1246: *Isoetes* type, UG-1253: Polypodiaceae, UG-1254: *Phaeoceros* cf. *carolianus*, UG-1259: *Pteridium aquilinum*, UG-1260: *Coniogramme africana* type, UG-1261: cf. *Pteris/Actiniopteris* sp., UG-1262: *Canalisporium* spp., UG-1277, UG-1286, UG-1303, UG-1307, UG-1309, UG-1311, UG-1316: *Asplenium* type, UG-1319, UG-1320.

d. Rare (<0.1%)

HdV-1018A: *Spegazzinia tessarthra*, HdV-1018B: *Spegazzinia tessarthra*, HdV-1022: *Clasterosporium* sp., HdV-1030: cf. *Byssothecium* sp., HdV-1032, HdV-1049: cf. *Mitteriella ziziphina* , HdV-1058A, UG-1065: Xylariaceae, UG-1071: cf. *Amphirosellinia* sp., UG-1075, UG-1076, UG-1079: *Urocystis* sp., UG-1081, UG-1082, UG-1083, UG-1085, UG-1089, UG-1090: *Sporidesmium* cf. *macrurum*, UG-1092, UG-1095, UG-1096, UG-1097, UG-1101, UG-1105, UG-1107, UG-1111, UG-1112: *Phaeosphaeria* type, UG-1113: *Meliola* sp., UG-1114, UG-1115, UG-1118: cf. *Savoryella lignicola*, UG-1120: *Savoryella curvispora*, UG-1121, UG-1122: cf. *Cookeina* sp., UG-1123, UG-1124, UG-1125, UG-1126, UG-1127, UG-1128: cf. *Kretzschmaria clavus/K. cetrarioides*, UG-1129, UG-1130, UG-1134, UG-1135: cf. Xylariaceae, UG-1137: *Meliola* sp., UG-1138, UG-1139: *Gelasinospora* sp., UG-1141, UG-1142, UG-1144, UG-1147, UG-1150, UG-1157: *Rosellinia* sp., UG-1158, UG-1159, UG-1162, UG-1168, UG-1171: *Apiosordaria* type, UG-1172, UG-1177, UG-1179, UG-1182, UG-1183: cf. *Cercophora* sp., UG-1187, UG-1188, UG-1191, UG-1192, UG-1194, UG-1195, UG-1197, UG-1199, UG-1203, UG-1204, UG-1206: cf. *Acroconidiellina loudetiae*, UG-1211, UG-1216: *Diporotheca* sp., UG-1217, UG-1221, UG-1222, UG-1225, UG-1229, UG-1230, UG-1239: *Scenedesmus* sp., UG-1240: *Spirogyra* sp., UG-1242: *Dryopteris* subg. *Dryopteris*, UG-1247, UG-1248, UG-1249: cf. *Ctenitis/Lastreopsis* sp., UG-1250: *Curvularia* cf. *comoriensis* , UG-1252, UG-1255: *Ophioglossum* subg. *Ophioglossum*, UG-1258, UG-1263: cf. *Grammitis* sp., UG-1264: *Pteris* sp., UG-1268: *Canalisporium variabile*, UG-1276, UG-1280, UG-1281, UG-1282, UG-1284, UG-1285: cf. *Ascodesmis* sp., UG-1288, UG-1291: *Glomus* type, UG-1300, UG-1306, UG-1310, UG-1312, UG-1326, UG-1329: cf. Xylariaceae, UG-1330, UG-1331, UG-1332, UG-1333, UG-1334, UG-1340, UG-1342, UG-1343: cf. *Cirrenalia* sp., UG-1346, UG-1352.

2.3.1. Descriptions and illustrations of African non-pollen palynomorphs

A. Spores and other remains of fungi

A.1. Septated spores

A.1.1. Uniseptate

Type HdV-1043: cf. *Lasiodiplodia theobromae* (Pat.) Griffon & Maubl. (Plate I)

Conidia ellipsoid, subequally and subsymmetrically 2-celled, reddish brown, 27 x 14 µm, slightly thick-walled, not constricted at the septum, with longitudinal ridges (3-4 on surface view). It is not always clear that it concerns conidia because the point of attachment can be indistinct due to unfavourable orientation. This morphotype strongly resembles *Lasiodiplodia theobromae*. It also resembles *Cainia desmazieri* C. Moreau & E. Müll. (syn. *Cainia incarcerata* (Desm.) E. Müll. & Arx), but *C. desmazieri* ascospores are smaller (22 x 7 µm), clearly constricted at the septum and not strictly ellipsoid (Moreau and Müller, 1963). Furthermore, the latter species is restricted to more temperate regions (Krug, 1978), whereas *Lasiodiplodia theobromae* has a worldwide distribution in tropical and subtropical regions. It has a very wide range of host plants, mainly woody plants including fruits and tree crops such as mango, peach, avocado, cacao and *Eucalyptus* (Mohali *et al.*, 2005; Mbenoun *et al.*, 2008).

Type UG-1066: *Delitschia* spp. (Plate I)

Ascospores ellipsoid to broadly fusiform, unequally and unsymmetrically 2-celled, brown to dark brown, 20-30(37) x 9-10(15) µm, smooth, thick-walled, often constricted at the septum; each cell with a straight germ slit parallel to the long axis of the ascospores. Based on differences in size of the ascospores and position of the germ slits (centred or not), this morphotype may include some *Delitschia* species. *Delitschia* species are mostly coprophilous, occurring worldwide on various kinds of dung (Bell, 1983; Hanlin, 1990).

Type UG-1081 (Plate I)

Spores ellipsoid, equally and symmetrically 2-celled, brown, 33 x 26 µm, smooth, very thick-walled, slightly constricted at the short (pseudo-)septum, with two points of attachment (truncate ends).

Type UG-1083 (Plate I)

Spores ellipsoid, equally and symmetrically 2-celled, brown, 52 x 30 µm, smooth, thick-walled, not constricted at the septum, with two points of attachment (truncate ends).

Type UG-1096 (Plate I)

Spores fusiform and slightly curved, subequally and subsymmetrically 2-celled, yellow, 86 x 10 µm, smooth, thick-walled, constricted at the septum, with nearly rounded ends.

Type UG-1105 (Plate I)

Ascospores ellipsoid, equally and symmetrically 2-celled, yellowish brown, 32 x 12 µm, smooth, thick-walled, constricted at the septum, with nearly rounded ends.

Type UG-1106 (Plate I)

Ascospores ellipsoid, (un)equally and (a)symmetrically 2-celled, yellow, 24-32 x 8-11 µm, smooth, slightly thick-walled, constricted at the septum, with slightly tapering ends. Based on small differences in the morphology of the single cells (symmetrical versus asymmetrical, small versus large), this type probably includes different species or genera.

Type UG-1107 (Plate I)

Spores ellipsoid, equally and symmetrically 2-celled, brown, 67 x 38 µm, finely striate, thick-walled, constricted at the septum, with bulged and rounded ends.

Type UG-1110 (Plate I)

Spores ellipsoid, equally and symmetrically 2-celled, yellowish brown, 37-39 x 15-17 µm, densely covered with small, cylindrical free standing processes, thick-walled, constricted at the septum, with slightly tapering ends.

Type UG-1121 (Plate I)

Spores ellipsoid, subequally and subsymmetrically 2-celled, yellow, 22 x 5 µm, covered with a pattern in which parallel or subparallel individual dots are cross-linked to form a reticulum in the grooves (striato-reticulate), thick-walled, constricted at the septum, nearly rounded ends.

Type UG-1122: cf. *Cookeina* sp. (Plate I)

Ascospores ellipsoid to fusiform, equally and symmetrically 2-celled, pale brown, 52 x 30 µm, slightly thick-walled, not constricted at the septum, with tapering ends. *Cookeina* is commonly distributed in the tropics and subtropics, and can be found on fallen angiosperm branches, trunks and occasionally on fruits (Weinstein *et al.*, 2002; Bera *et al.*, 2008).

Type UG-1123 (Plate I)

Spores fusiform, unequally and asymmetrically 2-celled, pale yellow, 42 x 9 µm, smooth, slightly thick-walled, slightly constricted at the septum, with tapering ends.

Type UG-1124 (Plate I)

Spores ellipsoid, subequally and subsymmetrically 2-celled, pale yellow, 32 x 15 µm, smooth, thick-walled, constricted at the septum, and with microreticulate hyaline sheath/coat, ornamented with circular and curving ridges, which are often hollow.

Type UG-1125 (Plate I)

Spores ellipsoid, subequally and subsymmetrically 2-celled, yellow, 19-32 x 6-11 µm, smooth, thick-walled, constricted at the septum. This rather nondescript morphotype probably includes several species or genera.

Type UG-1126 (Plate I)

Spores ellipsoid to fusiform, equally and symmetrically 2-celled, yellow, 24 x 7 µm, finely striate, slightly thick-walled, constricted at the septum, with slightly tapering ends.

Type UG-1129 (Plate I)

Spores ellipsoid to slightly dumbbell-shaped, equally and symmetrically 2-celled, brown, 34 x 14 µm, coarsely reticulate, thick-walled, constricted at the septum.

Type UG-1138 (Plate I)

Spores flask-shaped, unequally and asymmetrically 2-celled, brown to yellow, 37 x 28 µm, smooth, one cell large (28 µm in diameter), dark and thick-walled; other cell small (9 µm in diameter), pale and thin-walled.

Type UG-1148 (Plate I)

Spores flask-shaped, unequally and asymmetrically 2-celled, pale brown to yellow, 20 x 15 µm, smooth, one cell dark, large (15 µm in diameter) and very thick-walled; other cell pale, small (5 µm in diameter) and thin-walled; large cell surrounded by hyaline sheath (present or not) with scabrate pattern.

Type UG-1155 (Plate I)

Spores ellipsoid, equally and symmetrically 2-celled, brown, 23-32 x 12-15 µm, smooth, thick-walled, constricted at the septum; with slightly tapering ends; small opening/pore at one end (only visible in strictly polar or equatorial orientation).

Type UG-1159 (Plate I)

Spores fusiform, equally and symmetrically 2(4?)-celled (end cells may be missing), yellowish brown, 39-45 x 18-22 µm, smooth, thick-walled, constricted at the septum; single cells trapezoidal.

Type UG-1182 (Plate I)

Ascospores ellipsoid, subequally and subsymmetrically 2-celled, dark brown, 25 x 17 µm, smooth, thick-walled, not constricted at the septum; with pale septum.

Type UG-1183: cf. *Cercophora* sp. (Plate I)

Ascospores ellipsoid, unequally and asymmetrically 2-celled, dark brown, 23 x 12 µm, smooth, thick-walled, not con-

stricted at the septum, truncated at one end but tapering at the other, pale septum not truly median; covered with slightly ribbed subhyaline sheath; with apical pore. *Cercophora* species occur worldwide on dung or on decaying wood, culms and other plant debris (Bell, 1983; Hanlin, 1990).

Type UG-1191 (Plate I)

Spores ellipsoid, equally and symmetrically 2-celled, yellowish brown, 88 x 26 µm, smooth, relatively thick-walled, not constricted at the septum; central zone very dark; septum only visible with overexposure to light.

Type UG-1192 (Plate I)

Spores ellipsoid, equally and symmetrically 2-celled, brown, 38 x 18 µm, smooth, thick-walled, slightly constricted at the septum; with subhyaline verrucate sheath/coat.

Type UG-1194 (Plate I)

Spores ellipsoid, equally and asymmetrically 2-celled, yellow, 18 x 7 µm, smooth, thick-walled, slightly constricted at the septum, with point of attachment.

Type UG-1195 (Plate I)

Spores ellipsoid, equally and asymmetrically 2-celled, yellowish brown, 18 x 10 µm, smooth, thick-walled, not constricted at the septum, with thickened point of attachment.

Type UG-1206: cf. *Acroconidiellina loudetiae* M.B.Ellis (Plate I)

Conidia ellipsoid, subequally and subsymmetrically 2-celled, brown, 16-20 x 13 µm, with small echinae (~ 1 µm), thick-walled, sometimes slightly constricted at the septum. It is not always clear that it concerns conidia because the point of attachment can be indistinct due to unfavourable orientation. *Acroconidiellina loudetiae* occurs in Tanzania and can be found on leaves of *Loudetia arundinacea* (Hochst. ex A. Rich.) Steud. in grassland vegetation (Ellis, 1976).

Type UG-1217 (Plate I)

Ascospores ellipsoid, equally and symmetrically 2-celled, brown, 50 x 23 µm, smooth, thick-walled, constricted at the septum; with hyaline sheath (present or not).

Type UG-1252 (Plate II)

Ascospores ellipsoid, equally and symmetrically 2-celled, yellowish brown, 24 x 13 µm, smooth, thick-walled, not constricted at the septum.

Type UG-1333 (Plate II)

Conidia club-shaped, unequally and asymmetrically 2-celled, brown, 28-37 x 18 µm, smooth, not constricted at the septum, slightly ribbed in the central part of the large and thick-walled cell (23-29 x 18 µm), end cell subhyaline, small (5-8

x 5 µm) and thin-walled.

Type UG-1340 (Plate II)

Conidia inversely club-shaped, unequally and asymmetrically 2-celled, brown, 42 x 17 µm, smooth, thick-walled, not constricted at the septum, end cell subhyaline, small (3 x 8 µm) and trapezoidal.

Type UG-1352 (Plate II)

Ascospores fusiform, unequally and asymmetrically 2-celled, yellowish brown, 37 x 15 µm, finely reticulate, slightly thick-walled, slightly constricted at the septum, more tapering towards one end, one cell slightly broader than the other.

A.1.2. Diseptate

Type HdV-1005: *Brachydesmiella* sp. (Plate II)

Conidia lemon-shaped, unequally and symmetrically 3-celled, pale brown to brown, 30-47 x 13-18 µm, smooth, thick-walled; central cell larger (20-37 x 13-18 µm) and darker than end cells (5 x 7 µm), which are broadly trapezoidal. See also van Geel *et al.* (2011). *B. biseptata* has previously been reported from temperate regions (e.g. France, Japan, Canada, United Kingdom), but three *Brachydesmiella* (sub)species (*B. anthostomelloidea* Goh & K.D. Hyde, *B. biseptata* var. *orientalis* V. Rao & de Hoog and *B. caudata* V. Rao & de Hoog) are particularly known from submerged wood in tropical freshwater environments (Sivichai *et al.*, 1998). Based on spore characters, this East African morphotype may refer to *B. anthostomelloidea* or *B. biseptata* var. *orientalis*.

Type HdV-1048 (Plate II)

Ascospores ellipsoid to fusiform, unequally and symmetrically 3-celled, dark brown, 30-32(52) x 15-19(22) µm, smooth, thick-walled, surrounded by a hyaline sheath, central cell larger (22-24(48) x 15-19(22) µm) than end cells (4 x 8 µm), which are paler and conical to tapering. See also van Geel *et al.* (2011).

Type HdV-1049: cf. *Mitteriella ziziphina* Syd. (Plate II)

Conidia club-shaped, unequally and asymmetrically 3-celled, smooth, very thick-walled, with two pale to dark brown larger cells and one more subhyaline smaller and narrower basal cell, 27 x 13 µm, central zone very dark, septum only visible with overexposure to light, other (parts of) cells paler. See also van Geel *et al.* (2011). The genus *Mitteriella*, the anamorphic state of *Schiffnerula*, is parasitic on different species of *Ziziphus*, a genus of spiny shrubs and small trees in the family of Rhamnaceae (Tandon, 1935).

Type UG-1076 (Plate II)

Spores ellipsoid, unequally and subsymmetrically 3-celled, pale brown to brown, 38 x 18 µm, smooth, very thick-walled; two (pseudo-)septa almost invisible; not constricted at the septa; central cell large, end cells small and tapering.

Type UG-1084 (Plate II)

Spores inversely egg-shaped, unequally and asymmetrically 3-celled, 38-50 x 29-30 µm, smooth, thick-walled, slightly constricted at the septa; two cells dark brown and broad; basal cell paler and narrow.

Type UG-1085 (Plate II)

Spores ellipsoid, unequally and asymmetrically 3-celled, dark brown, 36-40 x 24-28 µm, smooth, not constricted at the septa; basal cell paler and thinner. This morphotype may be related to Type UG-1084 (Plate II).

Type UG-1142 (Plate II)

Spores ellipsoid to slightly curved, unequally and asymmetrically 3-celled, brown, 38 x 13 µm, smooth, thick-walled, slightly constricted at the septa, surrounded by a hyaline sheath; cells differing in size; basal cell small, conical to tapering.

Type UG-1151 (Plate II)

Spores flask-shaped, unequally and asymmetrically 3-celled, 21-25 x 14 µm, smooth, thick-walled, constricted at the septa, cells differing in size; one cell very large and almost globose, brown; basal cell subhyaline, small and conical.

Type UG-1199 (Plate II)

Spores flask-shaped, unequally and asymmetrically 3-celled, 46 x 34 µm, smooth, very thick-walled, constricted at the septa, cells differing in size, one cell dark brown, very large and almost globose, basal cell (partly broken) subhyaline and small.

Type UG-1230 (Plate II)

Spores awl-shaped, unequally and asymmetrically 3-celled, yellow, 87 x 10 µm, smooth, thick-walled, with 2 septa at one end and an apiculate appendage at the other end.

Type UG-1331 (Plate II)

Ascospores ellipsoid to fusiform, unequally and subsymmetrically 3-celled, pale brown, 48 x 17 µm, smooth, very thick-walled (thickest in the center), with a small hyaline projection at the base forming a so-called foot cell, not constricted at the septa; (pseudo-)septa thickened.

Type UG-1332 (Plate II)

Conidia ellipsoid, unequally and asymmetrically 3-celled, brown, 34-50 x 21-28 µm (length dependent on the number of preserved cells), smooth or verrucate, thick-walled, not constricted at the septa; zone around widest septum dark; basal cell subhyaline, small and tapering (often missing or partly broken).

Type UG-1334 (Plate II)

Spores inversely egg-shaped, unequally and asymmetrically 3-celled, 18 x 13 µm, smooth, thick-walled, not constricted at the septa; one cell brown, large and almost globose; basal cells subhyaline and tapering.

A.1.3. Triseptate

Type HdV-1029A: *Curvularia* cf. *intermedia* Boedijn (Plate II)

Conidia ellipsoid to fusiform, unequally and asymmetrically 4-celled, yellow, 25-39 x 13-19 µm, smooth, not constricted at the septa, middle septum usually positioned along the median; slightly thick-walled. This *Curvularia* species has currently been differentiated from the Types HdV-1029A-B (see van Geel *et al.*, 2011), which include a symmetrical (i.e. Type HdV-1029A) and asymmetrical (i.e. Type HdV-1029B) 4-celled *Curvularia* species. *Curvularia intermedia*, an anamorphic state of *Cochliobolus*, has been reported from Australia, Papua-New Guinea, Tanzania and the USA, and occurs on *Triticum*, *Zea*, *Oryza* and *Cynodon* (Ellis, 1971).

Type HdV-1030: cf. *Byssothecium* sp. (Plate II)

Ascospores fusiform, oblong and slightly curved, unequally and asymmetrically 4-celled, pale yellow, 60 x 13 µm, smooth, constricted at the middle septum; one central cell more elongated and slightly broader than the other; central cells with thickened walls; end cells subhyaline, with thinner wall. See also van Geel *et al.* (2011). *Byssothecium* can be found on (submerged) wood (Crane *et al.*, 1992).

Type UG-1068 (Plate II)

Spores fusiform, unequally and subsymmetrically 4-celled, 30-38 x 14-15 µm, smooth, not constricted at the septa; central cells dark brown and thick-walled; end cells subhyaline and thinner (frequently absent).

Type UG-1080 (Plate II)

Ascopores ellipsoid, unequally and asymmetrically 4-celled, 45-50(65) x 27-30(40) µm, verrucate, slightly constricted at the septa; central cells large (17-20(27) x 27-30(40), dark brown and thick-walled; end cells 5 µm long, 7-9 µm wide, subhyaline and thin-walled. This morphotype resembles *Savoryella verrucosa* Minoura & T.Muroi, but the ascospores of the latter species are clearly smaller (Ho *et al.*, 1997).

Type UG-1082 (Plate II)

Ascospores ellipsoid, unequally and asymmetrically 4-celled, 42 x 18 µm, smooth (but some protuberances may be caused by corrosion, see Plate II), constricted at the septa; central cells brown, large (18 x 18 µm) and thick-walled; end cells subhyaline, small (3 x 5 µm) and thin-walled. This morphotype may be related to Type UG-1080 (Plate II), which is ornamented, larger and thick-walled. Also some resemblance with Type HdV-1001 (see van Geel *et al.*, 2011) is apparent, but Type UG-1082 is slightly smaller and thin-walled.

Type UG-1089 (Plate II)

Spores ellipsoid to narrowly inversely club-shaped, unequally and asymmetrically 4-celled, pale brown, 23 x 14 µm, smooth, not constricted at the septa, thick-walled; basal cell subhyaline and thin-walled.

Type UG-1090: *Sporidesmium* cf. *macrurum* (Sacc.) M.B.Ellis (Plate II)

Conidia straight, curved or inversely club-shaped to beaklike; conico-truncate and protuberant at the base, unequally and asymmetrically 4-celled, 63-36 x 13-12 µm, smooth, slightly constricted at the septa, thick-walled; cells brown and gradually decreasing in size and colour towards apical part of conidia; end cell subhyaline and strongly tapering. *Sporidesmium macrurum* is mainly distributed in tropical areas (e.g., Brazil, Ceylon, Papua) and occurs on the leaves and leaf-stalks of palms such as *Areca*, *Borassus*, *Cocos*, *Elaeis*, *Licuala*, *Mauritia* and *Phoenix* (Ellis, 1971).

Type UG-1091: *Bactrodesmium* type (Plate II)

Conidia ellipsoid, unequally and asymmetrically 4-celled, 30-45 x 17-30 µm, smooth, thick-walled, slightly constricted at the septa, rounded at one end; septa dark; one central cell often darker than other cells; basal cell subhyaline, truncate and slightly thin-walled. Based on size and morphological variation, this morphotype probably includes different *Bactrodesmium* species, and maybe also other representatives of unknown but similarly looking genera. *Bactrodesmium* can be found worldwide on the wood and bark of various deciduous trees (Ellis, 1971).

Type UG-1092 (Plate II)

Spores ellipsoid, unequally and asymmetrically 4-celled, brown, 25 x 13 µm, smooth, thick-walled, constricted at the septa; basal cell much paler and subhyaline, somewhat smaller and thin-walled.

Type UG-1098 (Plate II)

Ascospores lemon-shaped, unequally and subsymmetrically 4-celled, smooth, dark yellow to pale brown, 50 x 20 µm, slightly constricted at the septa, thick-walled; with microreticulate hyaline sheath; central cells dark and large; end cells paler, conical and rather acute.

Type UG-1111 (Plate II)

Ascospores cylindrical to slightly dumbbell-shaped, unequally and asymmetrically 4-celled, yellow, 38-45 x 10-11 µm, striate, thick-walled, slightly constricted at the septa, end cells slightly broader and swollen.

Type UG-1112: *Phaeosphaeria* type (Plate III)

Ascospores narrowly fusiform, unequally and asymmetrically 4-celled, brown, 25 x 6 µm, longitudinally and finely striate, thick-walled, slightly constricted at the septa; one central cell enlarged; end cells tapering. This morphotype resembles *Phaeosphaeria*, in which one central cell is commonly enlarged (Shoemaker and Babcock, 1989), but may also be related to other genera, which have similarly looking ascospores (such as *Lophiostoma* and *Leptosphaeria*) (Ellis and Ellis, 1985). Species of *Phaeosphaeria* are known as pathogens on cereals, wild grasses, sedges and rushes (Shoemaker and Babcock, 1989).

Type UG-1118: cf. *Savoryella lignicola* E.B.G.Jones & R.A.Eaton (Plate III)

Ascospores ellipsoid to fusiform, unequally and asymmetrically 4-celled, 27-30 x 11-12 µm, smooth, slightly constricted at the septa; central cells brown, large (12-18 x 11-12 µm) and thick walled; end cells subhyaline, small (2 µm long, 5 µm wide) and thin-walled. Based on shape and the length to width ratio this morphotype may refer to *Savoryella lignicola*, which was first reported from a water cooling tower, but has now been recorded from natural habitats throughout the world (e.g., Australië, Brunei, Hong Kong, Sri Lanka, United Kingdom). It appears to be the only *Savoryella* species encountered in both marine and freshwater habitats, although it is doubtful at the molecular level if the similarly looking ascospores from both habitats in fact belong to the same species (Ho *et al.*, 1997).

Type UG-1120: *Savoryella curvispora* W.H.Ho, K.D.Hyde & Hodgkiss (Plate III)

Ascospores curved, unequally and symmetrically 4-celled, 30 x 8 µm, smooth; central cells yellow to brown, relatively large and thick-walled; end cells subhyaline, small and thin-walled. This type may be related to the European type HdV-715. *Savoryella curvispora* has been reported from submerged wood in Mauritius, Taiwan, Malaysia, Philippines and South Africa (Ho *et al.*, 1997).

Type UG-1137: *Meliola* sp. (Plate III)

Ascospores ellipsoid to oblong, unequally and asymmetrically 4-celled, slightly curved, brown, 53 x 16 µm, smooth, thick-walled, slightly constricted at the septa. *Meliola* species are found as parasites on leaves and stems of a wide range of hosts in the tropics. In East Africa they have been found on *Acacia*, *Cynanchum*, *Periploca*, *Secamone, Tylophora, Pergularia* and *Warburgia* (Mibey and Kokwaro, 1999).

Type UG-1145: cf. *Fusarium* sp. (Plate III)

Conidia narrowly fusiform, slightly curved, unequally and asymmetrically 4-celled, pale yellow, 37-42 x 9 µm, smooth, thick-walled, slightly constricted at the middle septum, and often with a small hyaline projection at the base forming a so-called foot cell. *Fusarium* species are anamorphic states of *Gibberella* sp. and commonly found on dead herbaceous plants (Ellis and Ellis, 1985). They occur in the normal mycoflora of staple foods such as rice, maize, bean and soybean. While most species are more frequent in tropical and subtropical areas, some inhabit soil in cold climates (Pitt *et al.*, 1994).

Type UG-1150 (Plate III)

Ascospores fusiform, subequally and symmetrically 2(4)-celled, 28 x 9 µm, smooth, slightly constricted at the septa; two central cells pale brown and thick-walled; subhyaline end cells probably absent. This morphotype may be related to Type UG-1068 (Plate II), but the wall of Type UG-1150 is thin-walled.

Type UG-1162 (Plate III)

Spores ellipsoid, unequally and subsymmetrically 4-celled, brown, 22 x 11 µm, smooth, slightly thick-walled, not constricted at the septa.

Type UG-1204 (Plate III)

Conidia narrowly club-shaped to oblong, unequally and asymmetrically 4-celled, yellow, 32 x 9 µm, smooth, thick-walled, slightly constricted at the septa; basal cells somewhat paler.

Type UG-1320 (Plate III)

Spores ellipsoid to lemon-shaped, unequally and subsymmetrically 4-celled, 50-57 x 29-31 µm, smooth, constricted at the septa; central cells dark brown, large and very thick-walled; end cells subhyaline, small and thin-walled (often damaged or absent). This morphotype may be related to Type UG-1080 (Plate II).

Type UG-1342 (Plate III)

Spores ellipsoid, unequally and asymmetrically 4-celled, 27 x 13 µm, striate in a slightly spiralic pattern, slightly constricted at the septa; central cells brown, large and thick-walled; end cells subhyaline, small and thin-walled (often damaged or absent).

A.1.4. Multiseptate

Type UG-1002: *Sporoschisma* spp. (Plate III)

Conidia cylindrical with flattened ends, unequally and subsymmetrically 4- or 6-celled, 50-61 x 12-14 µm, smooth, thick-walled, slightly constricted at the septa; central cells pale to dark brown, almost of equal size; end cells paler, short, discoid or somewhat truncate, flattened or slightly rounded at free ends (often absent). These conidia probably belong to *Sporoschisma saccardoi*. Specimens of which the end cells are missing, are possibly fragmented conidia of the same species (due to decay) or 3-septate conidia of other *Sporoschisma* species (e.g., *S. juvenile* Boud., *S. mirabile* Berk. & Broome). *Sporoschisma saccardoi* is distributed in tropical (e.g., Indonesia, Taiwan, Ecuador, and South Africa) and more temperate regions (e.g., Europe). It is mainly found on submerged wood in freshwater habitats (Goh *et al.*, 1997).

Type HdV-1022: *Clasterosporium* sp. (Plate III)

Conidia straight, curved or inversely club-shaped to beaklike; conico-truncate and protuberant at the base, unequally and asymmetrically 5- or more celled, ca. 40-75 x 8-9 µm (length dependent on the number of septa), striate, thick-walled, slightly constricted at the septa; cells brown and gradually decreasing in size and colour towards apical part of conidia; end cell subhyaline and strongly tapering. See also van Geel *et al.* (2011). *Clasterosporium* can be found on different plants, of which some are frequently subjected to periodic flooding, such as sedges (Ellis, 1971, Ellis and Ellis, 1985).
Type UG-1075 (Plate III)

Spores ellipsoid to broadly fusiform, unequally and subsymmetrically 5-celled, dark yellow to pale brown, 37-50 x 16-20 µm, microreticulate, thick-walled, costricted at the septa; with hyaline sheath (present or not).

Type UG-1078: *Sporidesmium* spp. (Plate III)

Conidia straight, slightly curved and narrower towards the ends, unequally and asymmetrically 11- or more celled (often

broken), dark yellow to pale brown, ca. 47-105 x 8-13 µm (length dependent on the number of septa), smooth, very thick-walled, constricted at the septa. This morphotype probably includes different *Sporidesmium* species. *Sporidesmium* has a worldwide distribution (e.g., Australia, England, India, Tanzania, and the United States) and is common on (fallen) leaves, rotten wood and dead culms of temperate (e.g., *Tilia*, *Sambucus*, *Alnus*) and tropical plants (e.g., *Cissus*, *Cordia*, *Cajanus*, *Eucalyptus, Jasminum*, and *Terminalia*) (Ellis, 1976).

Type UG-1097 (Plate III)

Spores (or hypha?) rod-shaped, pale yellow, unequally and asymmetrically 6- or more celled (partly broken), 125 x 10 µm, smooth, thick-walled, not constricted at the septa; individual cells variable in length.

Type UG-1099: *Brachysporium* spp. (Plate III)

Conidia broadly fusiform, unequally and subsymmetrically 5(6)-celled, 30-52 x 17-27 µm, smooth, thick-walled, not constricted at the septa; central cell dark brown and very large; other cells progressively paler and smaller towards the end. Younger conidia are generally paler than maturing ones. Based on size differences, this morphotype can probably be attributed to different (tropical) *Brachysporium* species, in which Type HdV-1024 (see van Geel *et al.*, 2011) is included. *Brachysporium* is distributed worldwide and is commonly isolated from rotten wood and bark of various trees and shrubs (Ellis, 1971).

Type UG-1104: cf. *Podosporium rigidum* Schwein. (Plate III)

Conidia straight, curved or inversely club-shaped to beaklike; funnel-shaped at the base, unequally and asymmetrically 5- or more celled (often broken), ca. 50-62 x 12 µm (length dependent on the number of septa), smooth, thick-walled, slightly constricted at the septa; cells brown and gradually decreasing in size and colour towards apical part of conidia; end cell subhyaline and strongly tapering. *Podosporium rigidum* can be found on dead stems and branches of plants, such as *Ampelopsis* and *Rhus* (Ellis, 1971).

Type UG-1113: *Meliola* sp. (Plate III)

Ascospores oblong to rarely subellipsoid, unequally and asymmetrically 5-celled, brown, 38-45 x 12-18 µm, smooth, thick-walled, constricted at the septa. For distribution and ecology of *Meliola* see Type UG-1137 (A.1.3.).

Type UG-1127 (Plate III)

Conidia inversely club-shaped, unequally and asymmetrically 5-celled, yellow, 33-41 x 6-11 µm, microreticulate, thick-walled, slightly constricted at the septa.

Type UG-1147 (Plate III)

Spores fusiform, unequally and symmetrically 6- or more celled (partly broken), pale yellow, 50 x 15 µm, smooth, thick-walled, slightly constricted at the septa; middle septum median.

Type UG-1203 (Plate III)

Conidia fusiform and slightly curved, unequally and asymmetrically 7- or more celled (partly broken), 99 x 13 µm, finely striate, thick-walled, slightly constricted at the septa; cells pale brown and large at the basis, subhyaline and smaller towards the ends.

Type UG-1250: *Curvularia* cf. *comoriensis* Bouriquet & Jauffret ex M.B.Ellis (Plate III)

Conidia inversely club-shaped and slightly curved, unequally and asymmetrically 5-celled, yellow, 45-60 x 13-15 µm, smooth, thick-walled, not constricted at the septa. *Curvularia comoriensis* has previously been found on *Cymbogon* in Congo and on the Comoro Islands (Ellis, 1971).

Type UG-1330 (Plate III)

Conidia inversely club-shaped, slightly curved, unequally and asymmetrically 7- or more celled, pale yellow, 50 x 15 µm, smooth, thick-walled, not constricted at the septa.

Type UG-1343: cf. *Cirrenalia* sp. (Plate III)

Conidia spiral-shaped, subglobose, unequally and asymmetrically 8-celled, brown, 31 µm in diameter, smooth, thick-walled, slightly constricted at the septa; cells increasing in diameter from base to end. Fourteen species are described in the genus *Cirrenalia*, of which 7 species are marine lignicolous and 7 are terrestrial, mostly occurring on bark and wood and often in wet habitats. This morphotype probably refers to one of the seven known terrestrial species (Ellis, 1976; Somrithipol *et al.*, 2002, Zhao and Liu, 2005)

A.1.5. Muriform

Type HdV-89: *Tetraploa aristata* Berk. & Broome (Plate IV)

Conidia ellipsoid to rectangular, 3-4 columns with 4 cells to each column, yellowish brown, 35-40 x 20-25 µm, verruculose, thick-walled; terminating in septate appendages, 12-80 µm long (frequently broken), 5-8 µm wide. See also van Geel *et al.* (2011). *Tetraploa aristata* is widespread, usually found on leaf bases and stems of host plants (such as *Andropogon*, *Carex*, *Cyperus*, *Juncus*, *Musa*, *Phaseolus*, *Phoenix*, *Phragmites* and *Zea*) just above the soil (Ellis, 1971).

Type HdV-1053: *Dictyosporium* cf. *heptasporum* (Garov.) Damon (Plate IV)

Conidia broadly ellipsoid, composed of ca. 7 rows of cells, pale yellow, 42-71 x 21-25 µm, smooth, slightly thick-walled, slightly constricted at the septa. See also van Geel *et al.* (2011). Contrary to other *Dictyosporium* species, the conidia of *D. heptasporum* are not flattened in one plane. *D. heptasporum* has been observed on decaying and submerged wood and stems in Europe, India and North America (Ellis, 1971).

Type UG-1109 (Plate IV)

Cluster of 5-10 globose fungal cells, brown, 34 x 30 µm, smooth, thick-walled; individual cells variable in size. This type

may be related to the European Type HdV-200, which suggests the presence of relatively dry microhabitats (van Geel *et al.*, 1989).

Type UG-1262*: *Canalisporium* spp. (Plate IV)

Conidia ellipsoid to inversely egg-shaped, pale to dark brown, 48-68 x 25-32 µm, smooth, thick-walled, slightly constricted at the septa; some septa strongly pigmented and heavily accentuated (septal canals often badly visible); with 3 columns of septa, and 4-6 rows of septa, a base comprising typically one or three thin-walled, subhyaline small cells (2-3 x 1.5-2 µm) in a row (sometimes missing). This type probably includes different *Canalisporium* species, such as *C. pulchrum* (Hol.-Jech. & Mercado) Nawawi & Kuthub. and *C. kenyense* Goh, W.H.Ho & K.D.Hyde (Goh et al, 1998). Species of *Canalisporium* are common saprophytes on rotten and submerged wood (e.g., on bamboo culms, palm rachis) and have a pan-tropical distribution. The genus has previously been recorded in Cuba, India, Kenya, Malaysia, Uganda and Australia (Goh *et al.*, 1998, see also table I in Goh and Hyde, 2000).

*Identification of *Canalisporium pulchrum* has been revised after Goh *et al.* (1998). *Canalisporium pulchrum* and *Canalisporium kenyense* were formerly comprised into the species *Berkleasmium pulchrum* Hol.-Jech & Mercado sensu P.M.Kirk.

Type UG-1268: *Canalisporium variabile* Goh & K.D.Hyde (Plate IV)

Conidia cubical, pale brown, 25 x 23 µm, smooth, thick-walled, moderately to strongly constricted at conidial septa (cells appear to bulge in outline); septa unpigmented, thin and septal canals clearly visible; with 2(-3) major columns of septa, 2 rows of septa, and a single basal cell, which is subhyaline and thin-walled. *C. variabile* is a recently described *Canalisporium* species, found on submerged wood and decaying palm raches in Australia (Goh and Hyde, 2000).

Type UG-1274 (Plate IV)

Conidia ellipsoid, subglobose or club-shaped, with more than 10 septated pale to dark brown cells (slightly variable in size and shape), and subhyaline basal cell(s) (sometimes missing), 26-33 x 17-22 µm, smooth, thick-walled, constricted at the septa. This morphotype may correspond with several different species due to its scarcity of diagnostic features.

Type UG-1276 (Plate IV)

Spores cylindrical, formed by a cluster of ~12 cells or more, variable in size and shape, dark brown, 50 x 17 µm, smooth, thick-walled, constricted at the septa; basal cells often slightly paler than central cells.

Type UG-1277 (Plate IV)

Spores globose to subglobose, 40-57 x 40-43 µm, smooth, with more than 20 brown, thick-walled septated cells (slightly variable in size and shape), and some subhyaline, thin-walled basal cell(s) (may be missing), slightly constricted at the septa. This morphotype differs from Type UG-1274 (Plate IV) by its bigger size and higher amount of cells. Type UG-1274 and UG-1277 may be produced by (morphologically) related species.

A.1.6. Tetrads

Type HdV-1018A-B: *Spegazzinia tessarthra* (Berk. & M.A.Curtis) Sacc. (Plate IV)

This fungal morphotype occurs in two more or less distinct types. Conidia of Type A are cruciately (cross-shaped) septate, equally and symmetrically 4-celled, brown, 10-16 µm in diameter, echinate (spines up to 3 µm long), thick-walled. Conidia of Type B are cruciately septate, equally and symmetrically 4-celled, brown, 14-18 µm in diameter, smooth, thick-walled. See also van Geel *et al.* (2011). *Spegazzinia tessarthra* is widespread in tropical and subtropical regions. It is particularly common on dead leaves and stems of various monocotyledonous plants, such as maize, grasses and *Andropogon* (Ellis, 1971; Subramanian, 1971).

A.2. Non-septated - Amerosporae

A.2.1. With one or more germ slits

A.2.1.1. One germ slit

Type HdV-1052: Xylariaceae (Plate IV)

Ascospores ellipsoid to subfusiform, inequilaterally one-celled, yellowish brown, 37-40 x 13-16 µm, smooth, thick-walled and with tapering ends; germ slit nearly straight and running over the entire spore-length near the flattened side. See also van Geel *et al.* (2011). This morphotype belongs to the family Xylariaceae, but further identification at the genus and species level is currently difficult because of possible affiliation with different genera (such as *Rosellinia* and *Hypoxylon*) or tropical species, which are still unknown. Xylariaceae are widely spread in temperate and tropical regions throughout the world. Apart from their endophytic existence, they are best known as saprotrophic wood-rotting fungi, as inhabitants of dung or litter and pathogens of a range of plants (Whalley, 1993).

Type UG-1065: Xylariaceae (Plate IV)

Ascospores slightly ellipsoid, inequilaterally one-celled, dark brown, 33-35 x 14-17 µm, smooth, thick-walled and with tapering ends; germ slit sigmoid and running over the entire spore-length near the less convex side (not always visible). For distribution and ecology see Type HdV-1052 (A.2.1.1).

Type UG-1071: cf. *Amphirosellinia* sp. (Plate IV)

Ascospores ellipsoid to cylindrical, inequilaterally one-celled, pale brown to brown, 29-30 x 8 µm, smooth, thick-walled and with narrowly to broadly rounded ends; germ slit sigmoid and running transversally over the entire width of the spore. Based on its size and the position and length of the germ slit on the ventral/transversal side, this morphotype may possibly refer to *Amphirosellinia*, a new Xylariaceae genus which currently includes two former *Rosellinia* species (*R. evansii* Læssøe & Spooner and *R. americana* (Petr.) Rappaz) and three new species, growing inside the bark of dicotyledonous trees (Ju *et al.*, 2004).

Type UG-1073 (Plate IV)

Ascospores globose to ellipsoid, equilaterally one-celled, brown, 17-24 x 13-17 µm, smooth, thick-walled, covered by a hyaline sheath (of which the slit may be a part); germ slit straight and running over the entire spore-length. This morphotype is probably strongly related to Type UG-1072 (Plate V).

Type UG-1077: cf. Xylariaceae/Sordariaceae/Coniochaetaceae (Plate IV)

Ascospores ellipsoid, equilaterally one-celled, brown to dark brown, 14-30 x 7-12 µm, smooth, thick-walled; germ slit straight and running over the entire spore-length. Based on size variability, this morphotype may include several species which possibly belong to the families Coniochaetaceae, Sordariaceae or Xylariaceae (Dennis, 1961; Hanlin, 1990; Lu *et al.*, 2000; Petrini, 2003).

Type UG-1128: cf. *Kretzschmaria clavus* (Fr.) Sacc./*K. cetrarioides* (Welw. & Curr.) Sacc. (Plate IV)

Ascospores ellipsoid to subfusiform, inequilaterally one-celled, pale brown, 32 x 10 µm, smooth, thick-walled and with tapering ends; germ slit straight and running about 1/2 of the spore-length near the flattened side. *Kretzschmaria* (syn. *Ustulina*) species are found worldwide throughout temperate and tropical regions and occur on plant debris and dead wood (Rogers and Ju, 1998). Only two distinct species, *K. clavus* and *K. cetrarioides*, seem to be distributed in tropical Africa (Dennis, 1961).

Type UG-1157: *Rosellinia* sp. (Plate IV)

Ascospores ellipsoid to fusiform, inequilaterally one-celled, brown to dark brown, 25 x 6 µm, smooth, thick-walled and with tapering ends; germ slit sigmoid and running about 3/4 of the spore-length. This morphotype resembles *R. dingleyae* L.E.Petrini, a new *Rosellinia* species encountered in New Zealand (Petrini, 2003), but the East African ascospores are slightly smaller and may thus represent an unknown tropical *Rosellinia* species. *Rosellinia* is widespread in temperate and tropical regions, and commonly found on decaying herbaceous stems and wood. In the tropics some species (such as *R. necatrix* Berl. ex Prill.) are particularly known as root pathogens, exclusively in plantations of cultivated trees and shrubs (Petrini, 1993).

Type UG-1174: *Rosellinia* sp. (Plate IV)

Ascospores ellipsoid to fusiform, inequilaterally one-celled, dark brown, 30-38 x 8-10 µm, smooth, with nearly rounded to slightly tapering ends, thick-walled; germ slit straight and running over the entire spore-length near the flattened side. For distribution and ecology see Type UG-1157 (A.2.1.1.).

Type UG-1177 (Plate IV)

Ascospores ellipsoid, inequilaterally one-celled, dark brown, 29 x 12 µm, smooth, thick-walled, truncate at one end but tapering at the other, covered by two polar hyaline caps, of which only the pedicel is clearly visible; germ slit straight and running over the entire spore-length.

Type UG-1208: *Coniochaeta* spp. (Plate IV)

Ascospores ellipsoid to globose, equilaterally one-celled, dark brown, 20-24 x 18-24 µm, smooth, thick-walled; germ slit straight, running over the entire spore-length and enclosed by a pale brown zone. When seen in polar view or a particular side view, the germ slit may be invisible; often the ascospore is also disrupted by a weakening of the germ slit. Based on small differences in size and shape, this morphotype may include *Coniochaeta ligniaria* (Grev.) Massee (Type HdV-172, see van Geel *et al.*, 2011) and several other *Coniochaeta* species (Hawksworth and Yip, 1981). *Coniochaeta* species are common on dead wood, plant material and dung (Hanlin, 1990; Asgari *et al.*, 2007).

Type UG-1211 (Plate IV)

Ascospores ellipsoid to lemon-shaped, inequilaterally one-celled, dark brown, 35-30 x 17-20 µm, smooth, very thick-walled, with slightly tapering ends; germ slit straight and running over the entire spore length. When seen from one particular side, the germ slit may be invisible.

Type UG-1329: cf. Xylariaceae (Plate IV)

Ascospores fusiform, inequilaterally one-celled, brown, smooth and thick-walled, cell 68 µm long, 10 µm wide, extremities needle-shaped and 35 µm long; germ slit (17 µm) short and centered near the flattened side. Apart from the atypical extremities, this morphotype appears to be affiliated with the family of Xylariaceae, and perhaps with the genus *Rosellinia* (Petrini, 2003).

A.2.1.2. Two germ slits

Type UG-1070: Xylariaceae (Plate IV)

Ascospores ellipsoid, inequilaterally one-celled, yellow, 18-21 x 7-9 µm, smooth, slightly thick-walled and with nearly rounded ends; two spiral germ slits running over the entire spore-length each at one side. This morphotype, which resembles the European Type EMA-55 (apart from the presence of one spiral germ slit, see Barthelmes *et al.*, 2006), is probably affiliated with the Xylariaceae. For distribution and ecology see Type HdV-1052 (A.2.1.1.).

A.2.2. Without germ slit

A.2.2.1. Aporate

A.2.2.1.1. Ornamented

Type HdV-1032 (Plate V)

Ascospores ellipsoid, equilaterally one-celled, brown, 20 x 14 µm, microreticulate, slightly thick-walled.

Type HdV-1058A (Plate V)

Spores globose to subglobose, equilaterally one-celled, yellowish brown, 12 µm in diameter, coarsely echinate (spines ~

1-2 µm), thick-walled. See also van Geel *et al.* (2011).

Type UG-1079: *Urocystis* sp. (Plate V)

Spore balls globose, composed of one yellowish brown spore, 11-14 µm in diameter, surrounded by small subhyaline cells, 3 µm in diameter, attached to the dark central cell; spore balls often preserved as clusters of two or more specimens. *Urocystis* is widespread, mostly found in leaves and stems, and less often in flowers, seeds and roots of different host plants within the families Cyperaceae, Brassicaceae, Poaceae, Ranunculaceae, etc. (Vánky, 1994; van Geel *et al.*, 2010).

Type UG-1095 (Plate V)

Spores ellipsoid, inequilaterally one-celled, yellow, 19 x 14 µm, thick-walled, tapering at one end, ornamented with a fingerprint pattern running predominantly in the longitudinal direction.

Type UG-1168 (Plate V)

Spores ellipsoid, inequilaterally one-celled, yellowish brown, 32 x 15 µm, thick-walled, with subhyaline sheath/coat forming high curving ridges which are partially anastosmosing.

Type UG-1281 (Plate V)

Conidia globose, equilaterally one-celled, yellowish brown, 18-20 µm in diameter, verrucose, thick-walled.

Type UG-1282 (Plate V)

Spores globose to subglobose, equilaterally one-celled, yellow, 15-20 µm in diameter, thick-walled, with the subhyaline sheath/coat developed into fairly high, coarse ridges which may or may not anastomose, and with small spines present on the tops of the ridges.

Type UG-1285: cf. *Ascodesmis* sp. (Plate V)

Ascospores subglobose, inequilaterally one-celled, dark brown, 38 µm in diameter, irregularly and coarsely verrucose (individual knobs ~7 µm thick), thick-walled. *Ascodesmis* is widespread on dung of both wild and domesticated animals (Hanlin, 1990).

A.2.2.1.2. Not ornamented

Type UG-1072 (Plate V)

Ascopores globose to ellipsoid, equilaterally one-celled, brown, 14-22 x 10-17 µm, smooth, thick-walled, mostly covered with a hyaline sheath. This morphotype may be strongly related to Type UG-1073 (Plate IV), which has a slit running over the entire spore-length (probably as part of the hyaline sheath).

Type UG-1101 (Plate V)

Spores subglobose, subequilaterally one-celled, brown to dark brown, 45 x 39 µm, smooth and thick-walled, often covered by a hyaline sheath.

Type HdV-1103: *Glomus* sp. (Plate V)

Chlamydospores globose to subglobose, subequilaterally one-celled, yellow, 55 x 50 µm, smooth and thick-walled, mostly with hyphate attachment. This East African type is almost certainly not *Glomus* cf. *fasciculatum* (Thaxt.) Gerd. & Trappe (European Type HdV-207), which occurs in more temperate regions (van Geel *et al.*, 1989) and is probably also related to Type UG-1291 (Plate V). The genus *Glomus* includes some 132 known species, which are hard to distinguish on the basis of their chlamydospores. *Glomus* is the largest genus of arbuscular mycorrhizal fungi, occurring on a variety of host plants and indirectly indicative for soil erosion when recorded in a lake deposit (van Geel *et al.*, 1989; van Geel *et al.*, 2011).

Type UG-1135: cf. Xylariaceae (Plate V)

Conidia ellipsoid, inequilaterally one-celled, yellow, 22 x 9 µm, smooth and thick-walled, truncate at one end but tapering at the other. This morphotype may be the anamorphic state of a Xylariaceae species. For distribution and ecology see Type HdV-1052 (A.2.1.1.).

Type UG-1141 (Plate V)

Spores globose to subglobose, subequilaterally one-celled, dark brown, 19-27 x 19-24 µm, smooth, very thick-walled (3-4 µm thick).

Type UG-1144 (Plate V)

Ascospores ellipsoid to fusiform, subequilaterally one-celled, pale brown, 20 x 7 µm, smooth and slightly thick-walled, tapering at both ends; with the paler and thinner girdle running transversally over the entire width of the spore.

Type UG-1173 (Plate V)

Ascospores ellipsoid to fusiform, (in)equilaterally one-celled, yellow to brown, 15-24 x 6-12 µm, smooth, slightly thick-walled and slightly tapering at both ends.

Type UG-1176 (Plate V)

Ascospores ellipsoid to fusiform, inequilaterally one-celled, yellow to brown, 11-27 x 4-10 µm, smooth, slightly thick-walled, slightly tapering at both ends, with one side flattened. Judging by observed variability in morphology and size, this morphotype probably represents various species.

Type UG-1188 (Plate V)

Conidia slightly pyriform, inequilaterally one-celled, brown to dark brown, 24-27 x 17-23 µm, smooth, thick-walled and

truncate at one end.

Type UG-1197 (Plate V)

Spores ellipsoid, inequilaterally one-celled, brown, 12-17 x 8-12 µm, smooth and thick-walled, often covered by hyaline sheath at truncate end.

Type UG-1291: *Glomus* type (Plate V)

Chlamydospores broadly ellipsoid, equilaterally one-celled, yellow, 72 x 57 µm, smooth, slightly thin-walled, with hypha-like attachment/appendix. This morphotype probably belongs to the mycorrhizal fungi, and may represent *Glomus* or a related tropical genus. It differs from the common *Glomus* chlamydospores (see Type HdV-1103, Plate V) by its distinctly ellipsoid shape and thinner wall. For distribution and ecology see Type HdV-1103 (A.2.2.1.).

A.2.2.2. Porate

A.2.2.2.1. Monoporate

Type HdV-1013: *Cercophora* type (Plate V)

Ascospores ellipsoid, inequilaterally one-celled, brown, 15-30 x 10-15 µm, smooth and thick-walled, tapering at one end but truncate at the other, often with one less convex side; pore often in a subpolar position and slightly protruding. See also van Geel *et al.* (2011). This morphotype differs from *Apiosordaria* type (Type UG-1171) by its more ellipsoid and often asymmetrically oblong form. This type probably represents different species which may be attributed to different genera such as *Cercophora*, *Podospora, Triangularia*, *Tripterospora* and *Zopfiella*. All of these genera are difficult to distinguish by their single ascospores (Bell, 1983; Khan and Krug, 1989b).

Type UG-1158 (Plate V)

Ascospores ellipsoid, inequilaterally one-celled, brown, 54 x 23 µm, smooth and thick-walled, tapering at one end but truncate at the other; pore slightly protruding.

Type UG-1171: *Apiosordaria* type (Plate V)

Ascospores broadly ellipsoid to subglobose, inequilaterally one-celled, brown, 20-30 x 15-20 µm, smooth and thick-walled, tapering at porate end but truncate at the other (originally with hyaline appendage); pore slightly protruding. This morphotype differs from *Cercophora* type (Type HdV-1013) by its more globose and shortened form. It superficially resembles the temperate-region species *Apiosordaria verruculosa* (C.N.Jensen) Arx & W.Gams (Type HdV-169, see van Geel and Aptroot, 2006), but ascospores of the latter are usually smaller. This East African type may therefore represent a tropical *Apiosordaria* species or an unknown tropical species of the Sordariales. *Apiosordaria* is particularly known from soil isolates, dung and plant debris (Bell, 1983; Hanlin, 1990).

Type UG-1172 (Plate V)

Ascospores ellipsoid, inequilaterally one-celled, brown, 32-35 x 14-19 µm, smooth and thick-walled, tapering at porate

end but truncate at the other; pore slightly protruding.

Type UG-1180: *Sordaria* spp. (Plate V)

Ascospores ellipsoid, equilaterally one-celled, brown, 17-36 x 11-24 µm, smooth and thick-walled, tapering at both ends; pore slightly protruding. Based on size variability, this type may include several Sordaria species. *Sordaria* mainly occurs on dung substrates, but it can also been found on seeds and in soil (Bell, 1983; Hanlin, 1990).

Type UG-1185 (Plate V)

Ascospores broadly fusiform, inequilaterally one-celled, yellowish brown to brown, 20-28 x 10-13 µm, smooth and thick-walled, tapering at both ends, often with one side flattened; pore slightly protruding. Based on small differences in size and morphology, this morphotype may represent several unknown species.

A.2.2.2.2. Diporate

[Ornamented]

Type HdV-1093: *Gelasinospora* cf. *cratophora* R.S.Khan & J.C.Krug (Plate VI)

Ascospores ellipsoid to subglobose, equilaterally one-celled, dark brown, 30-33 x 20-22 µm, covered by hyaline pits about 1 µm in diameter, thick-walled; with one or two slightly protruding pores, concentrated near both ends. See also van Geel *et al.* (2011). *Gelasinospora* is widely reported from both coprophilous and soil habitats. Judging from the available records it is more widely distributed in tropical and subtropical regions than in temperate climate zones (Krug *et al.*, 1994). Based on morphological features (size, form, surface pattern), this type may possibly belong to *Gelasinospora cratophora*, found on herbivore dung in Tanzania (Khan and Krug, 1989a).

Type UG-1179 (Plate VI)

Ascospores ellipsoid, equilaterally one-celled, brown, 28 x 14 µm, small longitudinal grooves (striae) alternating and running sub-parallel with lines of minute spheroidal projections (papillae), thick-walled; tapering ends with two protruding pores; surrounded by a hyaline sheath.

Type UG-1187 (Plate VI)

Ascospores ellipsoid, equilaterally one-celled, brown, 35 x 17 µm, longitudinal sub-parallel striae running over the entire spore-length, thick-walled; tapering ends with two protruding pores; surrounded by a hyaline sheath. This morphotype superficially resembles *Hypoxylon chestersii* J.D.Rogers & Whalley, but the latter species' ascospores are generally much smaller (14-17 x 6-7 µm) (Rogers and Whalley, 1978).

Type HdV-1245: *Diporotheca* sp. (Plate VI)

Ascospores broadly fusiform, equilaterally one-celled, pale brown to dark brown, 34-45 x 24-30 µm, with thick anastomosing ribs that are often broadly reticulate, very thick-walled; tapering ends with pores. It is previously known from European palaeoecological studies that a single *Diporotheca* fruitbody may include ascospores which are morphologically

very divers (van Geel *et al.*, 1986). This is also true for the East African *Diporotheca* findings, in which small morphological differences between specimens hamper solid classification of species. Contrary to the *Diporotheca* specimens found in the fossil record of lake Challa (see van Geel *et al.*, 2011), most ascospores reported from the Ugandan lake surface sediments are characterised by the absence of two (pale) septa. In temperate regions this parasitic genus of Meliolaceae regularly occurs in Holocene deposits formed in eutrophic to mesotrophic moist conditions (van Geel *et al.*, 1986).

[Not ornamented]

Type UG-1087 (Plate VI)

Ascospores ellipsoid, equilaterally one-celled, dark brown, 31 x 25 µm, smooth, very thick-walled; two protruding pores located in the center.

Type UG-1153 (Plate VI)

Ascospores ellipsoid to lemon-shaped, inequilaterally one-celled, dark brown, 23 x 14 µm, smooth and thick-walled; tapering ends with two protruding pores of which one is located is a more subpolar position.

Type UG-1178: *Sordaria* type (Plate VI)

Ascospores ellipsoid, equilaterally one-celled, pale brown to dark brown, 29-35 x 17-19 µm, smooth, thick-walled; slightly rounded ends with two protruding pores. This type differs from Type HdV-1012 (see van Geel *et al.*, 2011) by its larger size and more pronounced pores, and may include different Sordariaceous ascospores from genera, such as *Sordaria* and *Arnium*. Both genera have a worldwide distribution and have most frequently been encountered on dung (Bell, 1983).

Type UG-1216: *Diporotheca* sp. (Plate VI)

Ascospores broadly fusiform, equilaterally one-celled, pale brown to brown, 43 x 18 µm, smooth, thick-walled; tapering ends with two slightly protruding pores, covered by small hyaline end caps. *Diporotheca* ascospores with very diverse morphology (see above: Type HdV-1245, Plate VI) have also been recorded from Holocene deposits in more temperate regions (van Geel *et al.*, 1986). For distribution and ecology see Type HdV-1245 (A.2.2.2.2).

A.2.2.2.3. Multiporate

Type UG-1139: *Gelasinospora* sp. (Plate VI)

Ascospores ellipsoid to subglobose, inequilaterally one-celled, dark brown, 37 x 25 µm, surface sculpture reticulate (ridges and hollows of about 1 µm), thick-walled; at least three germ pores visible, concentrated near both ends. From an evolutionary perspective the occurrence of *Gelasinospora* spores with multiple germ pores is thought to be a recent development. Given that this genus is primarily known from tropical latitudes, and largely from Africa, the evolutionary origin of the genus may be situated in this continent (Krug *et al.*, 1994). *Gelasinospora* is mainly known from dung and dead wood (Hanlin, 1990).

B. Fern and moss spores

B.1. Monoletes

Type UG-1242: *Dryopteris* subg. *Dryopteris* Ching (Plate VII)

Spores bean-shaped, yellow, 40-45 x 15-18 µm, smooth, covered with perisporium forming curving and twisting subhyaline ridges and sacci (winglike compressed inflated folds). *Dryopteris* is distributed nearly worldwide in both temperate and tropical regions. Most African taxa, such as *D. kilemensis* (Kuhn) Kuntze, *D. inaequalis* (Schltdl.) Kuntze and *D. pentheri* (Krasser) C.Chr., have a smooth perine surface and typically inflated sacci with superficial ridges (Tryon and Lugardon, 1990). *Dryopteris* species are mainly found in shaded habitat along forest margins and streams in evergreen forest (Burrows, 1990).

Type UG-1243: cf. *Asplenium* sp. (Plate VII)

Spores bean-shaped, yellow to brown, 42-55 x 28-38 µm, smooth, covered with perisporium developed into fairly high and coarse, subhyaline ridges. These ridges anastomose or not, bear small echinae (spines) on top and columella-like structures underneath. *Asplenium* is one of the largest fern genera, distributed worldwide from Greenland and Europe to South America and New Zealand (Tryon and Lugardon, 1990). It occurs in a wide variety of exposed or partly shaded habitats, e.g., on rocks, in low-altitude semi-deciduous woodland, wet evergreen forest and (sub)montane rain forest (Burrows, 1990; Hemp, 2002).

Type UG-1246: *Isoetes* type (Plate VII)

Spores bean-shaped, brown, 32-37 x 15-28 µm, low, surface covered with broad disconnected muri mostly wider than high, and irregularly pitted. This morphotype may refer to *Isoetes*, which has similarly looking microspores. *Isoetes* is a heterosporous, usually lacustrine genus, occuring in aquatic habitats or saturated soils (Tryon and Lugardon, 1990).

Type UG-1247 (Plate VII)

Spores bean-shaped, brown, 40 x 33µm, smooth, covered with perisporium forming subhyaline to pale yellow echinae (~ 5 µm), densely arranged in a fimbriate (curtain-like) pattern.

Type UG-1248 (Plate VII)

Spores bean-shaped, brown, 45 x 30 µm, smooth, covered with perisporium forming large subhyaline folds with local wing-like extensions, areas between folds microreticulate to perforate.

Type UG-1249: cf. *Ctenitis/Lastreopsis* sp. (Plate VII)

Spores bean-shaped, yellow to brown, 33 x 23µm, surface covered with coarse and irregularly distributed echinae, varying in size but up to 5 µm tall. This spore strongly resembles both *Ctenitis* and *Lastreopsis*, which besides similar spore morphology have similar articulated trichomes on the leaves (Tryon and Lugardon, 1990). *Ctenitis* is widespread in tropical and south-temperate regions, such as Venezuela, Argentina and tropical Africa, and scattered in north-warm temperate regions of Asia, such as Ceylon. It usually occurs in mesic to wet forests. *Lastreopsis* has nearly the same distribution

range, and occurs in tropical/subtropical forests and moist lowlands (Tryon and Lugardon, 1990).

Type UG-1253: Polypodiaceae (Plate VII)

Spores bean-shaped, brown, 54-92 x 23-55 µm, surface covered with large and undulating, solid wart-like projections. Polypodiaceae are widely distributed throughout the world, with highest species diversity in tropical and subtropical regions. However, in Africa only 11 genera (*Belvisia*, *Drynaria*, *Loxogramme*, *Lepisorus*, *Microgramma*, *Microsorum*, *Phytomatosorus*, *Platecyrium*, *Pleopeltis*, *Polypodium*, and *Pyrrosia*) are encountered, of which most species occur in forested areas, such as mixed evergreen forest, riverine forest, rainforest, gallery forest and woodland (Verdcourt, 2001).

Type UG-1315: monoletes undiff. (Plate VII)

Spores bean-shaped, yellow to brown, strongly varying in size from approximately 30 x 15 to 95 x 55 µm, smooth. This type comprises all monolete filicales without perispore.

Type UG-1316: *Asplenium* type (Plate VII)

Spores bean-shaped, brown, 35-45 x 22-26 µm, with smooth surface except low subhyaline plain folds. These type of spores are very common within the *Asplenium* genus, but affiliation with other genera is also apparent. For distribution and ecology see Type UG-1243 (B.1.).

B.2. Triletes

Type UG-1254: *Phaeoceros* cf. *carolianus* (Plate VII)

Spores tetrahedral-obtuse, brown, 37-50 x 23-37 µm, surface covered with small echinae, not joined by reticulum, some echinae forked and bent; arms of the trilete scar long (3/4 the radius) and appearing as prominent ridges. *Phaeoceros* is distributed nearly worldwide, growing in diverse open habitat such as moist slopes, cleared areas and (often) fallow land (Proskauer, 1951). Only *P. carolianus* (L.) Prosk. appears to have been reported from Uganda so far (Hodgetts, 2004).

Type UG-1255: *Ophioglossum* subg. *Ophioglossum* Linnaeus (Plate VII)

Spores globose, brown, 35 x 30 µm, surface covered with fine ridges developed into a dense reticulum, and irregularly spaced, depressed areolae (halos) underneath; trilete scar with short arms (1/2 to 2/3 the radius). The subgenus *Ophioglossum* is widely distributed in both tropical and temperate regions at low altitudes. It occurs in a wide range of habitats, from woodland and the margins of evergreen forest to wet grassland and sandy soils overlying granite sheet-rock (Burrows and Johns, 2001).

Type UG-1258 (Plate VII)

Spores tetrahedral-globose, brown, 36 x 34 µm, surface pitted and wrinkled with low coalescent ridges, trilete scar with long arms (3/4 the radius).

Type UG-1259: *Pteridium aquilinum* (L.) Kuhn (Plate VII)

Spores tetrahedral-globose, usually with concave sides, yellow, 30-38 x 20-28 µm, surface diffusely and irregularly granulate, trilete scar with relatively short arms (2/3 the radius). In subfossil specimens the sculptured perispore is often missing. *Pteridium aquilinum* has a worldwide distribution and occurs in a large variety of habitats (forest margins, grassland, woodland, rocky places and disturbed areas) in lowland to high montain regions (Friis and Vollesen, 1998; Verdcourt, 2000). It is definitely the most common African fern, often forming vast stands in eastern parts of southern Africa, and frequently becoming an invasive weed following land-clearance and fire (Burrows, 1990).

Type UG-1260: *Coniogramme africana* type (Plate VII)

Spores tetrahedral-globose, often deeply curved, yellow to brown, 37-30 x 30 µm, surface faintly patterned (rugate or irregularly papillate), trilete scar with relatively short arms (2/3 the radius). This type may be affiliated with *Coniogramme africana* Hieron., which occurs in tropical Africa and Madagascar in submontane and subalpine zones at altitudes ranging from ~1100 to 2200 m (Tryon and Lugardon, 1990; Hemp, 2002).

Type UG-1261: cf. *Pteris/Actiniopteris* sp. (Plate VII)

Spores tetrahedral-globose, yellow to brown, 43-48 x 40-45 µm, with prominent equatorial flange/rib, surface covered with low tubercles, trilete scar with long arms (3/4 the radius). This spore resembles some species of *Pteris* and *Actiniopteris*, which can be morphologically similar. *Pteris* is distributed in the tropics, subtropics and warm temperate regions, whereas *Actiniopteris* is primarily restricted to Africa, Madagascar and the adjacent islands extending northeastward to Afghanistan, Nepal, India and Sri Lanka (Tryon and Lugardon, 1990). Both taxa occur in a wide variety of habitats (rock outcrops, woodland, bushland), but *Actiniopteris* is apparently more favoured by dry conditions (Verdcourt, 1999, 2002).

Type UG-1263: cf. *Grammitis* sp. (Plate VII)

Spores tetrahedral-globose, brown, 32 x 30 µm, surface covered with prominent tubercles, with papillae near the aperture, and a trilete scar with long arms (1/3 to 3/4 the radius). *Grammitis* has a pantropic distribution across tropical, subtropical and warm temperate regions. These are small, often epiphytic ferns, usually growing in mossy substrates on trees (Tryon and Lugardon, 1990).

Type UG-1264: *Pteris* sp. (Plate VII)

Spores tetrahedral-globose, brown, 62 x 52 µm, surface covered with a very distinct coarse reticulum, with ridges (up to 2.5 µm tall) partly connected to each other and large papillae (2.5 µm in diameter) within areolae, trilete scar with long arms (3/4 the radius). The large papillae or tubercles within the aureolae of some *Pteris* spores (e.g., *P. vittata* L. and *P. longifolia* L.) are remarkably similar to those of *Onychium* species. However, *Pteris* is far more common in East Africa than *Onychium*, which is mostly distributed in the Sikkim-Himalayan area and southwest China. *Pteris* is widespread in tropical, subtropical and warm temperate regions and occurs in diverse habitat ranging from river banks, wet evergreen forest and stream-side vegetation to drier areas on limestone outcrops (Tryon and Lugardon, 1990; Verdcourt, 2002).

C. Microscopic zoological remains

Type UG-1221, UG-1222, UG-1223 and UG-1224 (Plate VIII) are oocytes with a size of ~100-190 µm belonging to various Neorhabdocoela (flatworm) species, which can be found worldwide in (semi-)aquatic habitats such as ponds, marshy pools, ditches, peat trenches and lakes (Haas, 1996). Type UG-1221, UG-1222 and UG-1223 are probably related to the oocyte types *Gyratrix hermaphroditus* Erhenberg 1831 (Type UG-1221) and *Microdalyellia armigera* O.Schmidt 1861 (Types UG-1222 and UG-1223) described by Haas (1996). However, since the oocyte morphology of these species is currently not well differentiated from those of other species, and since their palaeoecological significance is completely based on local Central European ecological conditions, we made no attempt to link the East African oocytes to these previously described types.

Type UG-1221 (Plate VIII)

Oocyte without operculum, yellow, funnel-shaped or oval, 125-150 x 120-150 µm, with smooth surface, smooth, stalk typical but often only partly or not preserved, with articulation just beneath the body.

Type UG-1222 (Plate VIII)

Oocyte without operculum, yellow, ellipsoid, 112-125 x 85-100 µm, with finely reticulated surface.

Type UG-1223 (Plate VIII)

Oocyte without operculum, yellow, oval to ellipsoid, 98-155 x 86-120 µm, with smooth surface.

Type UG-1224 (Plate VIII)

Oocyte without operculum, yellow, oval to ellipsoid, 137-188 x 110-150 µm, surface smooth or microreticulate, with parallel but slightly undulating, longitudinal ribs.

Types UG-1225, UG-1229, UG-1288 and UG-1326 (Plate VIII) are probably the external cases of diapausing eggs (cysts) of various aquatic invertebrates, excluding Rotifera and Branchiopoda. Considering the great variety of possible source organisms (microcrustaceans, arthropods, etc.) and enormous number of possible genera within each of these broad taxa we made no attempt to attribute these NPP types to a specific taxon. Their inclusion here mostly serves to help distinguish such NPP types from the spores of fungi, mosses and ferns.

Type UG-1225 (Plate VIII)

Cyst ellipsoid, hyaline to pale yellow, 110 x 85 µm, surface smooth with slightly undulating, transversely ribs, partly connected to each other and ornamented with regularly placed spines.

Type UG-1229 (Plate VIII)

Cyst subglobose, subhyaline to pale yellow, 64-73 x 55-61 µm, surface covered with striae finely arranged in a barely visible finger-print pattern.

Type UG-1288 (Plate VIII)

Cyst ellipsoid, subhyaline to pale yellow, 110 x 85 µm, surface ornamented with low reticulated flanges (honeycomb structure).

Type UG-1326 (Plate VIII)

Cyst globose, subhyaline, 41 µm in diameter, surface smooth but ornamented with rounded flanges (~4 µm).

D. Algal aplano-/zygospores, coenobia and colonies

Type UG-1231: *Botryococcus* cf. *neglectus* (W.West & G.S.West) (Plate IX)

Colonies (cells are arranged in a three-dimensional structure) yellow-brown to brown with irregularly sculpted surface, composed of sub-colonies (25–50 µm) connected by very short and thin undulating strings; cells (2 µm) obovoid, usually radially stacked up to a layer of larger (9 µm) and modified peripheral cells. Peripheral cells slightly distant one from another. This species of green alga (Chlorophyceae, Chlorococcales) strongly resembles *Botryococcus neglectus,* which is characteristic for small oligotrophic and mesotrophic aquatic environments in more temperate regions (Komárek and Marvan, 1992). However, the colonies and individual cells of this East African morphotype are more regularly arranged, which suggests it is a distinct *B. neglectus* variety or a *Botryococcus* species with more tropical ecological requirements. The genus *Botryococcus* is widely distributed in temperate and tropical regions, but the taxonomic classification of the species within the genus is still open for revision (Jankovská and Komárek, 2000).

Type UG-1233: *Coelastrum reticulatum* (P.A.Dang) Senn (Plate IX)

Coenobia (cells are arranged in a single layer) globose to ovoid, hyaline to pale yellow, 30-41 x 25-39 µm, covered by a hyaline envelope and built from 2, 4 or 8 cells that are globose to ellipsoid, each measuring up to 10 µm; neighbouring cells connected by 5-7 long, slender processes (up to 8 µm); intercellular spaces large. *Coelastrum reticulatum* (Chlorophyceae, Chlorococcales) has a worldwide distribution, and is common in the tropics. It mainly occurs planktonic in warm ponds and productive lakes (Jankovská and Komárek, 2000; John *et al.*, 2002).

Type UG-1235: *Pediastrum angulosum* (Ehrenb. ex) Menegh. (Plate IX)

Coenobia circular, slightly oval or irregular in outline, hyaline, 79-190 x 79-125 µm, comprised of 16-64 tightly packed cells. Peripheral cells with two short, conical processes flanking a U-shaped concave margin, cell wall with distinct irregular net-like sculpture. Peripheral and inner cells resp. 27 and 23 µm. *P. angulosum* is a cosmopolitan but not very common planktonic species with numerous varieties in need of taxonomic revision. Based on fossil records in temperate regions (Denmark, Finland, Germany, Russia), it seems indicative for both large and small lake habitats with slightly alkaline water and abundant submerged macrophyte vegetation (Komárek and Jankóvska, 2001). However, the specific ecological requirements of tropical populations is uncertain.

Type UG-1236: *Pediastrum boryanum* var. *brevicorne* A.Br. (Plate IX)

Coenobia circular, pale yellow, diameter 50-83 µm, comprised of 16-32 tightly packed cells. Peripheral cells with two triangular lobes flanking a wide V-shaped concave margin, processes very short cylindrical and hyaline, cell wall regularly

granular. Peripheral and inner cells resp. 12 and 8 µm. *P. boryanum* var. *brevicorne* is a planktonic thermophilic taxon, occurring in tropical regions and warmer areas of temperate zones (Komárek and Jankóvska, 2001).

Type UG-1237: *Pediastrum boryanum* cf. var. *forcipatum* (Corda) Chod. (Plate IX)

Coenobia nearly circular to irregular in outline, hyaline to pale yellow, 50-100 µm in diameter, comprised of 32-64 tightly packed cells. Peripheral cells with two long, narrow, hyaline processes on little developed lobes, margin between them shallowly concave, cell wall densely and distinctly granular. All cells 12-22 µm. *P. boryanum* var. *forcipatum* is a rare taxon and taxonomically not clearly defined, but probably more thermophilic than other *P. boryanum* varieties. It is mainly distributed in tropical and warm-temperate zones (Komárek and Jankovská, 2001). In Africa it has previously been reported from Chad (Compère, 1970).

Type UG-1239: *Scenedesmus* sp. (Plate IX)

Colonies linear, hyaline, 26(30) x 17µm, with four ellipsoid to oblong cells, arranged subparallel to each other, broadly rounded or slightly truncate, and with a smooth surface. Cells 5-8 x 17-22 µm. *Scenedesmus* species typically occur in freshwater ponds, lakes and/or slow-moving rivers, most abundantly in slightly eutrophic waters. The joint occurrence of *Scenedesmus* and *Pediastrum* species in small water bodies (wells, ditches, watering holes, etc.) and as fossils in lake deposits is indicative of eutrophication caused by human activities, and therefore has occasionally been used to infer past organic pollution (Cronberg, 1986).

Type UG-1240: *Spirogyra* sp. (Plate IX)

Zygo-/aplanospores yellow to dark yellow, 70-75 x 40-45 µm, oval, ellipsoid, ovoid or cylindrical-ovoid in shape, often split along its periphery. Surface with fine striate-rugulate pattern, smooth coating of the outer wall is occasionally present. This African green algae resembles Type 773 reported from a late-Holocene sediment record in The Netherlands (Bakker and van Smeerdijk, 1982). Species of *Spirogyra* have a worldwide distribution, and commonly occur in stagnant, shallow waters of mesotrophic to eutrophic small lakes and pools, or in the littoral zones of larger lakes. Many species seem to prefer rather extreme conditions, such as ephemeral standing waters, or strong daily fluctuations in pH and temperature. The sexual reproduction during which these zygospores are formed requires high temperatures, which can best be reached in shallow waters directly exposed to strong solar radiation. The optimum growth conditions for *Spirogyra* species lie above 20°C (Hoshaw, 1968).

E. Microscopic aquatic plant remains

Type UG-1241: Epidermis of *Nymphaea nouchali* Burm. f. (Plate X)

Globose to shaped like a rounded square in outline, subhyaline to pale yellow, 38-58 µm in diameter, consisting of 7-8 cells, each 17-25 x 14-22 µm. Cell walls covered by a very fine, wavy net-like sculpture, central cell globose, marginal cells tetragonal. Only occasionally found in assembled condition. This morphotype belongs to the epidermis of *Nymphaea nouchali*, which is the only living *Nymphaea* species found in the 20 lakes studied (Lebrun, unpublished CLANIMAE data), and can easily be mistaken for coenobia of the coccal green alga *Pediastrum privum* (Printz) E.Hegewald (see Komárek and Jankóvska, 2001). *Nymphaea nouchali* is a common macrophyte in tropical regions, occuring in shallow waters (Verdcourt, 1989).

F. Unknown microfossils

Type UG-1114 (Plate X)

Inversely club-shaped to broadly fusiform, yellow, 50-57 x 20 µm, smooth, thick-walled, truncate at both ends (partly broken off).

Type UG-1115 (Plate X)

Inversely club-shaped, yellow, 54 x 15 µm, smooth, thick-walled, at one end obliquely truncate with an aperture covered by a hyaline membrane (present or not), other end possibly broken off. This morphotype is probably related to Type UG-1114.

Type UG-1130 (Plate X)

Subglobose, subhyaline to pale yellow, 59-80 x 47-67 µm, slightly thin-walled, microreticulate.

Type UG-1234 (Plate X)

Globose, unicellular, pale yellow to yellow, 40 x 38 µm, smooth, consisting of 2 intricately lobed semi-cells with concave margins between them and a star-like pattern of projections pointing towards the center. This African morphotype superficially resembles *Micrasterias* (Chlorophyceae, Desmidiales) which is distinctly larger and of which the semi-cells are more complex and intricately lobed. However, experiments show that the size of some *Micrasterias* species, such as *M. rotata* Ralfs, consistently decreases at high temperatures, and the morphology is less elaborate than in cells grown at low temperature (Neustupa *et al.*, 2008). This NPP type may represent one or more tropical species of *Micrasterias*, but identification is severely hampered by the lack of a centrally placed nucleus, a typical feature of Desmidiaceae.

Type UG-1280 (Plate X)

Ellipsoid, yellow to brown, 100 x 187 µm, with small spines densely arranged across the surface. Possibly this is a swollen hair from an aquatic insect larva.

Type UG-1284 (Plate X)

Nearly triangular to obtuse, yellow to brown, 38 x 27 µm, covered with microreticulate knobs, thick-walled; two centrally located circular apertures are provided with annuli.

Type UG-1286 (Plate X)

Subglobose, yellow, 49-53 µm, with irregularly arranged linear and T-shaped appendages (1 to 3 µm), thick-walled.
Type UG-1300 (Plate X)

Globose, brown to dark brown, surface locally smooth but partly covered with small verrucae (~1 µm) grouped and restricted to some areas, 45 µm in diameter, thick-walled; with a long slit-like aperture.

Type UG-1303 (Plate X)

Globose to shaped like a rounded square, yellow to brown, 15 µm in diameter, thick-walled; with subhyaline outer coat covered with small protuberances (~1 µm).

Type UG-1306 (Plate X)

Globose, yellow to brown, 10 µm in diameter, very thick-walled (~2 µm); with a subhyaline net-like outer coat.

Type UG-1307 (Plate X)

Globose, brown, 25-15 µm in diameter, thick-walled, surface densely covered with long hairy appendages (3 to 5 µm); characteristic aperture/pore (~5 µm) with costa.

Type UG-1309 (Plate X)

Globose, brown, 25-20 µm in diameter, thick-walled, with minute spheroidal protuberances (papillae, 0,5-1 µm tall) irregularly distributed across the surface.

Type UG-1310 (Plate X)

Globose, brown, 28 µm in diameter, tthick-walled, with echinae (~3 µm tall) densely distributed.

Type UG-1311 (Plate X)

Globose, brown, 19-12 µm in diameter, thick-walled, with small protuberances (~1 µm tall) evenly distributed across the surface. This microfossil superficially resembles *Michrystridium* (Acritarcha, European NPP type HdV-115), which was first reported in lake sediment deposited on a subsoil of marine clay in The Netherlands (Pals *et al.*, 1980; Bakker and van Smeerdijk, 1982).

Type UG-1312 (Plate X)

Globose, yellow, 22 µm in diameter, smooth, slightly thick-walled; with a possible circular central aperture/hole (~10 µm). This microfossil superficially resembles the testate amoeba *Arcella*, which is clearly larger (~100-130 µm) and has a nucleus (Chardez, 1964).

Type UG-1319 (Plate X)

Globose, yellow, 20-26 µm in diameter, smooth, slightly thick-walled (~1 µm thick), often split. This microfossil resembles the European NPP type HdV-119, which is restricted to lake deposits (Pals *et al.*, 1980), but since its morphology is rather simple and nondescript we use a new type number.

Type UG-1346 (Plate X)

Subglobose, brown to dark brown, 50-55 µm, very thick-walled, with striae (~1 µm wide) arranged in a finger-print pattern; with thick and elongated V-shaped furrow (~3 µm wide); covered by a smooth subhyaline outer coat.

2.4. Discussion

In this early stage of NPP research in tropical Africa, it is not surprising that the taxonomic affinity of many NPP morphotypes remains unknown. Our ~28% success rate of identification in this Uganda crater-lake collection is, in fact, comparable to that achieved in studies of modern NPP assemblages elsewhere (Prager *et al.*, 2006). In part this is because identification of any microfossil to species or genus level is generally difficult when the range of possible source organisms is very wide. Most biological analysts have expertise in only a single group of organisms, and it already requires a much specialised study and accumulated experience to recognise (micro-)fragments of those organisms preserved in sediment samples. Often a single NPP morphotype can originate from different taxa, and depending on growth differentiation or body fragments a single organism can produce several NPP morphotypes (Prager *et al.*, 2006).

The fraction of identified morphotypes in this collection differs greatly among the main taxonomic groups, from ~26% in the fungi and ~68% in the ferns and mosses to 100% in the algae. The modest success rate in the fungi certainly can be attributed partly to the fact that only an estimated 5% of the 1.5 million fungal species worldwide have been formally described (Hawksworth, 1991, 1993). Smith and Waller (1992) even consider this total number as unrealistically low, and suggested that perhaps 1 million undescribed fungi exist on tropical plants alone. Based on summaries of plant species richness by floristic regions (White, 1983) and an estimated vascular plant-to-fungus species ratio of 1:6 (Hawksworth, 1991), up to 18,000 species of fungi may occur in the Lake Victoria regional mosaic (occupying most of Uganda, eastern Rwanda and Burundi, small parts of D.R. Congo, Kenya and Tanzania, and a small exclave in the Rusizi Valley north of Lake Tanganyika). However, this estimate may be susceptible to over-generalization, since the degree of host specificity in fungi likely differs between regions and between host plants (Lodge, 1997). For example, on tropical palms the mean ratio of host-specific fungi to palm species is 33:1 (Fröhlich and Hyde, 1999), much higher than the 6:1 ratio considered by Hawksworth (1991). Also other environmental factors (e.g., substrate, altitude, rainfall, seasonality) will certainly create regional variation in fungal diversity. The species diversity of non-lichenised fungi is known to be highest in sub-humid to humid tropical regions at low to middle elevation (Lodge *et al.*, 1995), i.e. the broad characteristics of our study area. A similar latitude effect in species richness has also been noted in the coprophilous mycobiota (Richardson, 2001), which are also present in our dataset (e.g., the Sordariales with *Sordaria*, *Gelasinospora* and *Coniochaeta* and possibly representatives of *Cercophora*, *Podospora, Zopfiella* or other morphologically related coprophilous fungi). In contrast, the diversity of fern and moss NPPs in our African collection (19 distinct types) is rather poor compared with other world areas. Some authors point to the scarcity of high-mountain habitats and the paucity of the continent's rain forest flora, as the main reason for the overall low diversity of Pteridophyta and Bryophyta in tropical Africa (Kornás, 1993; Moran, 1995; Pócs, 1998). Africa's total known species diversity in these groups is also strongly influenced by rich fern and moss communities in the Eastern Arc Mountains of Tanzania (Schelpe, 1983; Pócs, 1998; Aldasoro *et al.*, 2004), quite distant from our study area in western Uganda.

The true richness of a regional species pool can hardly be estimated *a priori*, but requires comprehensive investigation of the number of morphospecies in representative ecosystems (Foissner, 2006). Thus, given the wide range of both relatively undisturbed and disturbed ecosystems present near our lake sites, and the size of our fungal NPP collection (~7,430 specimens), it seems fair to assume that the 198 fungal morphotypes reported here represent a reasonable score of overall NPP diversity, which may occur in fossil assemblages of East African lake deposits. This may also be true for the 19 fern and moss morphotypes recognised in 725 specimens. In the other taxonomic groups the recovered

diversity (e.g., 7 morphotypes in 1115 specimens of algal NPPs) significantly underestimates regional species diversity because only a small fraction of species in those groups are composed of refractive organic materials (such as sporopollenine and thick chitine) which survive the chemically harsh palynological sample preparation. The preliminary results of phytoplankton analyses of 29 western Ugandan crater lakes, of which 12 of the lakes are also included in this present study, revealed a total species richness of approximately 220 algal taxa (Cocquyt, unpublished CLANIMAE data) which is in sharp contrast to the 7 morphotypes found in our NPP dataset of 20 study lakes. Representation of these microfossil groups in NPP collections is highly selective and incomplete; other, more appropiate sample-processing techniques are required to reveal their full species diversity and to optimally exploit their palaeoecological indicator value.

Overall NPP taxon richness is certainly also affected by *in situ* decay processes, since after burial in bottom sediments the microfossils are differentially sensitive to chemical (oxidation), mechanical (abrasion) and biological (feeding) degradation. Differential preservation is well known in pollen (Dimbleby, 1957; Havinga, 1984), but to our knowledge it has not been experimentally studied in a wide range of fungal spores. Nevertheless, the results of the present study clearly indicate that pigmented, thick-walled fungal spores are far better preserved in (East African) lake sediments than hyaline, thin-walled species, which are totally absent. Since thin-walled fungal spores can mainly be attributed to species with airborne dispersal, it would seem that fungal NPP assemblages in lake sediments mainly reflect the local aquatic ecosystem and any immediately surrounding terrestrial ecosystems. Among the zoological remains, we recovered both smooth or modestly ornamented eggs of Neorhabdocoela (flatworms) and more strongly ornamented diapausing eggs (cysts) attributable to various groups of aquatic arthropods (copepods, ostracods, etc.). Cyst ornamentation (honeycombing, flanges, spines, etc.) in aquatic invertebrates is thought to help protect against predation (Dumont *et al.*, 2002), consequently the relative abundance of aquatic invertebrate groups recorded in fossil NPP assemblages is biased in favour of those groups producing ornamented cysts.

Finally, experimental studies on modern NPP origin and deposition (Gaillard *et al.*, 1994; Wilmshurst and McGlone, 2005; Prager *et al.*, 2006) also reveal differences in microfossil diversity between substrate types (e.g., lake sediments, moss cushions, terrestrial soils). The high diversity of pollen and spore types typically found in lake sediments compared to terrestrial substrates (Wilmshurst and McGlone, 2005) has been attributed to a more diverse biotic influx from multiple lakeshore habitats and substrates, supplemented by important wind dispersal (see also Prentice, 1985; Sugita, 1993; DeBusk, 1997). However, at our study sites at least, wind dispersal appears to contribute less to lake-bottom NPP assemblages than entrainment from the surrounding landscape by water flow across it; and a significant portion of total NPP diversity is derived from local, (semi-) aquatic saprotrophic fungi, algae and aquatic invertebrates. We estimate that at least 24% of the 73 identified African NPPs in our dataset are (semi-)aquatic species, but even these two fundamental ecological groups of terrestrial versus aquatic biota cannot be reliably separated. The group of algal NPPs and most zoological NPPs are fully aquatic, whereas the fern and moss NPPs are presumably mostly derived from terrestrial or riparian habitats. The terrestrial or aquatic affinity of fungal remains, however, is less tractable. Of the 53 fungal NPP taxa that could be (tentatively) identified to species, genus or family level, about 20% have worldwide distributions in both terrestrial environments and (sometimes fortuitously) freshwater environments. Terrestrial and aquatic fungi do not form separate monophyletic groups, but each comprise a diverse assemblage of species with representatives from various orders. Among the predominantly terrestrial fungi, Sordariales (e.g., *Apiosordaria*, *Coniochaeta*, *Cercophora*, *Gelasinospora* and *Sordaria*), Pleosporales (e.g., *Byssothecium*, *Curvularia*, *Delitschia* and *Sporidesmium*) and Xylariales (e.g. *Rosellinia*, *Kretzschmaria* and a few other unknown Xylariaceae*)* are well represented, whereas Chaetosphaeriales (e.g., *Sporoschisma*), Glomerales (*Glomus*), Phyllachorales (e.g., *Bactrodesmium* and *Clasterosporium*) and Ustilaginales (e.g., *Urocystis*) are less well represented. Only four or five (~10%) of the identified fungal genera in our dataset have previously been reported from tropical freshwater habitats (Goh, 1997; Hyde *et al.*, 1997). Among the Ascomycota and Hyphomycetes, it is known that some species within genera such as *Brachydesmiella*, *Clasterosporium, Dictyosporium, Sporidesmium, Sporoschisma* and *Tetraploa* live on (partially) submerged dead stems, leaves and wood. Unfortunately, tropical Africa remains one of the least studied biogeographical regions for fungal diversity in aquatic habitats (Shearer

et al., 2007). This problem of differentiation between aquatic NPPs (reflecting habitat conditions in the local lake system) and terrestrial NPPs (reflecting habitat conditions in the surrounding landscape), together with the biologically heterogeneous nature of NPP assemblages, hampers quantitative evaluation of the ecological parameters controlling the distribution of individual taxa, on the basis of which their palaeoecological indicator value must be established.

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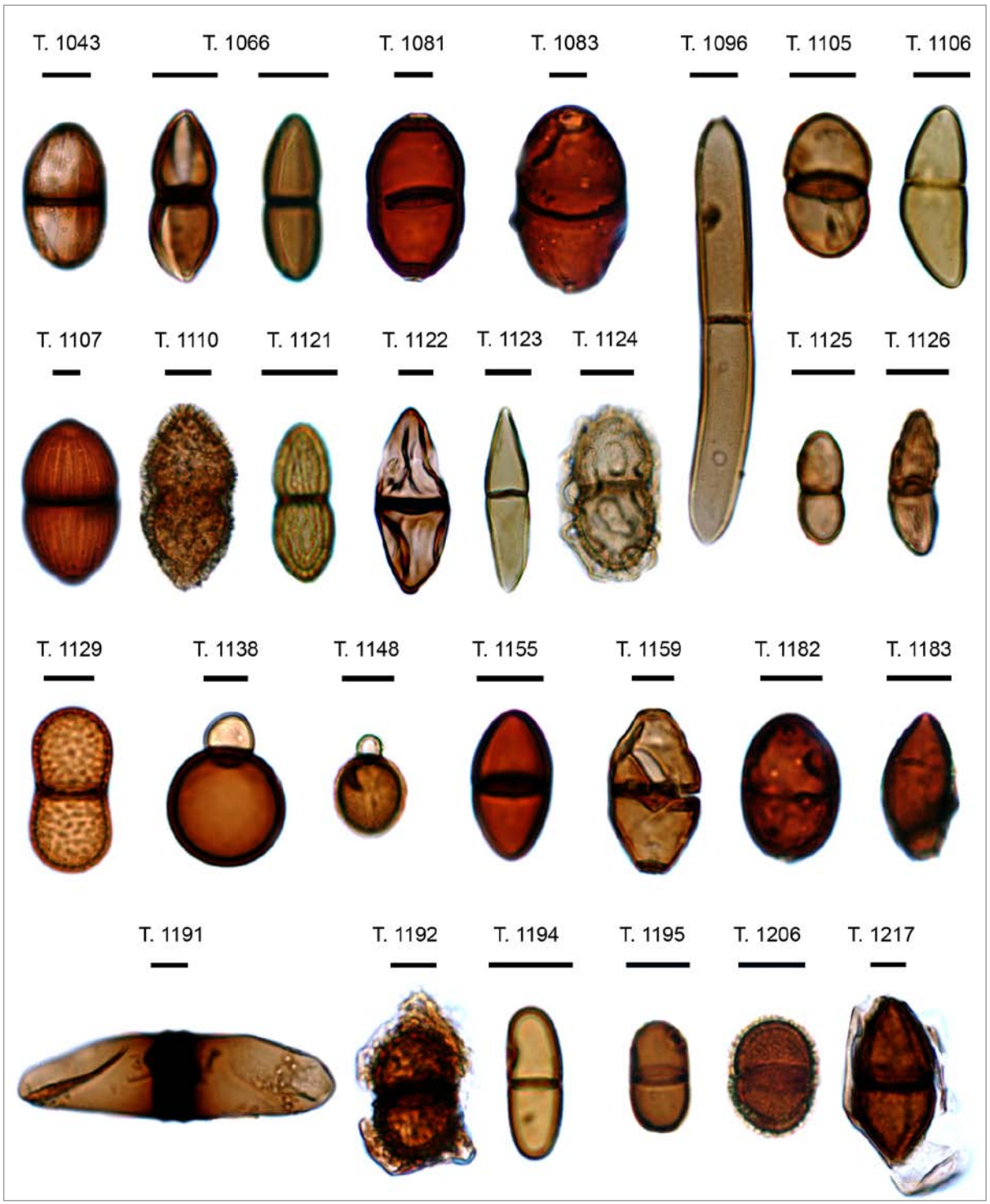

Plate I. Septate fungal spores: uniseptate: T. HdV-1043: cf. *Lasiodiplodia theobromae*, T. UG-1066: *Delitschia* spp., T. UG-1081, T. UG-1083, T. UG-1096, T. UG-1105, T. UG-1106, T. UG-1107, T. UG-1110, T. UG-1121, T. UG-1122: cf. *Cookeina* sp., T. UG-1123, T. UG-1124, T. UG-1125, T. UG-1126, T. UG-1129, T. UG-1138, T. UG-1148, T. UG-1155, T. UG-1159, T. UG-1182, T. UG-1183: cf. *Cercophora* sp., T. UG-1191, T. UG-1192, T. UG-1194, T. UG-1195, T. UG-1206: cf. *Acroconidiellina loudetiae*, T. UG-1217. All scale bars are 10 µm.

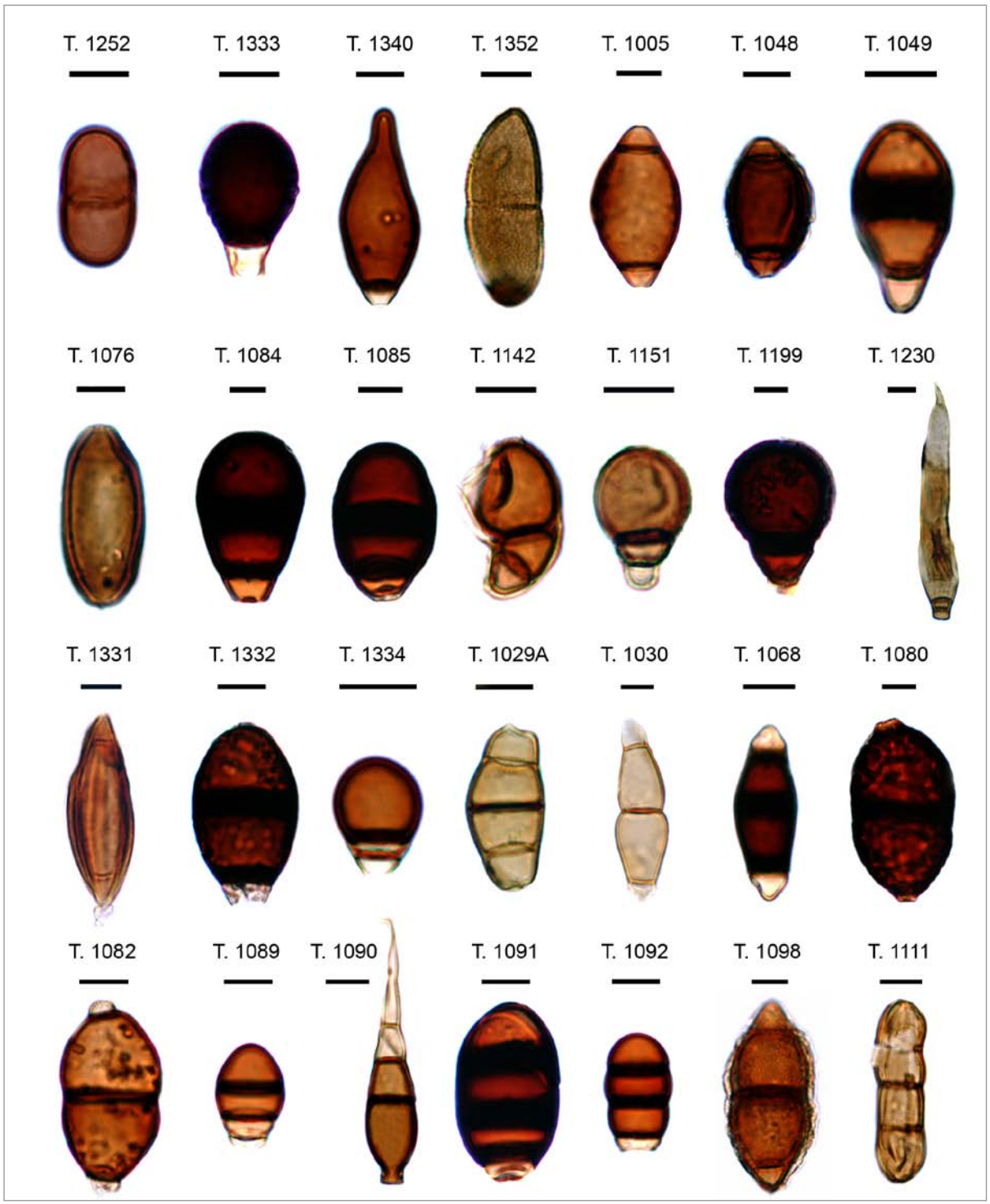

Plate II. Septate fungal spores: uniseptate: T. UG-1252, T. UG-1333, T. UG-1340, T. UG-1352; Diseptate: T. HdV-1005: *Brachydesmiella* sp., T. HdV-1048, T. HdV-1049: cf. *Mitteriella ziziphina*, T. UG-1076, T. UG-1084, T. UG-1085, T. UG-1142, T. UG-1151, T. UG-1199, T. UG-1230, T. UG-1331, T. UG-1332, T. UG-1334; Triseptate: T. HdV-1029A: *Curvularia* cf. *intermedia*, T. HdV-1030: cf. *Byssothecium* sp., T. UG-1068, T. UG-1080, T. UG-1082, T. UG-1089, T. UG-1090: *Sporidesmium* cf. *macrurum*, T. UG-1091: *Bactrodesmium* type, T. UG-1092, T. UG-1098, T. UG-1111. All scale bars are 10 µm.

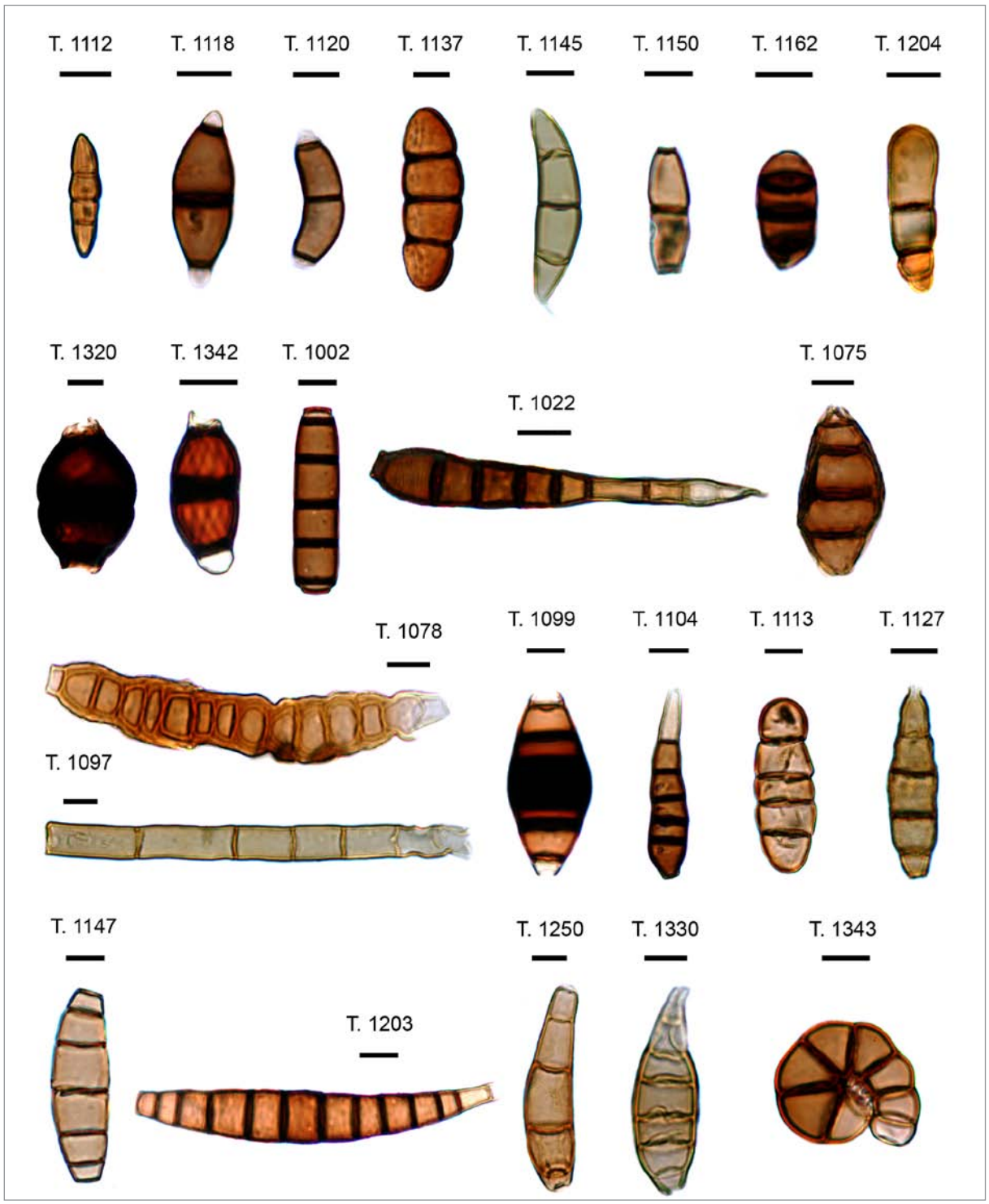

Plate III. Septate fungal spores: triseptate: T. UG-1112: *Phaeosphaeria* type, T. UG-1118: cf. *Savoryella lignicola*, T. UG-1120: *Savoryella curvispora*, T. UG-1137: *Meliola* sp., T. UG-1145: cf. *Fusarium* sp., T. UG-1150, T. UG-1162, T. UG-1204, T. UG-1320, T. UG-1342; Multiseptate: T. UG-1002: *Sporoschisma* spp., T. HdV-1022: *Clasterosporium* sp., T. UG-1075, T. UG-1078: *Sporidesmium* spp., T. UG-1097, T. UG-1099: *Brachysporium* spp., T. UG-1104: cf. *Podosporium rigidum,* T. UG-1113: *Meliola* sp., T. UG-1127, T. UG-1147, T. UG-1203, T. UG-1250: *Curvularia* cf. *comoriensis*, T. UG-1330, T. UG-1343: cf. *Cirrenalia* sp. All scale bars are 10 µm.

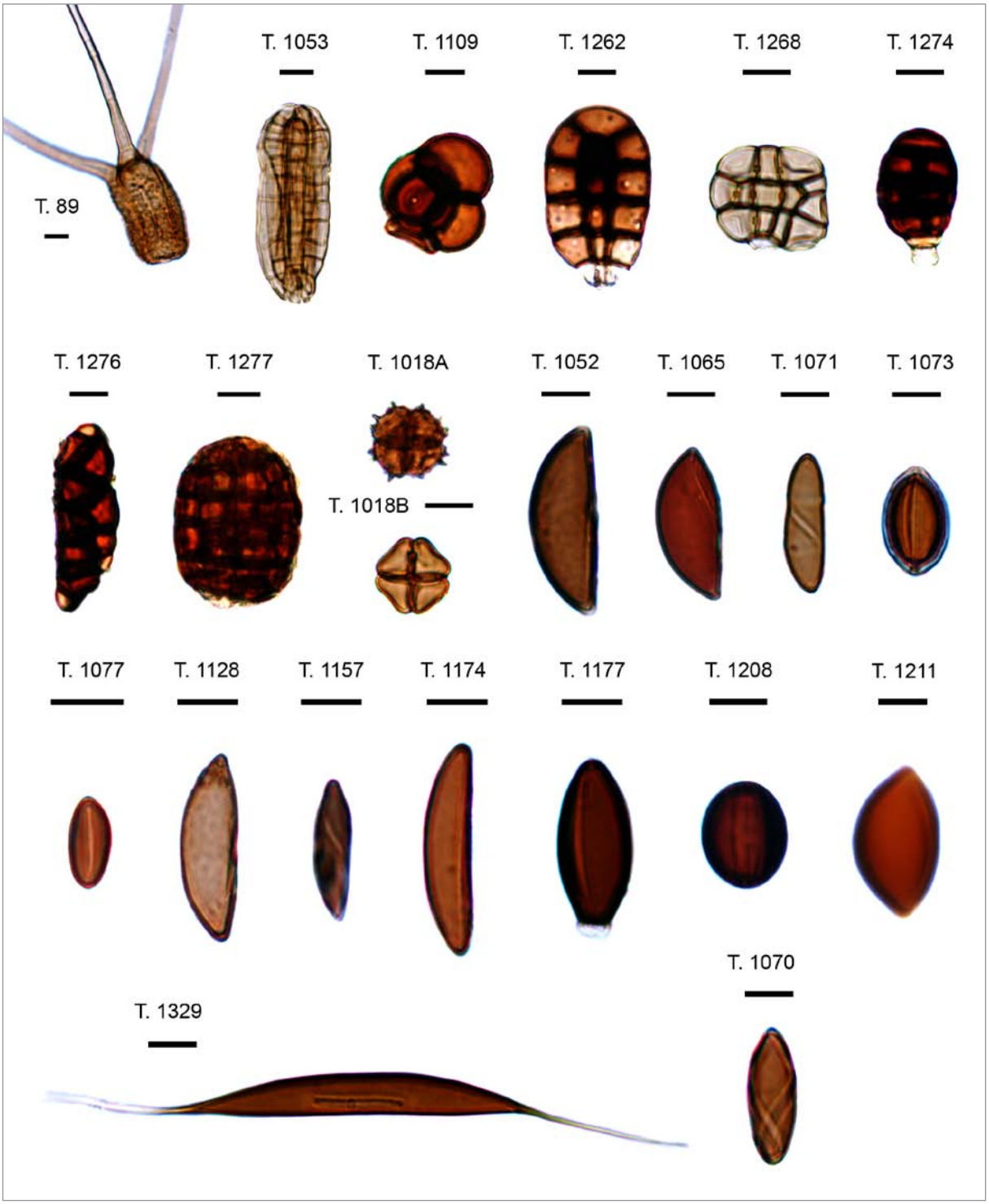

Plate IV. Septate fungal spores: muriform: T. HdV-89: *Tetraploa aristata*, T. HdV-1053: *Dictyosporium* cf. *heptasporum*, T UG-1109, T. UG-1262: *Canalisporium cf. kenyense*, T. UG-1268: *Canalisporium variabile*, T. UG-1274, T. UG-1276, T. UG-1277; Tetrads: T. HdV-1018A-B: *Spegazzinia tessarthra*; Non-septated spores/Amerosporae: with one or more germ slits: one germ slit: T. HdV-1052: Xylariaceae, T. UG-1065: Xylariaceae, T. UG-1071: cf. *Amphirosellinia* sp., T. UG-1073, T. UG-1077: cf. Xylariaceae/Sordariaceae/Coniochaetaceae, T. UG-1128: cf. *Kretzschmaria clavus/cetrarioides*, T. UG-1157: *Rosellinia* sp., T. UG-1174: *Rosellinia* sp., T. UG-1177, T. UG-1208: *Coniochaeta* spp., T. UG-1211, T. UG-1329: cf. Xylariaceae; Two germ slits: T. UG-1070: Xylariaceae. All scale bars are 10 µm.

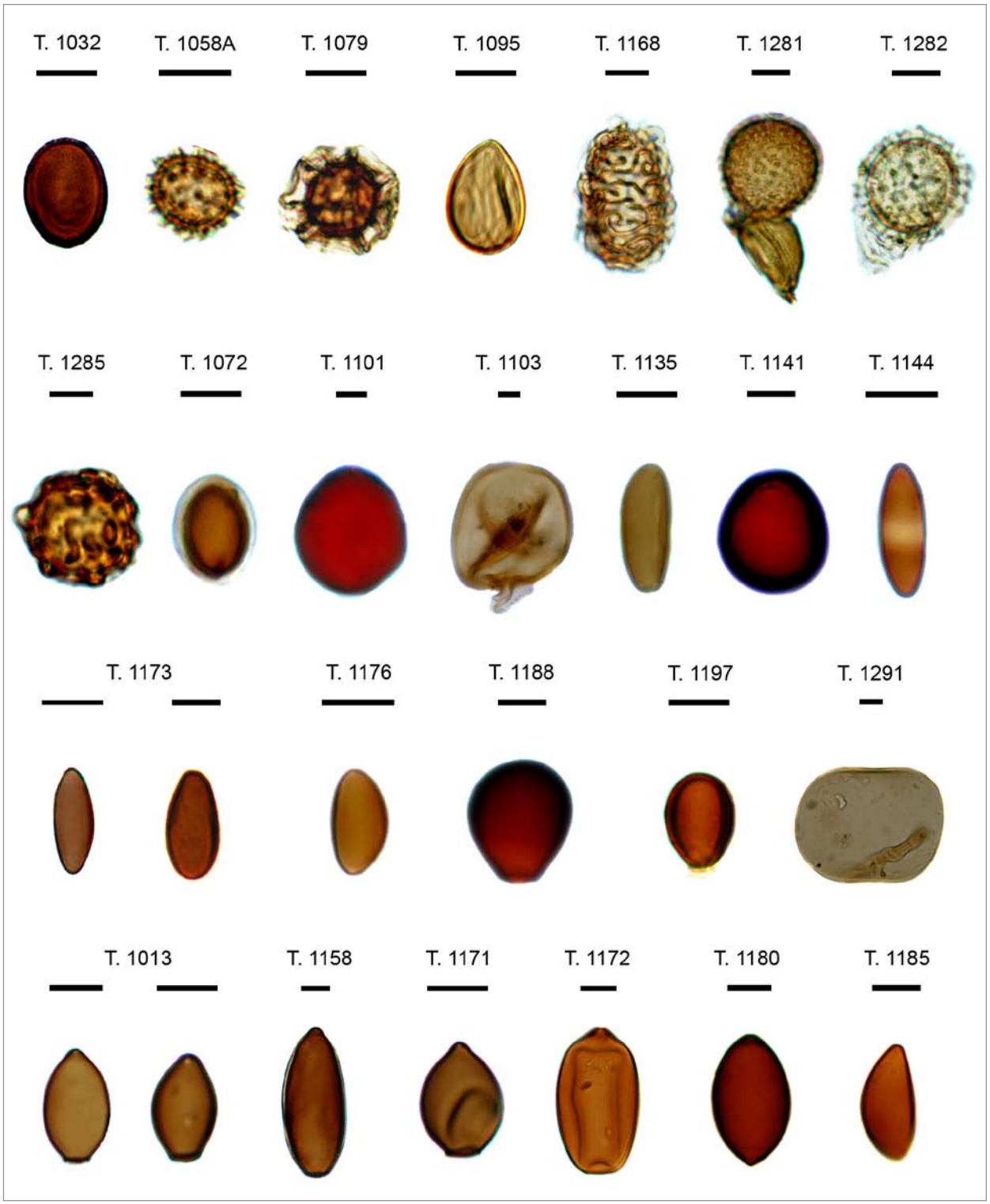

Plate V. Non-septated spores/Amerosporae: without germ slit: aporate: ornamented: T. HdV-1032, T. HdV-1058A, T. UG-1079: *Urocystis* sp., T. UG-1095, T. UG-1168, T. UG-1281, T. UG-1282, T. UG-1285: cf. *Ascodesmis* sp.; Aporate: not ornamented: T. UG-1072, T. UG-1101, T. HdV-1103: *Glomus* sp., T. UG-1135: cf. Xylariaceae, T. UG-1141, T. UG-1144, T. UG-1173, T. UG-1176, T. UG-1188, T. UG-1197, T. UG-1291: *Glomus* type; Porate: monoporate: T. HdV-1013: *Cercophora* type, T. UG-1158, T. UG-1171: *Apiosordaria* type, T. UG-1172, T. UG-1180: *Sordaria* spp., T. UG-1185. All scale bars are 10 µm.

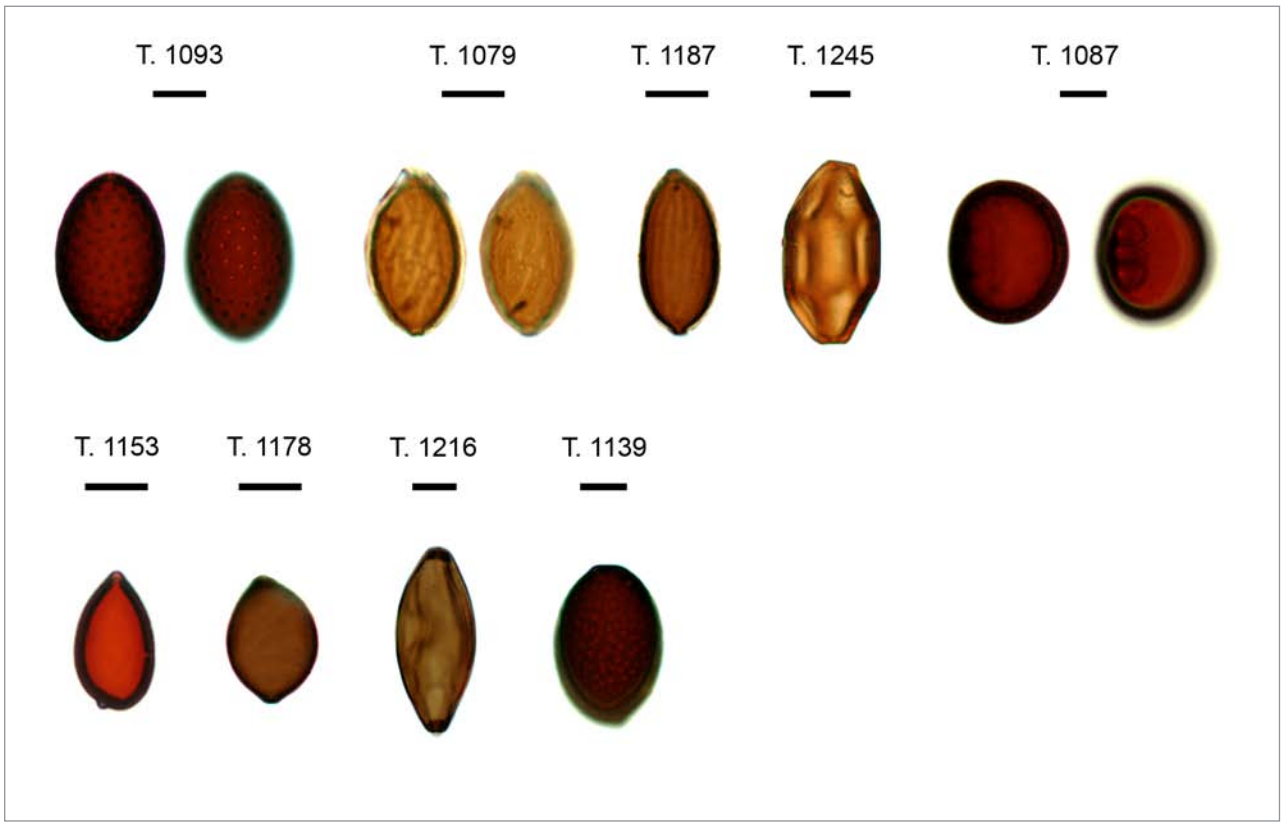

Plate VI. Non-septated spores/Amerosporae: without germ slit: diporate: ornamented: T. HdV-1093: *Gelasinospora* cf. *cratophora*, T. UG-1179, T. UG-1187, T. HdV-1245: *Diporotheca* sp.; Diporate: not ornamented: T. UG-1087, T. UG-1153, T. UG-1178: cf. *Sordaria* sp., T. UG-1216: *Diporotheca* sp.; Multiporate: T. UG-1139: *Gelasinospora* sp. All scale bars are 10 µm.

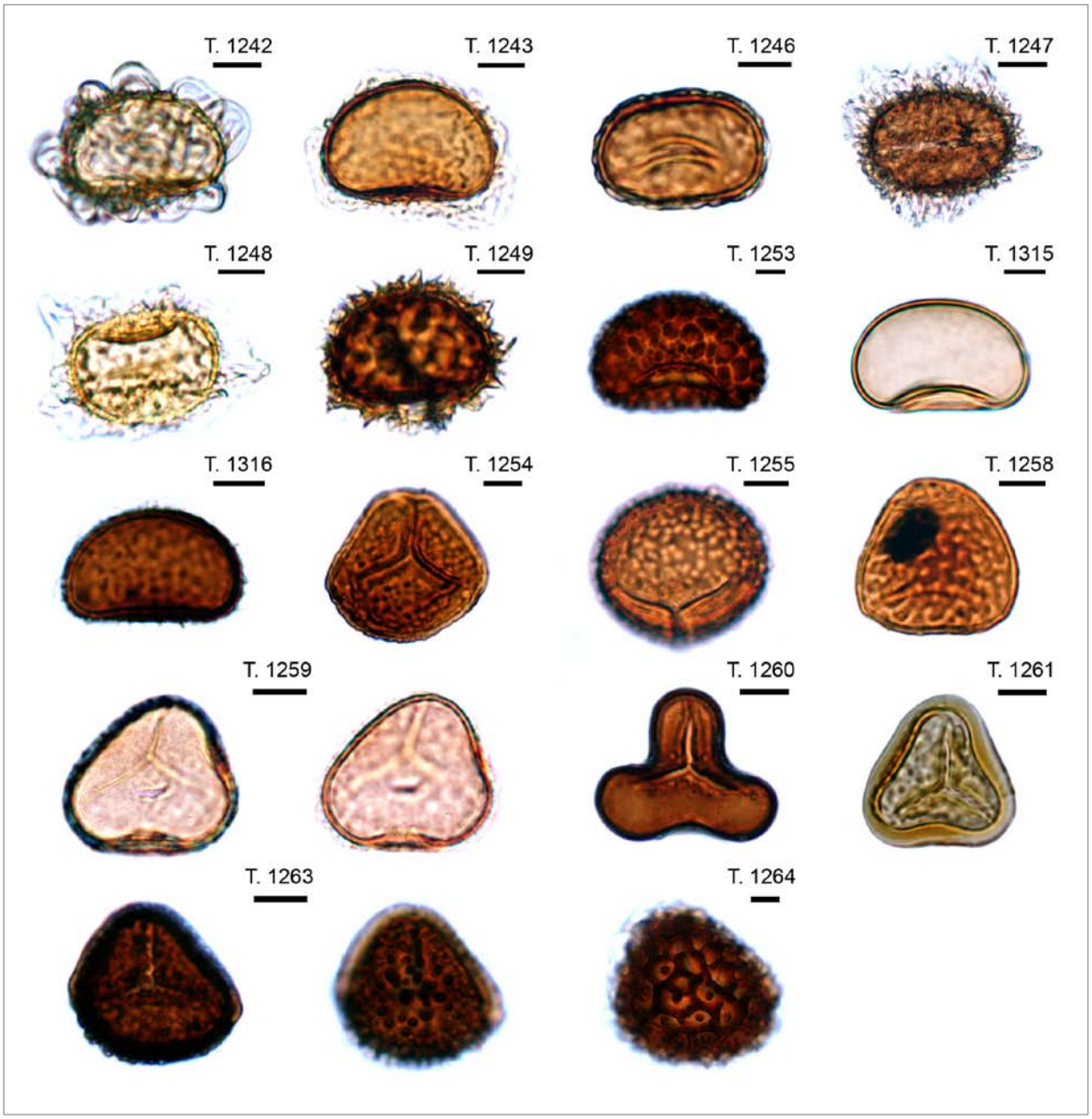

Plate VII. Fern and moss spores: Monoletes: T. UG-1242: *Dryopteris* subg. *Dryopteris,* T. UG-1243: cf. *Asplenium* sp., T. UG-1246: *Isoetes* type, T. UG-1247, T. UG-1248, T. UG-1249: cf. *Ctenitis/Lastreopsis* sp., T. UG-1253: Polypodiaceae, T. UG-1315: monoletes undiff., T. UG-1316: *Asplenium* type; Triletes: T. UG-1254: *Phaeoceros* cf. *carolianus*, T. UG-1255: *Ophioglossum* subg. *Ophioglossum*, T. UG-1258, T. UG-1259: *Pteridium aquilinum*, T. UG-1260: *Coniogramme africana* type, T. UG-1261: cf. *Pteris/Actiniopteris* sp., T. UG-1263: cf. *Grammitis* sp., T. UG-1264: *Pteris* sp. All scale bars are 10 µm.

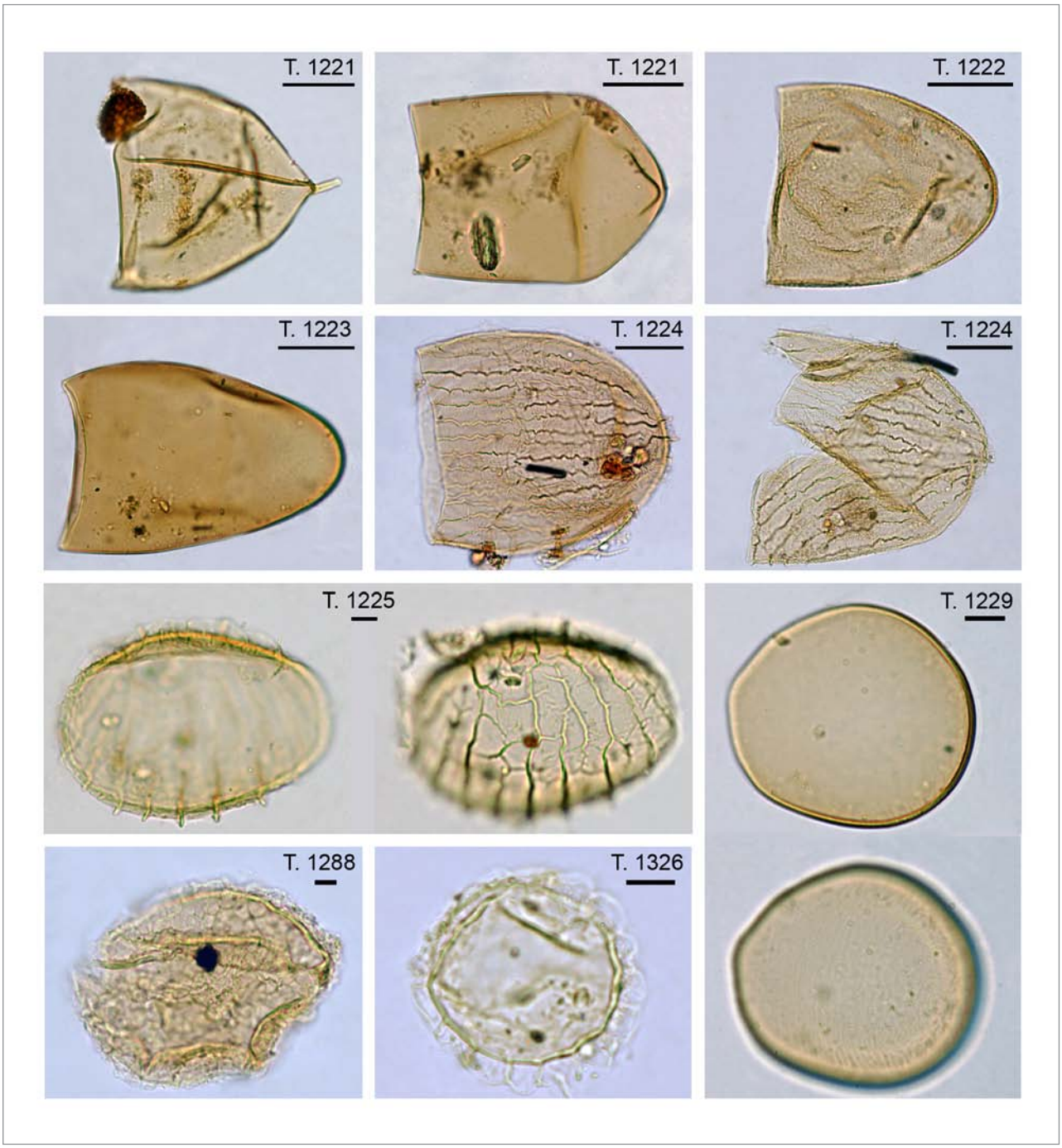

Plate VIII. Microscopic zoological remains: oocytes from *Neorhabdocoela* (flatworm) species: T. UG-1221, T. UG-1222, T. UG-1223, T. UG-1224; External cases of diapausing eggs (cysts) of unknown aquatic invertebrates: T. UG-1225, T. UG-1229, T. UG-1288, T. UG-1326. All scale bars are 10 µm, except for the *Neorhabdocoela* oocytes, which are 50 µm.

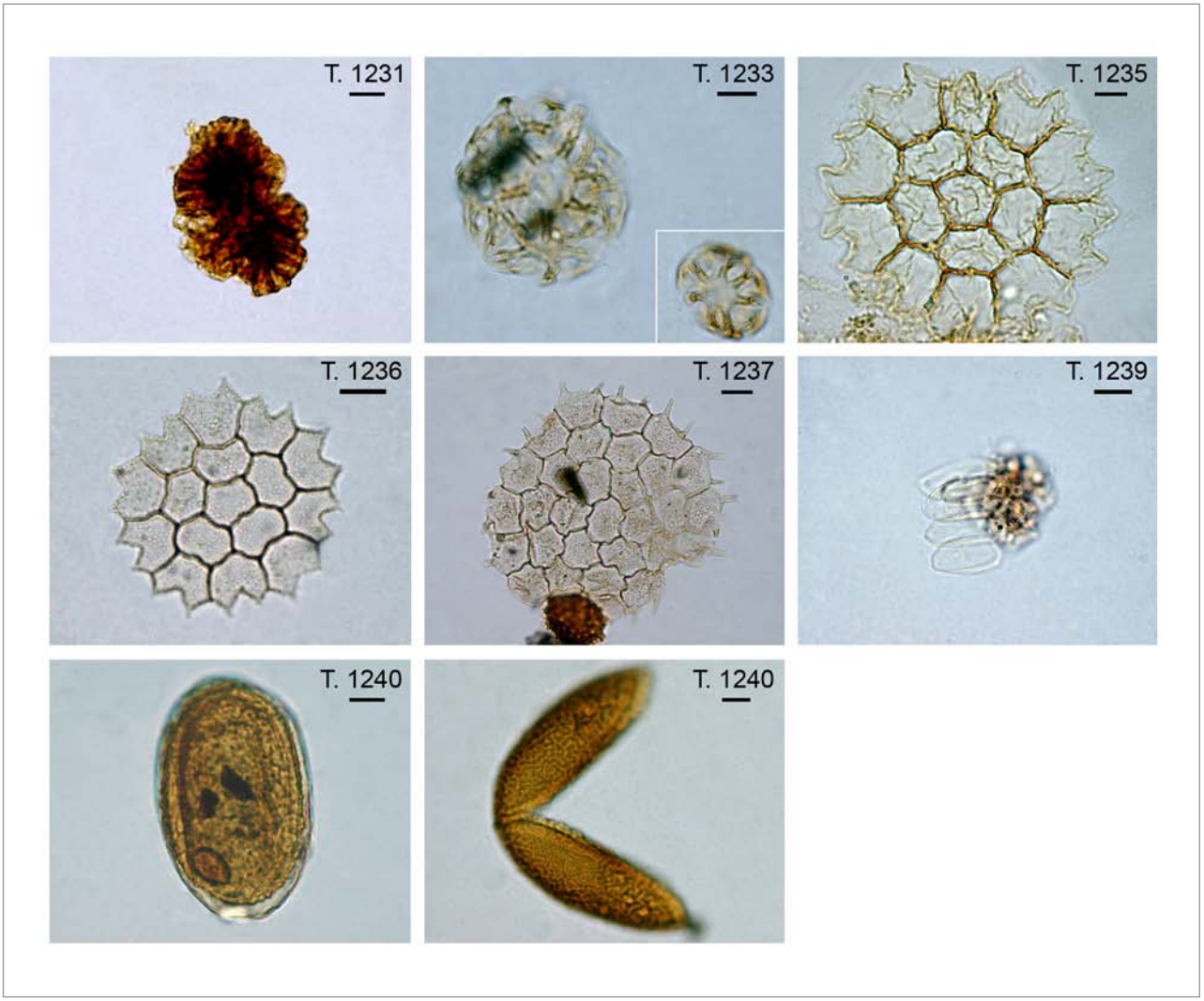

Plate IX. Algal zygospores, coenobia and colonies: T. UG-1231: *Botryococcus* cf. *neglectus*, T. UG-1233: *Coelastrum reticulatum*, T. UG-1235: *Pediastrum angulosum*, T. UG-1236: *Pediastrum boryanum* var. *brevicorne*, T. UG-1237: *Pediastrum boryanum* var. *forcipatum*, T. UG-1239: *Scenedesmus* sp., T. UG-1240: *Spirogyra* sp. All scale bars are 10 µm.

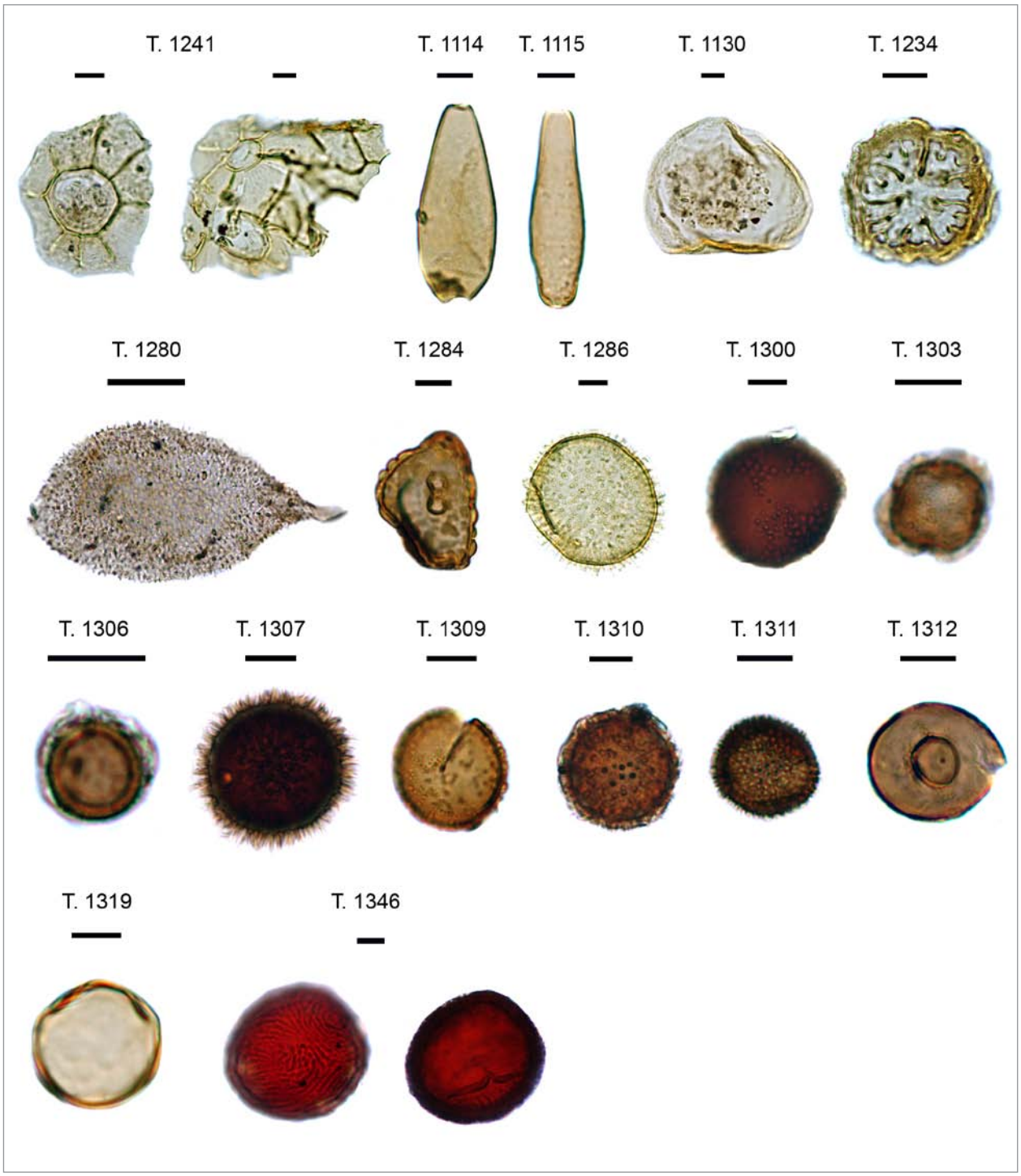

Plate X. Microscopic aquatic plant remains: T. UG-1241: Epidermis of *Nymphaea nouchali*; Unknown microfossils: T. UG-1114, T. UG-1115, T. UG-1130, T. UG-1234, T. UG-1280, T. UG-1284, T. UG-1286, T. UG-1300, T. UG-1303, T. UG-1306, T. UG-1307, T. UG-1309, T. UG-1310, T. UG-1311, T. UG-1312, T. UG-1319, T. UG-1346. All scale bars are 10 µm, except for T. UG-1280, which is 50 µm.

Effects of Land use on the fungal spore diversity of small crater-lake basins in western Uganda

Gelorini, V., Verbeken, A., Lens, L., Eggermont, H., Odgaard, B.V., Verschuren, D., in preparation. Fungal Diversity.

Abstract

Mycological tools to estimate the effects of diverse land-use practices on fungal diversity are scarce, because of poor knowledge of the taxonomic diversity of tropical fungi and their response to anthropogenic habitat change. Here, we investigate assemblages of fungal spores, recently deposited in the bottom sediments of 24 small crater lakes in western Uganda, to assess the relationship between the local diversity (richness and evenness) of fungi and environmental variation in the crater basin along regional gradients of natural vegetation and land use. We recovered ~9500 fungal spore specimens, which could be discriminated into 216 morphotypes. Using an information-theoretic approach based on the Akaike Information Criterion (AIC), we determined the environmental factors which best explained variation in richness and evenness of fungal spores among three datasets: (i) the full set of 24 crater basins, (ii) the subset of 22 basins with freshwater lakes, and (iii) the subset of 17 basins partly or completely in agricultural use (cropland, fallow land, pasture and plantation). In these 17 human-impacted crater basins our results revealed a negative relationship between fungal spore richness and the percent area of the basin in agricultural use. However, this detrimental effect of land use on fungal spore richness was not apparent across the full set of both disturbed and (presently) undisturbed basins. This was due to large variation in fungal spore richness among the undisturbed basins covered either with forest or savannah vegetation, probably resulting from site-specific controls on fungal habitat diversity such as climatic moisture balance and the composition of natural and/or secondary vegetation. In all crater basins and the freshwater lake basins only, variation in the evenness of the fungal spore assemblages is primarily explained by size characteristics of the undisturbed crater basins, possibly reflecting an association with the nutrient budget and productivity of these more stable ecosystems. The land-use effects on fungal spore diversity, as documented in this study, suggest that communities of tropical fungi progressively exposed to land-use practices are threatened by species loss. Hence, our study demonstrates the need to develop conservation strategies mitigating the impacts of agriculture on the biodiversity of tropical fungi.

Keywords: fungal spores, diversity, richness, evenness, land use, lake basins, western Uganda

3.1. Introduction

The rapidly accelerating extinction of plant and animal species is an increasing threat to the functioning of Earth's natural ecosystems (Vitousek *et al.*, 1997; Gaston, 2005). By the year 2100, land-use change will probably be the principal driver of overall biodiversity loss, particularly in the tropics where agricultural conversion of natural ecosystems and the overall intensity of anthropogenic land use continues unabated (Sala *et al.*, 2000). Conversion of tropical forests into agricultural land results in disappearance of many species of animals and fungi whose habitat is largely determined by the species composition of local plant communities (Vitousek *et al.*, 1997; Brooks *et al.*, 2002; Wright and Muller-Landau, 2006). Various studies in Europe (e.g., The Netherlands, Germany, Sweden and Finland) have documented significant loss of species diversity in macrofungi and ectomycorrhizal fungi coincident with forest decline (Arnolds, 1991; Amaranthus, 1998). In the tropics, the threat of extinction may be particularly acute for the more than a million estimated species of fungi living in direct association with plants (e.g., Hawksworth, 1991; Smith and Waller, 1992; Hyde and Hawksworth, 1997; Tsui *et al.*, 1998). Although more surveys are definitely needed to assess the true taxonomic diversity of tropical

fungi (Hawksworth, 2001; Mueller and Schmit, 2007; O'Brien *et al.*, 2005), recent studies suggest that the abundance and diversity of endophytes (e.g., Arnold *et al.*, 2000; Banerjee, 2011), soil fungi (e.g., Satish *et al.*, 2007), palm fungi (e.g., Fröhlich and Hyde, 1999) and ectomycorrhizal fungi (e.g., Verbeken and Buyck, 2002) in tropical forests and woodlands are much higher than previously recognised.

Assessing the diversity of tropical fungal communities is inherently labour-intensive, consequently most studies on modern fungi are strongly constrained in time and space by their particular objectives, sampling strategies and opportunities for culturing (O'Dell *et al.*, 1996; Hawksworth, 1993; Hyde and Hawksworth, 1997; Zak and Willig, 2004). Because of poor knowledge of the taxonomic diversity of tropical fungi and their response to habitat changes, mycological tools to estimate the effects of diverse land-use practices on fungal diversity are also scarce (Hyde and Hawksworth, 1997; Miller and Lodge 1997; Tsui *et al.*, 1998). The number of mycological studies quantifying land-use impacts on tropical fungi is growing (Hyde *et al.*, 1997; Pfenning, 1997; Persiani *et al.*, 1998; Cabello and Arambarri, 2002; Tchabi *et al.*, 2008), but they mostly refer to specific fungal communities in well-defined habitats. From these studies it appears that agricultural impacts together with variation in soil moisture related to natural rainfall variability may determine the level of diversity in fungal communities. Loss of fungal diversity is expected to affect the healthy balance of ecosystems (Arnolds, 1991), as well as human welfare by reducing important contributions of fungi to food production and biotechnological applications (e.g., Fox, 1993; Hyde and Hawksworth, 1997; Tsui *et al.*, 1998). As such, understanding the impact of human disturbance on fungal diversity in the tropics is of paramount importance for sustainable management of natural resources and ecosystems in developing regions.

Microfossil records preserved in lake and bog sediments provide keys to understand fundamentally important questions about ecosystem dynamics and environmental change at long temporal scales (Jackson and Williams, 2004; Willis and Birks, 2006). Fossil fungal remains mostly concern their small, well-preserved chitinous parts, the fungal spores. Today, exploitation of fossil assemblages of fungal spores using palaeoecological methods are increasingly shedding light on factors controlling the diversity and distribution of fungi (e.g., Blackford and Innes, 2006; Prager *et al.*, 2006; Yeloff *et al.*, 2007; Cugny *et al.*, 2010). These methods offer an interesting adjunct to the selective isolation and culturing of living fungi from spores (Sherwood-Pike, 1988), and can thus help to comprehensively assess the response of living fungal communities to human impacts on land cover. However, complicating effects of differential spore productivity, dispersal and preservation evidently create a somewhat biased picture of the composition and relative species abundances of the actual fungal communities living within the spores' source area. In lakes and pools, spores of terrestrial fungi are passively introduced via inflowing streams, rainwater, wind and insects (Smirnov, 1964; Ingold and Hudson, 1993). Due to the high difficulty level of taxonomic discrimination, it remains often unclear whether they are truly terrestrial or (semi-) aquatic. The reflected diversity is only a fragment of the true diversity, since the hyaline, thin-walled spores of aquatic and airborne fungi are mostly poorly preserved in lake deposits and are completely lacking in our samples (Gelorini *et al.*, 2011). Besides effects of taphonomic processes (e.g., rapid decay after dispersal) (Ingold and Hudson, 1993), this can be attributed to their physical degradation by the harsh chemical treatment of pollen preparation (e.g., Wolf 1966, 1967a,b; van Geel and Aptroot, 2006; Gelorini *et al.*, 2011; van Geel *et al.*, 2011). Also, the imperfect taxonomic discrimination allowed by the analysis of fungal spores makes it difficult to draw strong conclusions about the actual species diversity of fungi present. Nevertheless, documented relationships between fungal spore diversity and environmental variables may provide insights into baseline species diversity patterns and ecological processes at the landscape scale (e.g., Odgaard, 1999; Purvis and Hector, 2000; Whittaker *et al.*, 2001).

In this study we use an information-theoretic approach based on the Akaike Information Criterion (AIC; Akaike, 1974) to statistically evaluate the effect of anthropogenic land use on the taxonomic richness and evenness of fungal communities in western Uganda. Our study sites are 24 small crater basins selected to cover the main regional vegetation and habitat gradients from moist evergreen forest to grass savannah, and from relatively undisturbed to severely impacted by diverse types of agriculture. We investigated these fungal communities using the assemblages of fungal spores that are currently deposited in the lakes' bottom sediments, and which thus integrate habitat diversity

in space (across the lake catchment) and in time (across seasons and the last few years). As such, this study aims to comprehensively evaluate the response of tropical fungal communities to agricultural impacts at the landscape scale.

3.2. Material and methods

3.2.1. Study area

The 24 study sites (Fig. 3.1) are located in the Lake Edward-George branch of the East African Rift Valley in southwestern Uganda (0°43′N-0°15′S, 29°50′-30°21′E), which encompasses about 80 maar crater basins distributed over four main lake districts (Fort Portal, Kasenda, Katwe-Kikorongo and Bunyaruguru; see Melack, 1978) situated between ~900 and 1500 m elevation. Since the beginning of the 20th century, increasing population growth (3.3% per year) and intensifying land use, mainly driven by the growing demand for food and fuel, have reduced the natural vegetation (including lowland rain forest, dry semi-evergreen Guineo-Congolian rain forest, afromontane forest, swamp forest, and evergreen bushlands; White, 1983) from 45% to 20% of Uganda's total land area. Most of the natural tropical forest in the crater-lake regions has only been preserved in national parks, wildlife reserves and forest reserves such as Queen Elisabeth and Kibale National Parks. The still existing natural forest on public and private land is largely degraded and threatened by uncontrolled harvesting and forest clearance. Commercial and small-scale subsistence farming now comprise the dominant land use in Uganda (both 35%, Andrua, 2002). Moreover, poor agricultural practices, such as over-exploitation of rangelands and cultivation on steep slopes, have contributed to erosion and siltation of surface waters (Winterbottom and Eilu, 2006). Within the crater basins, gently sloping crater walls are often occupied by plantations (banana, coffee, eucalyptus, pine and cotton), annual food crops (sorghum, millet, maize), mixed vegetable gardens (potatoes, beans, cabbage) and meadows grazed by cows, sheep and goats. On more steeply sloping crater walls the natural vegetation of (secondary) deciduous forest, succulent plants and light-demanding ferns has remained more or less intact. The disturbed study sites are all located near human settlements, but seven crater basins are at present undisturbed by human activity because they are located inside protected areas, such as the secondary *Acacia* wooded grasslands and grass savannah of Queen Elizabeth National Park (Langdale-Brown *et al.*, 1964; Harrington, 1974) which has remained largely unaffected by human activity over at least the last 60 years; and the partly natural, partly secondary semi-deciduous and moist evergreen forests of Kibale National Park. All 24 crater-lake basins (with total surface area A) are small (lake surface area A_0 = 0.01-0.92 km^2; catchment area A-A_0 = 0.02-0.71 km^2; Table 3.1). Of these, 22 basins contain a freshwater lake (surface-water conductivity ranging from 56 to 920 µS/cm) and two basins a saline lake (with surface water conductivity of 22,400 and 61,100 µS/cm; Table 3.1). To comprehensively evaluate the effects of land use on the local diversity of fungal communities, we considered three datasets for this study: (i) the full set of 24 basins, (ii) the subset of 22 basins with freshwater lakes, and (iii) the subset of 17 basins with land cover slightly to severely impacted by anthropogenic land use.

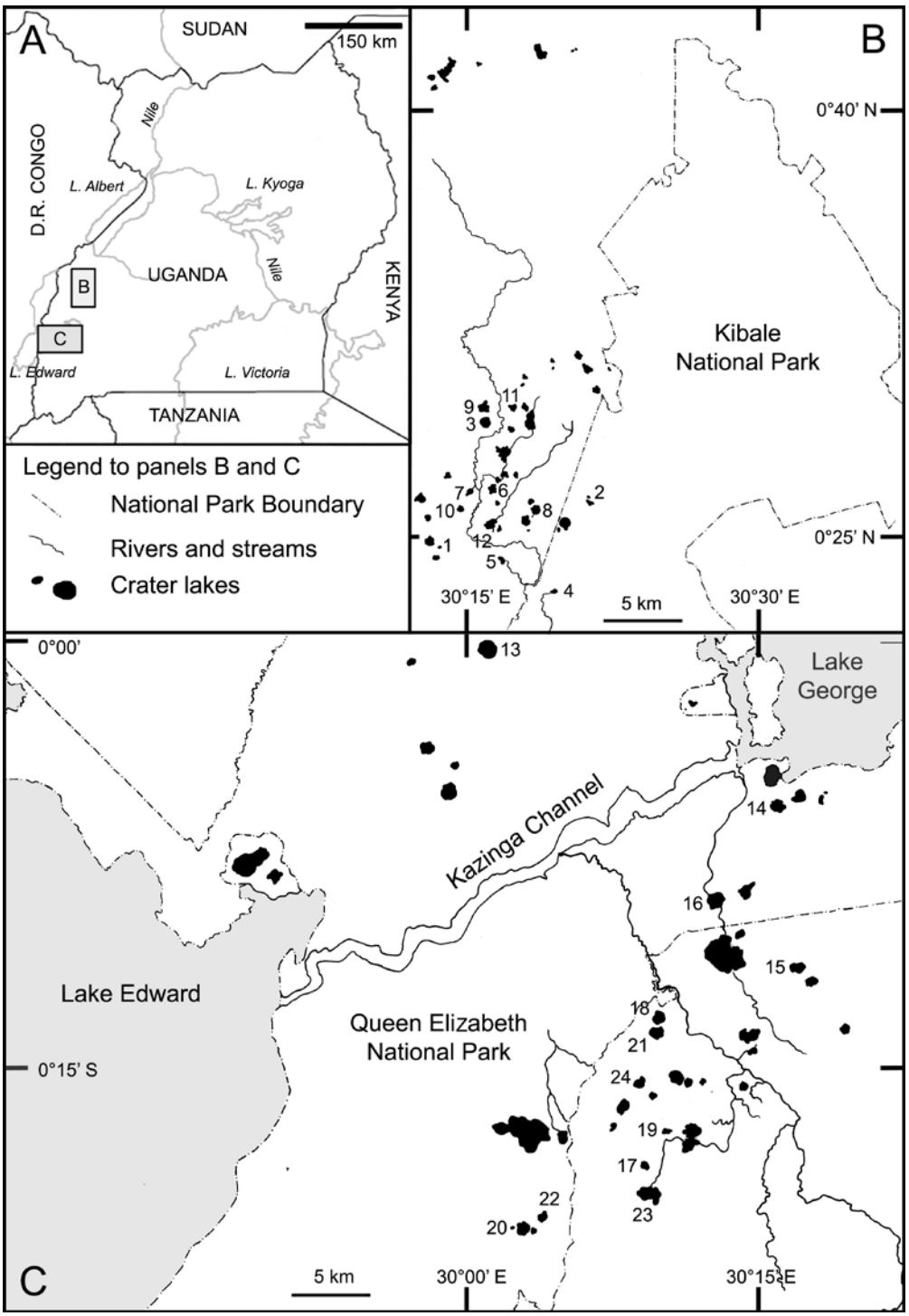

Fig. 3.1. General situation map of Uganda, with location of the 24 study sites in western Uganda (study regions B and C); modified from Rumes *et al.* (submitted). Lake basins in the Kasenda-cluster: 1. Kanyamukali, 2. Kanyanchu, 3. Katanda, 4. Kisibendi, 5. Kitere, 6. Mahuhura, 7. Mubiro, 8. Murusi, 9. Mwengenyi, 10. Nyarayabana, 11. Nyantonde, 12. Wankenzi. Katwe-Kikorongo-cluster: 13. Kikorongo. Bunyaruguru-cluster: 14. Bagusa, 15. Bugwagi, 16. Chibwera, 17. Kako, 18. Katinda, 19. Kigezi, 20. Kyogo, 21. Mirambi, 22. Murabyo, 23. Nkugute, 24. Nyungu.

Table 3.1. Sample list with lake names, environmental code (*D*: disturbed, *U-Fo*: Undisturbed-Forest, *U-Sa*: Undisturbed-Savannah), crater basin properties (*A-A0*: catchment area, *A0*: lake surface area, *Cond*: surface-water conductivity), fungal spore variables (*N*: number of counted specimens, F_s: observed richness, EF_{200}: rarefacted richness, and $E_{1/D}$: evenness) and environmental variables (*HAB*: number of habitat types, *AREA*: (A-A0)/A0, and *ANT*: fractional area (%) of crater basins in agricultural use).

#	Lake/Cluster	Env	A-A0 *km2*	A0 *km2*	Cond *µS/cm*	N	Fs *n*	EF200 *n*	E1/D	HAB *n*	AREA	ANT *%*
Kasenda												
1	Kanyamukali	D	0,05	0,02	920	783	50	25	0,04	11	2,53	82
2	Kanyanchu	U-Fo	0,02	0,01	568	208	44	43	0,26	2	2,28	0
3	Katanda	D	0,35	0,37	419	358	44	32	0,06	9	0,97	35
4	Kisibendi	U-Fo	0,05	0,04	277	212	38	37	0,14	2	1,29	0
5	Kitere	D	0,07	0,10	711	251	38	33	0,06	11	0,70	35
6	Mahuhura	D	0,19	0,19	600	432	45	32	0,06	10	1,00	45
7	Mubiro	D	0,14	0,16	718	206	24	24	0,07	7	0,88	60
8	Murusi	D	0,12	0,21	382	387	45	32	0,04	10	0,58	75
9	Mwengenyi	D	0,34	0,29	352	205	37	37	0,11	11	1,17	75
10	Nyarayabana	D	0,08	0,12	857	304	35	30	0,06	6	0,63	40
11	Nyantonde	D	0,06	0,12	501	309	32	27	0,06	12	0,49	82
12	Wankenzi	D	0,19	0,16	496	680	72	42	0,05	10	1,17	45
Katwe-Kikorongo												
13	Kikorongo	U-Sa	0,36	0,92	22400	204	14	14	0,08	2	0,40	0
Bunyaruguru												
14	Bagusa	U-Sa	0,71	0,33	61100	268	23	19	0,09	2	2,16	0
15	Bugwagi	D	0,34	0,60	441	486	41	26	0,05	15	0,56	75
16	Chibwera	U-Sa	0,22	0,76	457	261	40	34	0,05	2	0,29	0
17	Kako	D	0,15	0,17	89	371	25	19	0,09	11	0,88	100
18	Katinda	D	0,34	0,44	746	635	47	30	0,05	8	0,75	95
19	Kigezi	D	0,26	0,08	265	1045	53	30	0,07	10	3,35	99
20	Kyogo	U-Fo	0,04	0,02	56	221	23	22	0,06	2	2,24	0
21	Mirambi	D	0,31	0,53	642	245	28	26	0,07	8	0,58	90
22	Murabyo	U-Fo	0,32	0,27	141	537	50	33	0,06	2	1,22	0
23	Nkugute	D	0,26	0,89	121	613	39	24	0,07	15	0,29	97
24	Nyungu	D	0,34	0,14	430	319	18	15	0,10	7	2,35	100
	Min		0,02	0,01	56	204	14	14	0,04	2	0,29	0
	Max		0,71	0,92	61100	1045	72	43	0,26	15	3,35	100
	Avg		0,22	0,29	3904	398	38	29	0,08	8	1,20	51
	SD		0,16	0,27	12980,3	218,4	13,0	7,6	0,05	4,3	0,8	39,2

3.2.2. Vegetation mapping and sampling of fungal spores

In January-February and August-September 2008, land-cover data were collected to complement lake data and samples collected during two previous field campaigns in January-February and August-September 2007. We surveyed 24 crater basins to document the distribution of (at present) undisturbed and disturbed natural vegetation, and various types of anthropogenic land use. We also recorded the absolute numbers of livestock and, if traceable, of any large wild herbivores which use the lakes as watering hole. The land-cover distribution of different vegetation types (higher terrestrial plants, ferns and aquatic macrophytes) and land-use practices were sketched in radial sectors from a GPS-fixed vantage point in the center of the lake, with reference to topographic maps and Google Earth images. Interviews with local farmers and comparison with earlier vegetation surveys (1999-2007) that are available for some of the basins showed that vegetation and land use within the crater basins have remained more or less constant over at least the last decade, except for seasonal harvesting cycles and crop rotation.

Surface-sediment cores were recovered from the central, deepest part of each lake by means of a UWITEC gravity corer. In most lakes, each core top (5 cm sediment depth) was extruded upright and successively sectioned in 0-1 cm, 1-3 cm and 3-5 cm increments; in some deep lakes the removal of hydrostatic pressure during core recovery caused ebullition of methane contained in the soft sediment, and required the core top to be extruded in a single 0-5 cm increment. ^{210}Pb-dating in several lakes of the area (Russell *et al.*, 2007; Bessems *et al.*, 2008) suggests that the upper 5 cm of uncompacted surface muds typically represent the last eight to ten years of sedimentation.

3.2.3. Fungal spore analysis

We analysed ~2g wet sediment of the topmost layer from each lake according to standard palynological extraction techniques (Faegri *et al.*, 1989) which included sieving through 212 µm mesh, soaking in 10% KOH, acetolysis, heavy liquid separation (density: 2.0) with sodium polytungstate, and mounting in glycerin jelly. Scanning and counting was performed with an Olympus CX 31 light microscope at 400x and 1000x magnification. Conform to palynological methods, the abundance of fungal spores in each sample was counted relative to ~500 pollen grains of vascular plants (Birks and Birks, 1980). When fungal spore abundance was low (<100 spores per ~500 pollen grains: lakes Kikorongo, Kanyanchu, Kisibendi and Mubiro), we continued counting until at least 200 fungal spore specimens were encountered. Hence, the number of fungal spores analysed varied between 204 and 1045 specimens per sample. Identification of fungal spores was mainly based on comparison with descriptions and illustrations in primary taxonomic literature, including Ellis (1971, 1976), Subramanian (1971), Ellis and Ellis (1985), and Bell (1983), and specialised taxonomic literature on tropical fungi (e.g. Dennis, 1961; Goh *et al.*, 1997; Goh *et al.*, 1998; Sivichai *et al.*, 1998; Mibey and Kokwaro, 1999). Fungal spores were attributed to known species or genera only when they fully agreed with published morphological descriptions, and their presence in tropical regions had been confirmed by other studies (Gelorini *et al.*, 2011). All identified fungal remains were classified with reference to the latest taxonomic developments, implemented in the *Index fungorum* (CABI database, Index Fungorum Partnership, 2004) and the *Dictionary of fungi* (Kirk *et al.*, 2008).

3.2.4. Observed and rarefacted fungal spore richness

Taxon richness was evaluated using the observed number of taxa present (F_s), and the number of taxa expected with constant sample size (EF_n) using Hurlbert's rarefaction method (Magurran, 2004). The latter was used to compensate for the different sample yields when comparing fungal spore richness among samples (Hurlbert, 1971; Gotelli and Colwell, 2001; Magurran, 2004). Since Hurlbert's rarefaction method cannot be used for extrapolation (Gotelli and Colwell, 2001), we estimated richness relative to a constant sample size of 200 specimens (EF_{200}), approximating the lowest number of specimens (204) recovered at any site. Using Primer version 5.2.2 (Primer-E Ltd, 2001), we calculated the rarefaction

estimate, defined by

$$EF_n = \sum_{i=1}^{F_S} 1 - \left[\frac{(N - N_i)!(N - n)!}{(N - N_i - n)!N!} \right]$$

where EF_n is the rarefacted fungal spore richness at sample size n, N the sum of counted spores in the original sample, F_s the actual fungal spore richness in the original sample, and N_i the number of spores of type i.

Although rarefaction measures are widely used as indices of species richness in palaeoecological studies (Tipper, 1979; Birks and Line, 1992; Berglund *et al.*, 2007), these richness estimates are influenced by the evenness of the distribution of species abundances' across assemblages. Evenness is high when all species present have comparable relative abundances; evenness is low when one or a few species are over-abundant while all other species are comparatively rare. Evenness determines the shape of the species accumulation curve (Fig. 3.2). Presence of a few abundant taxa may impede detection of lower frequency taxa compared to samples where taxon frequencies are more even (Peros and Gajewski, 2008). Since palaeoecological samples are invariably small in relation to the total population from which they originate, the recovered species richness will be much lower in a sample of low evenness than in one with high evenness, even though population richness is identical (Odgaard, 2001). To ensure statistical robustness of our results, we therefore integrated an evenness index into our study.

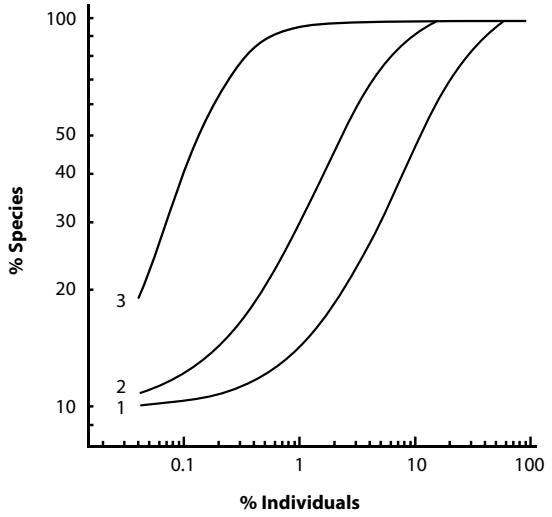

Fig. 3.2. Species accumulation curves showing the relationship between the number of species and the number of individuals, when using rarefaction techniques; both expressed as percentages on a logarithmic scale. Curves for three different populations with the same total species richness are shown with (1) low, (2) intermediate, and (3) high evenness, indicating that the observed number of species for small sample sizes is determined by the evenness (modified from Odgaard, 2001, 2007).

3.2.5. Evenness

Numerous evenness indices exist, but their applicability mainly depends on the biological structure of the dataset and the index properties favoured by users. To be adequate, an evenness index must satisfy three criteria: (i) independence from species richness, (ii) independence from sample size, and (iii) unambiguous relationship to evenness (Molinari, 1996). In this study we used the evenness measure $E_{1/D}$, which conforms most closely to these three criteria (Smith and Wilson, 1996). It is one of three known indices unaffected by species richness and only slightly affected by sample size (Smith and Wilson, 1996; Beisel *et al.*, 2003; Magurran, 2004). Contrary to E_Q and E_{var}, the shape of $E_{1/D}$ also responds most coherently to an evenness gradient (i.e., it has an excellent Molinari shape), which underscores its distinct relationship to evenness. According to Biesel *et al.* (2003), $E_{1/D}$ is sensitive to density variations of 'rare' taxa (here defined as N_i<5%, following Biesel *et al.*, 2003), which may be advantageous for assessing spatial or temporal changes in the abundance of important indicator species, which are feebly represented in a community. We used the Ecological Evenness Calculator (Smith and Wilson, 1996) to calculate $E_{1/D}$ as

$$E_{1/D} = \frac{1/D}{F_s}$$

where D represents the Simpson's dominance index (Simpson, 1949)

$$D = \sum_{i=1}^{F_S} \left(\frac{n_i}{N} \right)^2$$

and F_s the observed fungal richness in the sample. To detect possible influences of evenness on rarefacted richness, we also calculated Pearson correlation coefficients between richness (EF_{200}) and evenness ($E_{1/D}$).

3.2.6. Environmental data processing

To assess if values for rarefacted fungal spore richness (EF_{200}) and evenness ($E_{1/D}$) recorded in the sediment samples were affected by the size of the putative source area of the fungal spores, we integrated measurements of crater-basin morphometry into the analysis. Small lake-surface areas (A_0) were calculated using GPS-guided field data of either circumference or average diameter. Larger, irregularly shaped lake-surface areas and all terrestrial catchment areas (A-A_0) were determined by analysis of topographic maps (scale 1:50 000) overlain with a mm-scale grid (Claessens, 2002). Because the influx of fungal spores to the mid-lake coring site may be influenced by its mean distance to the source area, we used the catchment area/lake area ratio $(A\text{-}A_0)/A_0$ as a quantitative measure for relative basin size (*AREA*).

We further employed two different quantitative measures for the severity of human impact: (i) for the datasets including either all 24 basins or the 22 basins with freshwater lakes only, we used the categorical variable (1/0) for presence/absence of anthropogenic landscape disturbance (*DIST*) based on the occurrence of anthropogenic land-cover types, such as *Eucalyptus* or pine plantations, crop cultivation, fallow land, pasture and bare land; and (ii) for the dataset of only the 17 disturbed basins, we calculated the summed areal percentage of all these anthropogenic land-cover types as a measure for the magnitude/intensity of human activity in the crater basins (*ANT*). Habitat diversity in each basin (*HAB*) was defined as the total number of distinct natural and anthropogenic land-cover types present. To accurately interpret patterns of diversity in (semi-) aquatic fungi and dung fungi, we also included two near-shore habitat types: emergent riparian vegetation (usually *Phragmites*, *Cyperus* and/or *Typha*) and the excrements of cattle or wild animals using the lake as watering hole.

3.2.7. Model building and selection

For each dataset separately, sets of candidate models were constructed a priori with a (combinations of) explanatory variables (*AREA*, *DIST*, *HAB*, *ANT*) hypothesised to influence fungal spore diversity (EF_{200} and $E_{1/D}$). We used an information-theoretic statistical approach (Burnham and Anderson, 2002) to examine which models considered within these sets of candidate models best described variation in the rarefacted richness (EF_{200}) and evenness ($E_{1/D}$) among samples. Fit statistics of random-effect models based on pseudo-likelihoods are not useful for model comparison (SAS Institute Inc, 2008), and a general approach to select random-effect models remains elusive (Burnham and Anderson, 2002). We therefore fitted generalised linear models (Proc GLM in SAS 9.2) to the fungal assemblage data, in which the following variables were treated as fixed effects: *AREA*, *DIST*, *HAB*, *ANT* and all relevant two-factor interactions. Separate model selections were performed for the full set of 24 crater basins (main effects *AREA*, *DIST*, *HAB*), the 22 basins with freshwater lakes only (main effects *AREA*, *DIST*, *HAB*) and the 17 disturbed basins only (main effects *AREA, ANT, HAB*). Prior to model selection, intercept-only models were fitted to assess whether models including combinations of the fixed variables better explained the fungal assemblage data than a model without these variables (results not shown).

Model weights based on Akaike Information Criterion (AIC) values corrected for small sample size (AICc, Burnham and Anderson, 2002) were calculated for each model within the set of candidate models. Each model that differed less than two AICc units (ΔAICc) from the most parsimonious model was considered to fit the data equally well. Since in this data analysis the best model had no definitive and differing interpretation, and several models might fit the data well, inference was based on best estimates of the set of model effects (*AREA, HAB, DIST, ANT, AREA*HAB, AREA*DIST, AREA*ANT* and *ANT*HAB*) included in the candidate models. We applied model averaging to all candidate models which contained these model effects to estimate the direction and strength of each parameter separately according to their relative fit (Burnham and Anderson, 2002). This procedure allowed us to include model selection uncertainty in estimating the precision of each effect, and to calculate unconditional standard errors (*SE*) following the method outlined in Mazerolle (2004).

3.3. Results

3.3.1. Fungal spore analysis

The 24 lake-sediment samples yielded between 204 and 1045 fungal spores (Table 3.1) for a grand total of ~9500 specimens, which could be discriminated into 216 different morphotypes. Among the 64 morphotypes (30%) that could be identified at the species, genus or family level, only five belonged to taxa which are known to include fungi living on submerged wood substrates in freshwater aquatic habitat: *Brachydesmiella* sp. (Sivichai *et al.*, 1998), cf. *Byssothecium* sp. (Crane *et al.*, 1992), cf. *Savoryella lignicola* (Ho *et al.*, 1997), *Sporoschisma* spp. (Goh *et al.*, 1997) and *Canalisporium* spp. (Goh *et al.*, 1998). All identified fungal spores (mostly conidia and ascospores) were thick-walled, and mainly derived from saprotrophic, mycorrhizal or dung fungi of which the spores are transported into the lakes by mainly wind and water (with soil, plant debris and/or dung). Fifty-three of these identified fungal taxa were described, illustrated and provided with a taxonomic discussion by Gelorini *et al.* (2011) (Fig. 3.3).

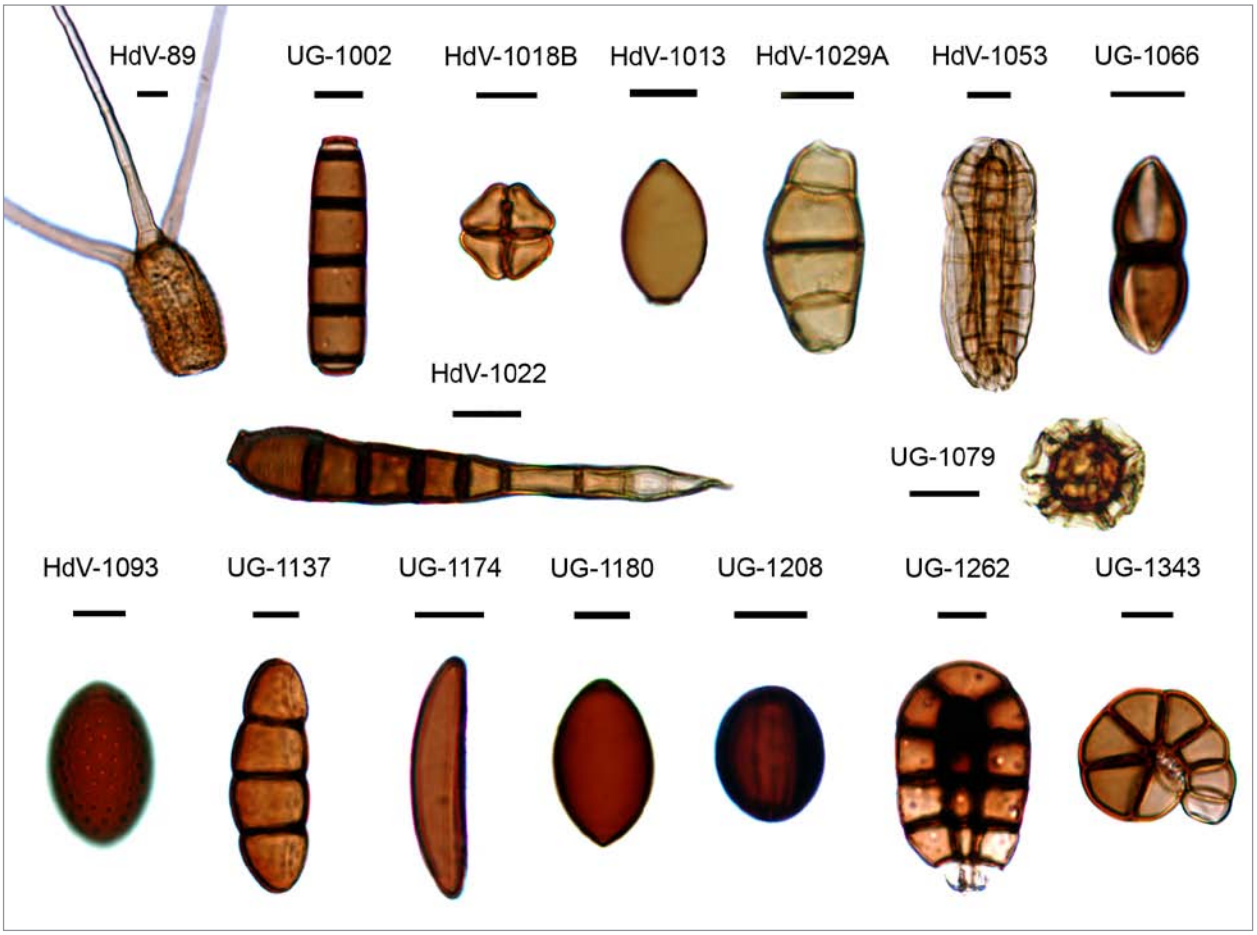

Fig. 3.3. Selection of fungal spore types recovered from Ugandan crater-lake sediments in this study. HdV-89: *Tetraploa aristata*, UG-1002: *Sporoschisma* spp. (*S. saccardoi*, illustrated here), HdV-1013: *Cercophora* type, HdV-1018B: *Spegazzinia tessarthra*, HdV-1022: *Clasterosporium* sp., HdV-1029A: *Curvularia* cf. *intermedia*, HdV-1053: *Dictyosporium* cf. *heptasporum*, UG-1066: *Delitschia* spp., UG-1079: *Urocystis* sp., HdV-1093: *Gelasinospora* cf. *cratophora*, UG-1137: *Meliola* sp., UG-1174: *Rosellinia* sp., UG-1180: *Sordaria* spp., UG-1208: *Coniochaeta* spp., UG-1262*: *Canalisporium* spp., UG-1343: cf. *Cirrenalia* sp. All scale bars are 10 µm. Abbreviations of lab codes: HdV (previously Hugo de Vries laboratory, now IBED, University of Amsterdam), UG (Universiteit Gent).

*Revision of the type *Canalisporium pulchrum* (Gelorini *et al.*, 2011) after Goh *et al.* (1998), which probably includes several *Canalisporium* species, such as *C. pulchrum* and *C. kenyense* (illustrated here).

3.3.2. Richness and evenness

F_s varied from 14 fungal spore morphotypes in Kikorongo to 72 morphotypes in Wankenzi, with a mean of 38 (SD = 13) over the 24 sampled basins. Values of EF_{200} ranged from 14 morphotypes in Kikorongo to 43 morphotypes in Kanyanchu, with a mean of 29 (SD = 7.6). Among the seven undisturbed basins (Table 3.1; Fig. 3.4), the expected spore richness was relatively low in the two savannah sites with saline lakes (Kikorongo and Bagusa: EF_{200} = 14 and 19, respectively) compared to the five basins with freshwater lakes (EF_{200} = 22-43), which besides four forest sites includes Chibwera (EF_{200}= 34), the only savannah site in our dataset occupied by a freshwater lake. Due to the over-abundance of *Coniochaeta* spp. in most samples (between 19.2 and 92.2% of the counted spores, on average 63.1%), and rare taxa (here defined as N_i <0.5%) representing between 31.3 and 78.6% of the observed richness per sample (Fig. 3.5, and details in Appendix 3.2), $E_{1/D}$ was extremely low, ranging from 0.04 to 0.26, with a mean of 0.08 (SD = 0.05) (Table 3.1; Fig. 3.6). $E_{1/D}$ was not significantly correlated with the number of rare taxa (R^2=0.002, p=0.59), despite the claimed sensitivity of $E_{1/D}$ to rare taxa (Biesel *et al.* 2003). The inverse correlation between $E_{1/D}$ and %*Coniochaeta* spp. (R^2=0.48, p=0.0002; Fig. 3.7) highlights the dependence of $E_{1/D}$ on the exact relative abundance of *Coniochaeta* spp. in our samples, and the effect of variation in %*Coniochaeta* spp. on the relative abundance of all the less common taxa. As a result the number of rare taxa in each sample was significantly correlated with %*Coniochaeta* spp. (R^2=0.17, p=0.05) confirming the predicted effect of low evenness on observed taxon richness (Fig. 3.8; Odgaard, 2001; Peros and Gajewski, 2008). No significant correlation occurs between $E_{1/D}$ and EF_{200} (R^2=0.08, p=0.17), satisfying in principle the criterion of independence between both diversity indices. However, when excluding *Coniochaeta* spp. from all datasets and recalculating both diversity measures for the 15 crater-lake basins where N remains above 100 (F_s=25-72; N=101-538), EF_{100} (22-43) and the now much higher evenness values for $E_{1/D}$ (0.19-0.62) were significantly correlated (R^2=0.32, p=0.03) (Fig. 3.9).

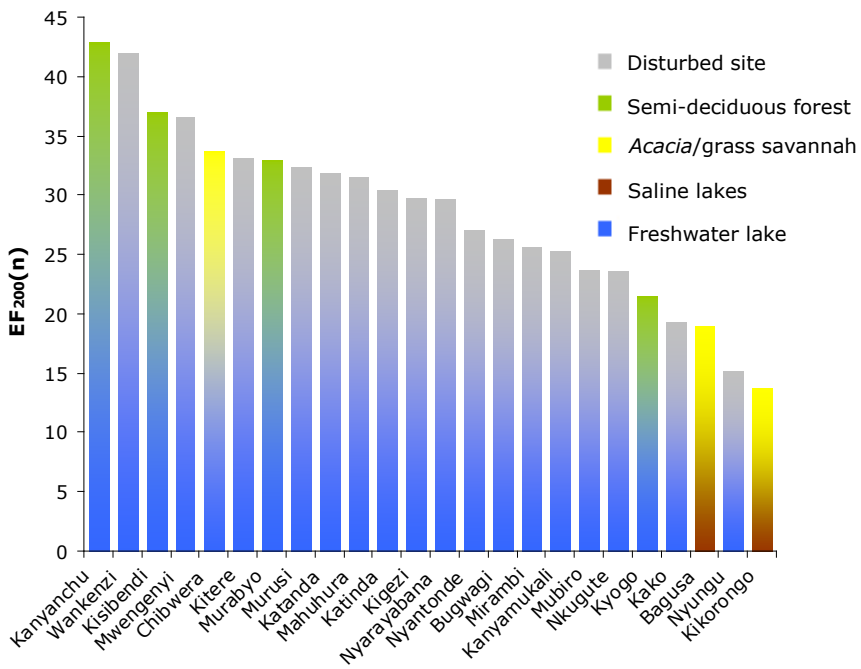

Fig. 3.4. The 24 study basins ordered from high to low expected spore richness (EF_{200}), with colour codes for undisturbed sites (forest or savannah), disturbed sites and the type of lake (saline or fresh), showing that undisturbed sites generally have high fungal-spore diversity, but not when occupied by a saline lake.

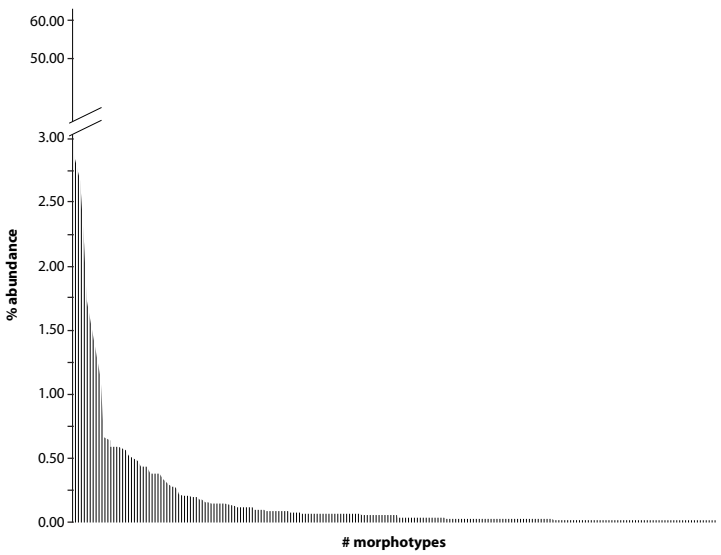

Fig. 3.5. Overall % abundance of the 216 types of fungal spores (bars) recovered from the sediments of 24 study sites, relative to the total sum of ~9500 counted spores. *Coniochaeta* spp. represents 63.1% of the total fungal spore inventory; other morphotypes account for at most 3%, and all but 20 taxa are rare (< 0.5%).

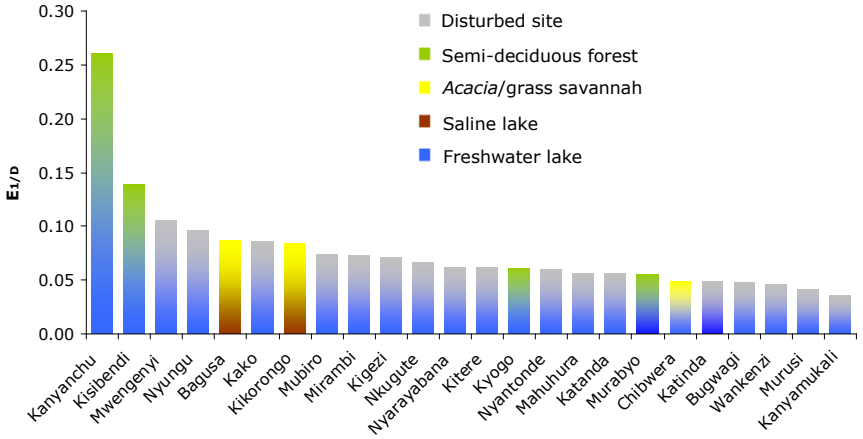

Fig. 3.6. The 24 study basins ordered from high to low evenness ($E_{1/D}$), with colour codes for undisturbed sites (forest or savannah), disturbed sites and the type of lake (saline or fresh), showing little relationship between fungal spore evenness and disturbance.

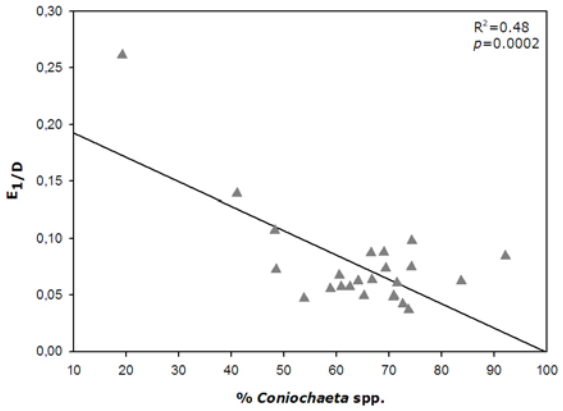

Fig. 3.7. Negative relationship between evenness ($E_{1/D}$) and %*Coniochaeta* spp. in our 24 crater-lake basins.

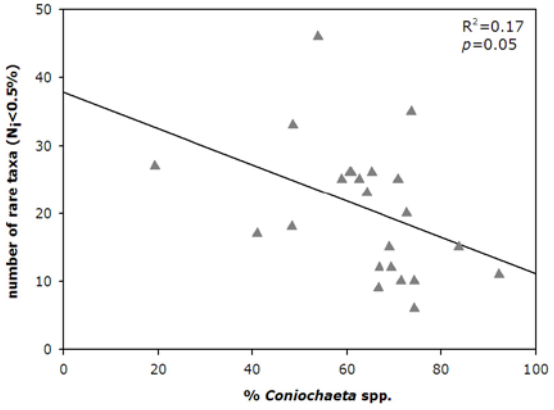

Fig. 3.8. Negative relationship between the number of rare taxa (*Ni*<0.5%) and %*Coniochaeta* spp. in our 24 crater-lake basins.

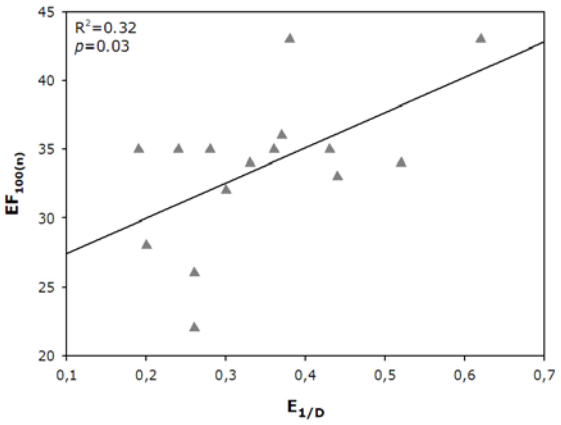

Fig. 3.9. Positive relationship between rarefacted fungal spore richness (*EF100*) and evenness (*E1/D*) for the 15 crater-lake basins with *N*>100 individuals, when %*Coniochaeta* spp. is excluded.

3.3.3. Relative effects of the environmental variables on richness and evenness

Appendix 3.1 shows the results of the model selections for the three datasets (all basins, the freshwater lake basins only and disturbed basins only) for EF_{200} and $E_{1/D}$, highlighting the models which fit the data (almost) equally well (ΔAICc values ≤ 2). The most parsimonious model in each set of candidate models (12 models for all basins and the freshwater lake basins only, 17 models for the disturbed basins only) explained between 0.1 and 19% of the variation in fungal spore richness (EF_{200}) and between 10 and 43% of the variation in fungal spore evenness ($E_{1/D}$).

Model-averaged parameter estimates, unconditional SE and 95% confidence intervals are calculated for all model effects (*AREA, HAB, DIST, ANT, AREA*HAB, AREA*DIST, AREA*ANT* and *ANT*HAB*) included in the candidate models, and are listed in Table 3.2. When modelling variation in EF_{200} among all sites (i.e., the full dataset), the environmental variables *AREA*, *HAB* and *DIST* were all retained within the selected models, however the 95% confidence intervals around the parameter estimates included zero in all cases, suggesting weak effects only. We attribute this result to high variability in fungal spore richness among the seven undisturbed sites (Table 3.1). More specifically, fungal spore richness in the two *Acacia*/grass savannah basins with saline lakes (Kikorongo and Bagusa) is much lower than that in the five basins occupied by freshwater lakes, from which one is located in *Acacia*/grass savannah (L. Chibwera) and four in semi-deciduous forest (Fig. 3.4). In the dataset without the two saline-lake basins, variation in EF_{200} showed a strong negative relationship to the categorical variable *DIST* (model-averaged slope= -5.39± 2.50). This negative impact of disturbance on EF_{200} was smaller but also apparent (model-average slope= -0.15 ± 0.10) in the models testing fungal assemblage response to environmental variation within the subset of disturbed basins only, where *DIST* was replaced by the continuous variable *ANT*. Linear regression of EF_{200} on *ANT* shows that the areal proportion of a crater basin disturbed by human activity explains 35% of the variation in EF_{200} (p=0.01; Fig. 3.10). It thus appears that the more a crater catchment is converted into agricultural land, the more fungal spore richness is reduced. Habitat diversity (*HAB*) was not retained by the most parsimonious models for EF_{200} in the subset of disturbed basins, and thus does not seem to have an effect on fungal spore richness. This somewhat counter-intuitive result can be explained by the fact that besides the presence of forest or savannah remnants, *HAB* is mainly determined by the local diversity of anthropogenic habitat types, which by itself does not appear to influence fungal spore richness decisively.

When modelling variation in the evenness ($E_{1/D}$) of fungal diversity among sites for the full dataset and the dataset of freshwater lake basins only, effects of the relative size of the basins' catchment (*AREA*), linked to *DIST* and *HAB* separately, had a negative effect on evenness (Table 3.2). However, again these relationships were mainly driven by variation in evenness among the undisturbed basins (Figs. 3.6 and 3.11). When focusing on the disturbed basins only, evenness was not affected by any variable retained within the selected models (Table 3.2: the 95% confidence intervals included zero in all cases).

Table 3.2. AICc and associated measures recomputed to obtain the model-averaged estimate (MA est), precision (unconditional SE) and 95% confidence intervals (CI=2σ) of the main model effects, explaining the variation in richness (EF_{200}) and evenness ($E_{1/D}$) for the three datasets (all crater basins, the freshwater lake basins and the disturbed crater basins). Only model effects included in the (near-) parsimonious models (ΔAICc ≤ 2, see Appendix 3.1), are displayed; those where the 95% confidence interval of the parameter estimates excludes zero are highlighted in bold.

Model selection	**All crater basins**				**Freshwater lake basins**				**Disturbed crater basins**			
Model effects	*MA est*	*Uncon SE*	*-95% CI*	*+95% CI*	*MA est*	*Uncon SE*	*-95% CI*	*+95% CI*	*MA est*	*Uncon SE*	*-95% CI*	*+95% CI*
AREA	-0,46	0,94	-2,29	1,38	-	-	-	-	-	-	-	-
HAB	0,01	0,20	-0,38	0,39	-0,32	0,21	-0,74	0,09	-	-	-	-
DIST	-0,28	1,86	-3,90	3,38	**-5,39**	**2,49**	**-10,28**	**-0,50**				
ANT									**-0,15**	**0,07**	**-0,28**	**-0,02**
AREA*HAB	-	-	-	-	-	-	-	-	-	-	-	-
AREA*DIST	-	-	-	-	-	-	-	-				
AREA*ANT									-	-	-	-
ANT*HAB									-	-	-	-
AREA	0,02	0,01	-0,003	0,05	0,04	0,03	-0,01	0,09	0,0047	0,0049	-0,0049	0,0144
HAB	-0,001	0,002	-0,005	0,003	0,001	0,003	-0,005	0,006	-0,0014	0,0010	-0,0033	0,0006
DIST	-0,02	0,02	-0,06	0,01	-0,01	0,03	-0,06	0,04				
ANT									0,0002	0,0001	-0,00003	0,0005
AREA*HAB	**-0,005**	**0,0005**	**-0,01**	**-0,004**	**-0,01**	**0,001**	**-0,009**	**-0,005**	-	-	-	-
AREA*DIST	**-0,04**	**0,003**	**-0,04**	**-0,03**	**-0,06**	**0,01**	**-0,07**	**-0,04**				
AREA*ANT									-	-	-	-
ANT*HAB									-	-	-	-

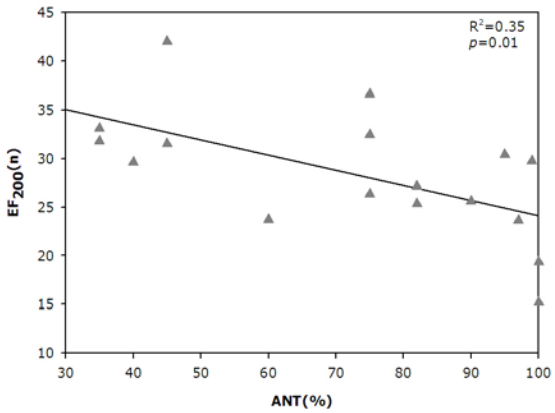

Fig. 3.10. Negative relationship between the rarefacted fungal spore richness (EF_{200}) and the areal fraction of disturbed crater basins affected by anthropogenic land use (*ANT)*.

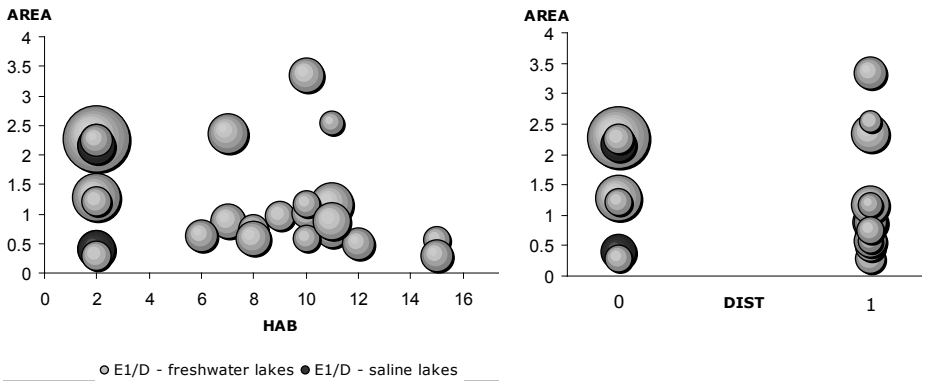

Fig. 3.11. Evenness ($E_{1/D}$; bubble size) of fungal spore assemblages in relation to the relative size of the catchment (*AREA*), habitat diversity (*HAB*; left panel) and disturbance (*DIST*; right panel) for the full 24-lake dataset. All undisturbed sites have a *HAB* value of 2 and a *DIST* value of 0 (Table 3.1).

3.4. Discussion

3.4.1. Fungal spore richness and evenness

The overall richness of fungal spore morphotypes recovered from the 24 studied samples of Uganda crater-lake sediments was very high, totaling 216 morphotypes on a total of ~9500 fungal spore specimens. Fungal spore richness per crater basin was substantially lower, varying between 14 and 72 morphotypes. This difference suggests that the tropical fungal communities which produced these spores are strongly heterogeneous along the sampled regional environmental gradients of natural vegetation and human impact. The high richness and abundance of fungal spores recovered in this study seemingly support the hypothesis that fungal spores in lake ecosystems are numerous and diverse (Wurzbacher *et al.*, 2010). However, the recovered spores are typically robust and thick-walled, and most of those we could identify originate from terrestrial saprotrophic, mycorrhizal and coprophilous fungi growing on sub-aerial substrates (e.g., plant debris, dead wood, macrophytes and dung). Since only very few belong to taxa with known aquatic representatives, we treat our fungal spore data to represent the communities of fungi living in terrestrial habitat within the crater basins.

At present, it is hardly feasible to compare the results of this study to other studies dealing with fungal spore diversity. Analogous studies from Europe (e.g., Blackford and Innes, 2006; Prager *et al.*, 2006; Yeloff *et al.*, 2007; Cugny *et al.*, 2010) are exclusively concerned with fungal spore archives contained in the subsoil of (semi-)terrestrial ecosystems (e.g., oak woodland, alder carr, raised bogs and mountainous pasture-woodland). Moreover, all these efforts to calibrate the modern distribution of fungal spores have focused on the ecological significance of only the most common fungal types or groups found in the assemblages, producing a distorted view of the true taxonomic richness of fungal spores in the datasets. Further, to our knowledge only two previous studies have assessed fungal spore diversity in tropical African environments: Wolf (1966) dealt with fungal spore distribution in the surface sediments of lakes and ponds in Kenya, and Jarzen and Elsik (1986) examined fungal spores from recently deposited river sediments in Zambia. However, it is uncertain whether these studies accurately represented the true fungal spore richness present in the studied samples.

The low to extremely low (0.04 to 0.26) evenness of fungal spore diversity in all studied crater basins is mainly due to the over-dominance of *Coniochaeta* spp. at all sites; *Coniochaeta* species can be found on various substrates, such as bark, (submerged) wood, dung and plant remains, the latter particularly from grasses (Romero *et al.*, 1999; Asgari *et al.*, 2007). This low evenness may have influenced the rarefacted richness (EF_{200} ranging from 14 to 43 morphotypes; Table 3.1), which was possibly underestimated. When excluding *Coniochaeta* spp. from the datasets, the evenness of fungal spore diversity increased by a factor of two to six, to $E_{1/D}$ values ranging between 0.19 and 0.62. Also, $E_{1/D}$ was significantly positively correlated with EF_{100} in the 15 crater-lake basins amenable to this analysis (cf. above). This suggests that higher evenness may exert a favourable effect on rarefacted richness estimates. Nevertheless, since both indices were integrated into the statistical analysis independently, and this study was designed to evaluate land-use effects on the entire inferred diversity of tropical fungi as represented by their spores (*Coniochaeta* spp. included), we decided to not correct for any such effects.

It is unclear whether taphonomic processes, such as differential transport and deposition of fungal spores across the lake bottom, may have affected the composition, richness and evenness of fungal spore assemblages recovered from the sampling location. However, several studies which modeled pollen dispersal and influx into small and medium-sized lakes (e.g., Prentice, 1985; Sugita, 1993) have found that pollen assemblages deposited at the center of a lake basin are the least affected by overloading from nearby pollen sources (e.g., the littoral zone) and represent a good overall estimate of plant species composition in the wider lake basin. The central bottom area is by its greater depth also generally well protected against sediment disturbance, in contrast to shallow, peripheral zones of the lake (Davis, 1973). Since the dispersal vectors (wind, water and insects) distributing pollen and spores of plant species are similar to those of mainly terrestrial fungi, their fungal spores are presumably transported and deposited into the lake in the same way.

3.4.2. Land-use effects on the richness and evenness of fungal diversity

Our study assessed the impact of agricultural land conversion on the diversity of tropical fungal communities at the landscape scale, i.e. along the full regional gradient from undisturbed to heavily disturbed environments as represented by a suite of crater-lake catchments. Given the spatial integration associated with the employed palaeoecological methods, this study was not concerned with effects on fungal diversity at the local scale (i.e. in-field and between-field variation in each catchment). In the full dataset of 24 undisturbed and disturbed basins, no detrimental effect of anthropogenic land use on fungal spore richness was found, because of great variability in observed fungal spore richness among the undisturbed forest and savannah sites. Local controls on fungal spore richness (vegetation composition, moisture balance, lake salinity, diversity of fungal habitat, etc.) may vary substantially between these (at present) natural sites. However, while savannah sites draining into saline lakes had significantly lower fungal spore richness than sites draining into freshwater lakes, savannah sites as such were not systematically poorer in fungal spore evenness than forest sites. In the subset of 17 disturbed basins, areal expansion of agricultural activity at the expense of local forest or savannah vegetation significantly affected fungal spore richness, indicating that tropical fungal communities exposed to increasingly intensive land-use impact experience species loss. Considering that fungal communities may account for 70 to 80% by weight of soil microbial biomass (Shields *et al.*, 1973; Lynch, 1983), agricultural practices such as tillage and clear-cut harvesting (e.g., slash-and-burn farming, logging) may severely damage the ecological niches available to fungi, and have a direct or indirect impact on the structure (e.g., species richness) and functioning (e.g., nutrient cycling and litter decomposition) of fungal communities (Miller and Lodge, 1997).

Given the host specificity of many fungi living in symbiotic or parasitic association with their host plants (Hawksworth, 2001), the negative effect of land use on fungal spore richness is not unexpected. Taking into account the estimated ratio of six fungus species to one host plant species (Hawksworth, 1991, 2001), which may even increase to 1:33 on tropical palms (Fröhlich and Hyde, 1999), the local species richness of fungal communities is much higher than that of vascular plants. This magnitude of fungal biodiversity can be expected to result in a very high rate of loss following land conversion for agriculture, especially in tropical rain forests, which account for over 70% of the world's fungal species (Fox, 1993). Fungal studies from temperate regions in Europe and North America showed that agricultural practices, and particularly the intense land management characteristic of modern-day industrial agriculture, severely affected the diversity and community structure of arbuscular mycorrhizal fungi (AMF) (e.g., Land and Schönbeck, 1991; Johnson and Pfleger, 1992; Douds and Millner, 1999; Franke-Snyder *et al.*, 2001; Oehl *et al.*, 2003). AMF species richness was less reduced on low-fertilised, organically managed lands with crop rotation, and significantly reduced on high-fertilised and continuous mono-cropping fields. While the farming system in our study region of western Uganda differs strongly from that of temperate regions in terms of mechanization and the use of chemical pesticides and fertilisers, the determining role of intensifying agriculture on fungal richness has already been observed in the tropics as well (e.g., Sieverding, 1989; Tsui *et al.*, 1998). On the other hand, studies from the Ivory Coast (Rambelli *et al.*, 1983, 1984; Persiani *et al.*, 1998) indicate that slash-and-burn farming does not seriously affect the diversity of soil fungi in tropical rainforest. Although agricultural activity caused sudden decrease in their biodiversity, iron- and aluminium-rich (i.e. lateritic) soil conditions seemed to help enhance rapid recovery of the pre-existing community when cultivation was abandoned.

Habitat diversity is considered another important factor determining species richness (e.g., Simpson, 1949; MacArthur and MacArthur, 1961; Köchy and Rydin, 1997). Only few species are found in all habitats (such as *Coniochaeta* spp.), the large majority being more or less habitat-specific. Thus a greater number of local habitat types present may enhance species richness across a landscape (e.g., Davidowitz and Rosenzweig, 1998; Kerr *et al.*, 2001; Tews *et al.*, 2004). Habitat diversity thus promotes biodiversity, with rare and specialist species appearing to benefit more than common and generalist species (MacArthur, 1958; Vivian-Smith, 1997). However, quantifying the habitat diversity shaped by vegetation is not straightforward, as its measurement is influenced by which habitat properties are focused upon (e.g., Wiens, 2000; Tews *et al.*, 2004). In this study, habitat diversity within a crater basin is measured as land-

cover diversity, in which the various types of anthropogenic activity (plantations, cropland, fallow land, pasture, etc.) are counted separately whereas potentially distinct microhabitats present within the remnants of natural/secondary forest and savannah are lumped together. As a result, habitat diversity in the 17 disturbed catchments ranged from 6 to 15, whereas all undisturbed catchments comprised only two major habitat types: either semi-deciduous forest and emergent riparian vegetation, or *Acacia*/grass savannah and the excrements of large wild herbivores. We propose that the observed lack of effect of habitat diversity on fungal spore richness occurs because this effect differs substantially on different environmental scales (suitability and composition of habitat types, microhabitat heterogeneity, plant species richness, soil type, the amount of phytomass, etc.) and for different fungal ecological groups (endophytes, saprobic soil fungi, ectomycorrhizal fungi, etc.) (Bills *et al.*, 2004; Zak and Willig, 2004). Combined with the different affect at different spatial scales (landscape, between-field and in-field; Benton *et al.*, 2003; Tews *et al.*, 2004) this may weaken the response of tropical fungi to habitat variation at the community level.

Because richness and evenness differ in their responses to ecological processes (e.g., nutrient loading, migration rates and competition of species, ecosystem stability and function) (Lundholm and Larson, 2003; Ma, 2005; Wilsey and Stirling, 2007; Reitalu *et al.*, 2009), changes in richness do not automatically result in changes in evenness and vice versa (Legendre and Legendre, 1998; Magurran, 2004). This is also corroborated by our results, wherein fungal spore evenness responded differently to the explanatory variables. Across all crater basins and the freshwater basins only, variation in evenness was negatively related to (i) the interaction between the catchment area/lake area ratio and habitat diversity, and (ii) the interaction between the catchment area/lake area ratio and the presence/absence of anthropogenic disturbance. These effects were mainly caused by an increase of evenness relative to a higher catchment/lake area ratio among the seven undisturbed sites, and consequently, did not affect variation in evenness across the disturbed basins only. Here, none of the selected variables had an influence on evenness. Since evenness represents the distribution of individuals among taxa (Wilsey and Potvin, 2000; Magurran, 2004), the fungal communities in undisturbed basins, having a large catchment surrounding the smaller lake, seemed slightly more even than in disturbed lake catchments, which are continuously exposed to environmental stress and only partially occupied by natural/secondary vegetation. The structure and functioning of fungi strongly depends on the availibility of nutrients and biomass (total primary productivity), which is most apparent in large, stable ecosystems (e.g., Vitousek and Hooper, 1993; Hooper and Vitousek, 1998; Wilsey and Potvin, 2000; Tilman *et al.*, 2001). As such, these natural ecosystems provide the necessary resources, goods and services to enhance biomass stability (e.g., Hughes and Roughgarden, 2000) of fungal communities. Our data tentatively suggest that the evenness of fungal communities is possibly more strongly associated with ecosystem stability and function than richness, as has been observed in studies on biota other than fungi (e.g., Wilsey and Potvin, 2000; Mattingly *et al.*, 2007; Reitalu *et al.*, 2009). However, we also need to consider the effect of the over-dominant *Coniochaeta* on the fungal spore evenness.

In conclusion, the results of this study show a negative effect of land use on the taxonomic richness of fungal spore assemblages deposited in the sediments of small crater lakes in western Uganda, which mostly originate from the fungal communities living in terrestrial habitat within the crater basins. Agricultural activity may substantially affect the community structure of tropical fungi, visible through changes in fungal spore representation. The areal expansion of agricultural activity at the expense of local forest or savannah vegetation significantly affected the richness of fungal spores, whereas biomass stability among the natural sites appears to have a more favourable effect on evenness. However, the latter is only tentative, given the strong effect of the dominant *Coniochaeta* on the evenness measures. We note that more efforts should be directed towards the use of integrative, analytical methodologies, such as palaeoecology, remote sensing and model selection criteria (e.g. Sherwood-Pike, 1988; Purvis and Hector, 2000; Caliman *et al.*, 2010) to study long- and short-term dynamics of fungal communities and ecosystem functioning. These integrated methods may improve understanding of the underlying environmental mechanisms, responsible for diversity loss. Palaeoecological records are of obvious relevance to assess Earth's biodiversity and ecosystem function and services more comprehensively (e.g., Dearing, 2006; Blackmore, 2007), and their added value to determine ecological processes

must be an integral part of management and conservation strategies (Willis and Bhagwat, 2010).

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Appendix 3.1. AICc values (based on Akaike's Information Criterion for small sample size) of the multiple lineair regression candidate models, selected to estimate the land-use effects on *EF200* and *E1/D* for the three datasets: all basins, the freshwater lake basins only and the disturbed lakes only. Models, considered to fit the data equally well ($\Delta AICc \leq 2$), are separated from the other candidate models by a dashed line; the most parsimonious models are highlighted in bold.

1. Fungal spore richness (EF_{200})

1.1. All crater basins and freshwater lake basins only

*Dist=0,1; no interaction Dist*Hab possible*

Model 1= Area Dist Hab Area*Hab Area*Dist
Model 2= Area Dist Hab Area*Dist
Model 3= Area Dist Hab Area*Hab
Model 4= Area Dist Hab
Model 5= Area Dist Area*Dist
Model 6= Area Hab Area*Hab
Model 7= Area Dist
Model 8= Area Hab
Model 9= Dist Hab
Model 10= Area
Model 11= Hab
Model 12= Dist

All crater basins

Obs	Model	Parms	AICc	ΔAICc	Odds	Weight	Cum Weight	Variation (%)
1	**10**	**3**	**171.6**	**0.00000**	**1.000**	**0.25942**	**0.25942**	**0.1**
2	12	3	171.7	0.02040	1.010	0.25679	0.51622	0.03
3	11	3	171.7	0.02829	1.014	0.25578	0.77200	0.002
4	7	4	174.5	2.89113	4.244	0.06112	0.83312	
5	8	4	174.5	2.90326	4.270	0.06075	0.89388	
6	9	4	174.5	2.90412	4.272	0.06073	0.95460	
7	5	5	177.4	5.72751	17.527	0.01480	0.96940	
8	4	5	177.7	6.10519	21.170	0.01225	0.98166	
9	6	5	177.8	6.13079	21.443	0.01210	0.99376	
10	2	6	181.0	9.33230	106.288	0.00244	0.99620	
11	3	6	181.3	9.70497	128.058	0.00203	0.99822	
12	1	7	181.6	9.96772	146.037	0.00178	1.00000	

Freshwater lake basins

Obs	Model	Parms	AICc	ΔAICc	Odds	Weight	Cum Weight	Variation (%)
1	**12**	**3**	**151.2**	**0.00000**	**1.000**	**0.36595**	**0.36595**	**11**
2	11	3	152.1	0.97263	1.626	0.22502	0.59097	7
3	10	3	153.5	2.38856	3.301	0.11085	0.70182	
4	7	4	153.8	2.63602	3.736	0.09795	0.79977	
5	9	4	154.1	2.99009	4.460	0.08206	0.88183	
6	8	4	154.8	3.59524	6.035	0.06064	0.94247	
7	4	5	157.2	6.02845	20.373	0.01796	0.96043	
8	5	5	157.2	6.03134	20.403	0.01794	0.97837	
9	6	5	158.0	6.86169	30.903	0.01184	0.99021	
10	3	6	160.3	9.10987	95.101	0.00385	0.99406	
11	1	7	160.6	9.40385	110.159	0.00332	0.99738	
12	2	6	161.0	9.87716	139.572	0.00262	1.00000	

1.2.. Disturbed crater basins

*Dist replaced by Int; interaction Ant*Hab possible; no 3-way interaction*

Model 1= Area Ant Hab Area*Hab Ant*Hab Area*Ant
Model 2= Area Ant Hab Area*Hab Area*Ant
Model 3= Area Ant Hab Area*Ant Ant*Hab
Model 4= Area Ant Hab Area*Hab Ant*Hab
Model 5= Area Ant Hab Area*Ant
Model 6= Area Ant Hab Area*Hab
Model 7= Area Ant Hab Ant*Hab
Model 8= Area Ant Hab
Model 9= Area Ant Area*Ant
Model 10= Area Hab Area*Hab
Model 11= Ant Hab Ant*Hab
Model 12= Area Ant
Model 13= Area Hab
Model 14= Ant Hab
Model 15= Area
Model 16= Hab
Model 17= Ant

Obs	Model	Parms	AICc	ΔAICc	Odds	Weight	Cum Weight	Variation (%)
1	**17**	**3**	**110.5**	**0.0000**	**1.00**	**0.60415**	**0.60415**	**19**
2	14	4	113.2	2.7290	3.91	0.15436	0.75851	
3	12	4	113.9	3.4580	5.64	0.10721	0.86572	
4	11	5	116.6	6.1532	21.68	0.02786	0.89358	
5	9	5	116.9	6.4324	24.93	0.02423	0.91781	
6	8	5	117.2	6.6677	28.05	0.02154	0.93935	
7	15	3	117.5	7.0534	34.01	0.01776	0.95712	
8	16	3	117.9	7.3730	39.90	0.01514	0.97226	
9	6	6	118.4	7.9141	52.30	0.01155	0.98381	
10	10	5	119.7	9.1877	98.87	0.00611	0.98992	
11	13	4	121.0	10.5361	194.04	0.00311	0.99303	
12	5	6	121.3	10.8233	224.00	0.00270	0.99573	
13	7	6	121.5	11.0414	249.81	0.00242	0.99815	
14	4	7	123.2	12.6756	565.54	0.00107	0.99922	
15	2	7	124.4	13.8728	1029.04	0.00059	0.99980	
16	3	7	126.8	16.3260	3508.74	0.00017	0.99998	
17	1	8	130.7	20.1927	24253.93	0.00002	1.00000	

2. Fungal spore evenness ($E_{1/D}$)

2.1. All crater basins and freshwater lake basins only

*Dist=0,1; no interaction Dist*Hab possible*

Model 1= Area Dist Hab Area*Hab Area*Dist
Model 2= Area Dist Hab Area*Dist
Model 3= Area Dist Hab Area*Hab
Model 4= Area Dist Hab
Model 5= Area Dist Area*Dist
Model 6= Area Hab Area*Hab
Model 7= Area Dist
Model 8= Area Hab
Model 9= Dist Hab
Model 10= Area
Model 11= Hab
Model 12= Dist

All crater basins

Obs	Model	Parms	AICc	ΔAICc	Odds	Weight	Cum Weight	Variation (%)
1	**12**	**3**	**-78.6**	**0.00000**	**1.0000**	**0.19774**	**0.19774**	**17**
2	11	3	-78.1	0.46874	1.2641	0.15642	0.35416	16
3	6	5	-78.1	0.48610	1.2751	0.15507	0.50923	35
4	7	4	-77.5	1.05272	1.6928	0.11681	0.62604	23
5	5	5	-77.3	1.31063	1.9257	0.10268	0.72873	32
6	8	4	-76.8	1.80156	2.4615	0.08033	0.80906	21
7	10	3	-76.5	2.05142	2.7891	0.07090	0.87995	
8	9	4	-75.8	2.77452	4.0039	0.04939	0.92934	
9	3	6	-74.5	4.07577	7.6744	0.02577	0.95511	
10	4	5	-74.3	4.25737	8.4038	0.02353	0.97863	
11	2	6	-73.8	4.79806	11.0125	0.01796	0.99659	
12	1	7	-70.5	8.12063	57.9926	0.00341	1.00000	

Freshwater lake basins

Obs	Model	Parms	AICc	ΔAICc	Odds	Weight	Cum Weight	Variation (%)
1	**6**	**5**	**-71.1**	**0.00000**	**1.0000**	**0.26417**	**0.26417**	**43**
2	5	5	-70.2	0.83772	1.5202	0.17377	0.43794	40
3	12	3	-70.0	1.09183	1.7262	0.15304	0.59098	19
4	11	3	-69.3	1.81794	2.4818	0.10645	0.69743	16
5	7	4	-68.7	2.34527	3.2305	0.08177	0.77920	
6	10	3	-67.8	3.31357	5.2424	0.05039	0.82959	
7	8	4	-67.7	3.35296	5.3467	0.04941	0.87900	
8	3	6	-67.2	3.84955	6.8536	0.03854	0.91755	
9	9	4	-67.1	3.98819	7.3456	0.03596	0.95351	
10	2	6	-66.5	4.56195	9.7862	0.02699	0.98050	
11	4	5	-65.4	5.72401	17.4965	0.01510	0.99560	
12	1	7	-62.9	8.19105	60.0707	0.00440	1.00000	

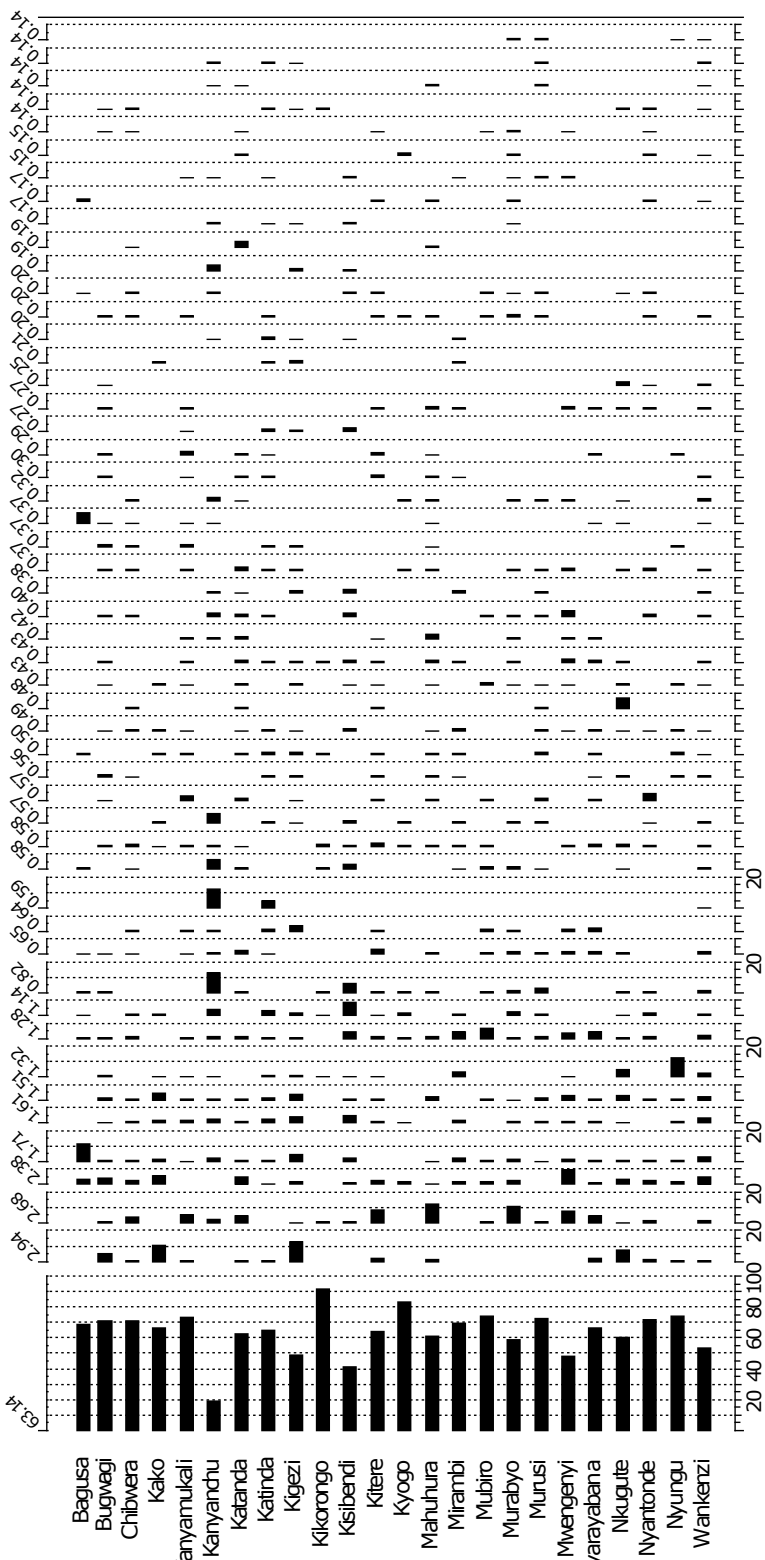
2.2. Disturbed crater basins

*Dist replaced by Int; interaction Ant*Hab possible; no 3-way interaction*

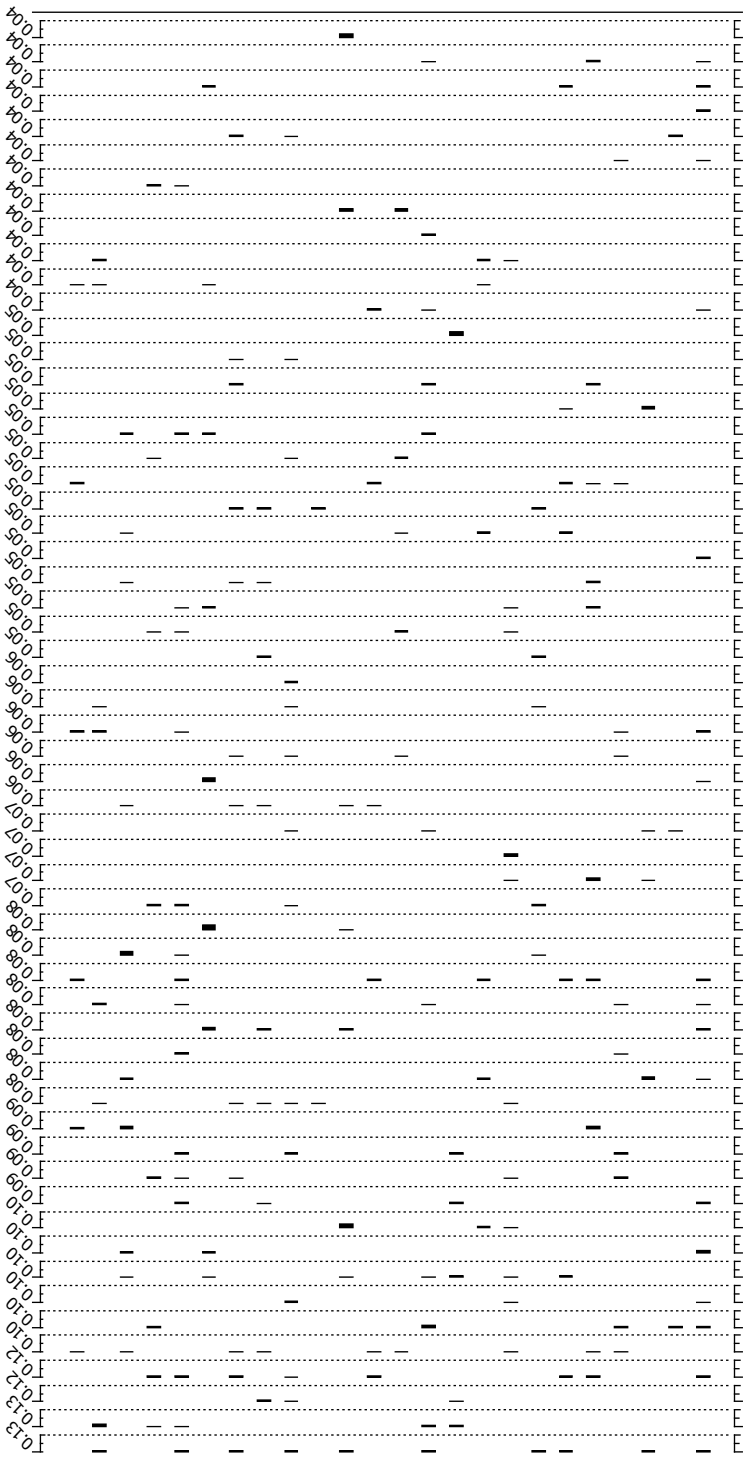
Model 1= Area Ant Hab Area*Hab Ant*Hab Area*Ant
Model 2= Area Ant Hab Area*Hab Area*Ant
Model 3= Area Ant Hab Area*Ant Ant*Hab
Model 4= Area Ant Hab Area*Hab Ant*Hab
Model 5= Area Ant Hab Area*Ant

Model 6= Area Ant Hab Area*Hab
Model 7= Area Ant Hab Ant*Hab
Model 8= Area Ant Hab
Model 9= Area Ant Area*Ant
Model 10= Area Hab Area*Hab
Model 11= Ant Hab Ant*Hab
Model 12= Area Ant
Model 13= Area Hab
Model 14= Ant Hab
Model 15= Area
Model 16= Hab
Model 17= Ant

Obs	Model	Parms	AICc	ΔAICc	Odds	Weight	Cum Weight	Variation (%)
1	**17**	**3**	**-81.2**	**0.0000**	**1.00**	**0.33735**	**0.33735**	**10**
2	16	3	-80.1	1.0678	1.71	0.19780	0.53515	4
3	15	3	-79.9	1.3236	1.94	0.17405	0.70920	2
4	14	4	-79.0	2.1661	2.95	0.11421	0.82341	
5	12	4	-77.8	3.4185	5.52	0.06106	0.88447	
6	13	4	-76.9	4.3235	8.69	0.03884	0.92331	
7	10	5	-76.0	5.1813	13.34	0.02529	0.94860	
8	9	5	-75.0	6.2308	22.54	0.01497	0.96357	
9	11	5	-74.9	6.2806	23.11	0.01460	0.97816	
10	8	5	-74.9	6.2855	23.17	0.01456	0.99273	
11	6	6	-72.2	9.0476	92.18	0.00366	0.99639	
12	5	6	-70.9	10.3593	177.62	0.00190	0.99829	
13	7	6	-70.0	11.2255	273.89	0.00123	0.99952	
14	2	7	-66.4	14.8566	1682.95	0.00020	0.99972	
15	4	7	-66.2	15.0130	1819.79	0.00019	0.99990	
16	3	7	-64.8	16.4024	3645.41	0.00009	1.00000	
17	1	8	-58.9	22.3554	71518.27	0.00000	1.00000	



Appendix 3.2. Percent abundances of represented morphotypes (bars) per assemblage, based on the fungal spore sum (204-1045 specimens) counted in each sample; the type number of each morphotype is replaced by its percent abundance throughout all assemblages, expressed as a proportion of the total fungal spore sum (~9500 specimens) (see also Fig. 3.4).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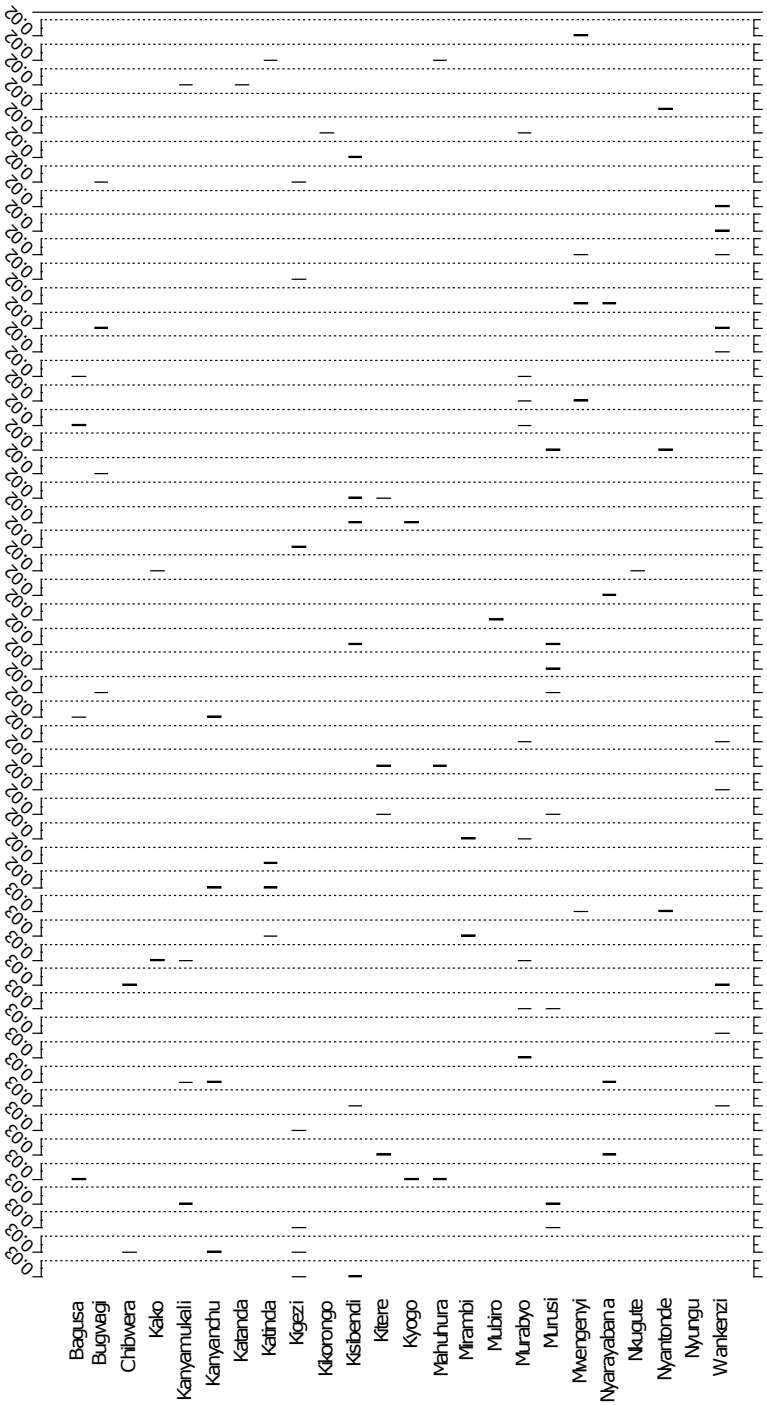
Bugwagi
Chibwera
Kako
Kanyamukali
Kanyanchu
Katanda
Katinda
Kigezi
Kikorongo
Kisibendi
Kitere
Kyogo
Mahuhura
Mirambi
Mubiro
Murabyo
Murusi
Mwengenyi
Nyarayabana
Nkugute
Nyantonde
Nyungu
Wankenzi


Bagusa
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Kyogo
Mahuhura
Mirambi
Mubiro
Murabyo
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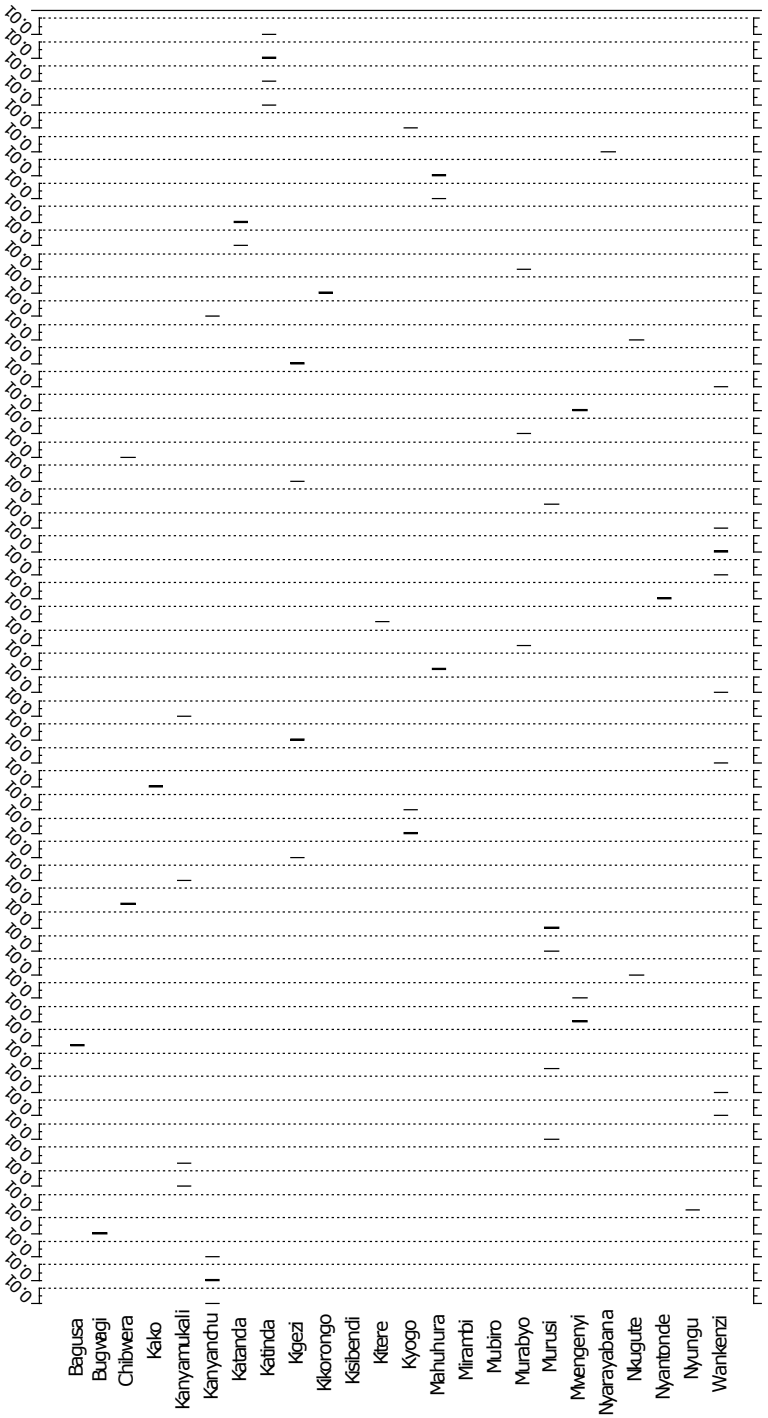
Mwengenyi
Nyarayabana
Nkugute
Nyantonde
Nyungu
Wankenzi


Bagusa
Bugwagi
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Katinda
Kigezi
Kikorongo
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Kyogo
Mahuhura
Mirambi
Mubiro
Murabyo
Murusi
Mwengenyi
Nyarayabana
Nkugute
Nyantonde
Nyungu
Wankenzi

Validation of non-pollen palynomorphs as palaeoenvironmental indicators in tropical Africa: contrasting ~200-yr palaeolimnological records of climate change and human impact

Gelorini, V., Ssemmanda, I., Verschuren, D., in preparation. Review of Palaeobotany and Palynology.

Abstract

Multi-proxy investigation of high-resolution ~200-yr sediment records from two shallow climate-sensitive crater lakes in western Uganda, surrounded by presently undisturbed (L. Chibwera) and severely human-disturbed (L. Kanyamukali) catchments, provides insights into lake ecosystem and vegetation response to short-term natural climate variability, as separate from local human impact. Here, we present and compare data on fossil non-pollen palynomorphs (NPPs) derived from spores of saprotrophic, coprophilous (dung-colonizing) and mycorrhizal fungi, zygo-/aplanospores and coenobia/colonies from chlorococcal algae, and fern and moss spores, from both of these sediment sequences to assess and validate the palaeoecological significance of fossil NPP assemblages for palaeoenvironmental reconstruction in a tropical African context. The NPP records of these two lakes display parallel responses to regional climate variability, expressed mainly through fluctuations in lake level and in soil moisture of terrestrial habitat within the lake catchments. However, some distinctly individualistic signals of local human activity were particularly observed at Kanyamukali. In both sediment sequences, high abundances of the saprotrophic ascomycete *Coniochaeta* broadly coincide with documented decade-scale episodes of increased humidity (early/mid-19th century, ~1870-1900 AD and late 20th century). During severe drought in the late 18th- and early-19th century, both lakes were reduced to ephemeral ponds and intensely visited by large wild and/or domestic herbivores to drink and bath. This is mainly indicated by high numbers of spores from *Sordaria* spp. and *Delitschia* spp., obligately growing on herbivore dung, in the desiccation horizon of both lakes. When the lakes gradually refilled during the 19th century, significantly lower percent abundances of these coprophilous fungal taxa suggest that the mammals became less dependent on these drinking spots for their water needs. In Chibwera evidence of large herbivore presence was (nearly) completely absent, in contrast with Kanyamukali where wild/domestic mammals continued to frequently use the lake. The current location of Lake Kanyamukali near the main road Kasese-Fort Portal, arisen from an ancient cattle trail and/or trading route, may underscore its stronger historical linkage with transhumant pastoralists, leading their cattle to watering places and productive grazing areas. Lake Chibwera became incorporated into Queen Elizabeth National Park from the 1960-70s, but at Kanyamukali intensified grazing and subsistence agriculture started from the mid-20th century. In the NPP assemblages, this historically documented agricultural activity is mainly reflected in slightly increased percentages of fungal taxa such as the coprophilous *Sordaria* spp. and *Glomus* sp., an endomycorrhizal fungus possibly indicative for increased land degradation in the lake catchment. Although these particular signals are clear, the overall change in NPP assemblage that can be uniquely attributed to this relatively intense human impact at Kanyamukali is modest compared to the change in NPP assemblage which occurred at both lakes due to changes in fungal habitat associated with regional climate change, including but not only the habitat change due to large herbivore response to drought. Thus, comparing these lake-sediment records allowed us to assess the intensity of past local agricultural activity required to produce an unambiguous signature in the non-pollen palynomorph assemblages recovered from East African lake sediment records.

Keywords: non-pollen palynomorphs, human impact, climate change, late Holocene, lake sediment records, western Uganda

4.1. Introduction

Natural resources and ecosystems in tropical Africa are increasingly vulnerable to human impact and climate change, threatening the services provided by these ecosystems to human society (e.g., Mendelsohn *et al.*, 2000; Conway *et al.*, 2005; Thomas and Twyman, 2005; Boko *et al.*, 2007). However, the role of human activities in ongoing ecosystem degradation is controversial, as it must be disentangled from large natural climate and ecosystem dynamics on short and longer time scales (e.g., Dearing, 2006; Costanza *et al.*, 2007; Pongratz *et al.*, 2008). Studies of historical land use tend to assume that pre-20th century human impact on natural ecosystems in East Africa was very low, due to the low density of indigenous people (Ramankutty and Foley, 1999; Klein Goldewijk, 2001). Yet, palaeoecological (e.g., Taylor, 1990; Jolly *et al.*, 1997; Kiage and Liu, 2006) and archaeological (e.g., Robertshaw and Taylor, 2000; Killick, 2009) evidence seem to indicate significant anthropogenic deforestation from at least 3000 years ago. Reflecting a lack of solid evidence, the notable discrepancy between these hypotheses must be resolved to properly assess the resilience, and recovery potential, of those natural ecosystems.

High-resolution palaeolimnological records of Ugandan crater lakes spanning the last 200 to ~1000 years (Ssemmanda *et al.*, 2005; Russell *et al.*, 2007; Bessems *et al.*, 2008; Ryves *et al.*, 2011) have provided strong evidence for regional complexity of natural climate variability and historical human impact. These lakes are particularly sensitive to short-term (decadal to century-scale) rainfall variability (Bessems *et al.*, 2008; Russell *et al.*, 2007), so that their records complement and fine-tune the climate change over longer timescales recorded by the sediment records of the larger Rift lakes Albert, George, Edward and Victoria (e.g., Beuning *et al.*, 1997; Stager *et al.*, 1997, 2003; Williams *et al.*, 2006). Human impact on lakes and their catchments can also create strong palaeoenvironmental signatures (Russell *et al.*, 2009; Ryves *et al.*, 2011), however these are often modified by simultaneous system response to climate fluctuation. This is mainly because the responses of vegetation proxies (pollen, charcoal and phytoliths) to land-use change are significantly mediated by basin-specific factors (e.g., hydrology, lake morphometry, catchment size) (Ryves *et al.*, 2011) and proxy-specific characteristics such as low pollen visibility of crop cultivation, variation in pollen and spore influxes, ambiguous pollen signals of increased Poaceae caused either by drought or agriculture, and uncertainty about whether charcoal signatures reflect natural or human-induced fire regimes (e.g., Lamb *et al.*, 2003; Lejju *et al.*, 2005; Ssemmanda *et al.*, 2005; Gillson and Ekblom, 2009). Multi-proxy investigation of paired or multiple lake-sediment records, however, may provide the comparison and replication needed to detect environmental changes more accurately (e.g., Fritz, 2008), and thus provide the means to more clearly separate local human impacts from regional-scale climatic impacts.

Here we investigate high-quality sediment records of two shallow crater lakes in western Uganda with a contrasting history (the presently undisturbed L. Chibwera and severely human-disturbed L. Kanyamukali) to unravel lake ecosystem and vegetation response to climatic fluctuations and human impact over the past 200 years. Multi-proxy analyses of sedimentary parameters (bulk sediment composition, texture (% sand and coarse organic detritus), C/N ratio and magnetic susceptibility) and biotic remains (pollen, diatoms, aquatic macrofyte fossils and aquatic invertebrates) have revealed distinct patterns of short-term rainfall variability over the whole time span of both sediment sequences (Bessems *et al.*, 2008; Audenaert *et al.*, in prep.; Ssemmanda *et al.*, in prep.; Ssemmanda, unpublished CLANIMAE data). In the sediment record of the Lake Kanyamukali, the appearance of two diatom species (*Amphora pediculus* and *Sellaphora pupula)* also indicated increased aquatic productivity during the past 60-70 years, possibly due to cultural eutrophication linked to usage of the crater basin by pastoralists and farmers since the mid-20th century (Audenaert *et al.*, in prep.). Increased human impact was also suggested by the pollen record, which shows regional presence of cereals and exotic plantation trees (*Eucalyptus* and pine) in the past 50 years (Ssemmanda, unpublished CLANIMAE data).

In this particular study, we exploit the contrasting histories of these two lakes to test and validate fossil non-pollen palynomorphs (NPPs) as proxies for palaeoenvironmental reconstruction in a tropical African context. These NPPS include spores of saprotrophic, coprophilous and mycorrhizal fungi, zygo-/aplanospores, coenobia and colonies from chlorococcal algae and fern and moss spores. During the last two decades, NPPs have received increased attention

in palaeoecological studies worldwide (e.g., special issue of the *Review of Palaeobotany and Palynology*: van Geel, 2006, and *Vegetation history and Archaeobotany*: Haas, 2010), but only recently comprehensive surveys of their diversity (Gelorini *et al.*, 2011; van Geel *et al.*, 2011) have become available which permit their firm introduction in the African palaeoecological research field. These microfossils are common in all sorts of habitats (e.g., wetlands, grasslands, tropical and temperate forests) and may provide complementary insights into climate and/or human-driven soil and hydrological processes (e.g., moisture balance, erosion, etc.) and vegetation shifts (e.g., crop cultivation, pasture and fire frequency). We compare the fossil NPP assemblages from lakes Chibwera and Kanyamukali to assess and validate their role for unraveling past climatic and human impacts on tropical African lake ecosystems. However, terrestrial pollen data are not included in this study, since this will be part of a vegetation-related paper, and this exploratory research is primarily focused on our understanding of tracing environmental changes, based on tropical non-pollen palynomorphs as valuable indicators per se. Aquatic pollen data are only discussed to support local habitat changes. More specifically, this study aims to critically test the purported link between spores of coprophilous fungi and pastoralism in a tropical African context.

4.2. The study lakes and their environmental setting

Our two study lakes are located in southwestern Uganda, in the Edward-George branch of the East African Rift System southeast of the Ruwenzori Mountains (Bessems *et al.*, 2008) (Fig. 4.1a). This tropical sub-humid region experiences a seasonally bimodal rainfall regime, with long rains during boreal spring (March-May) and short rains during boreal autumn (October-December). The wet seasons are strongly driven by monsoonal wind systems from the Indian Ocean, modulated by the passage of the Intertropical Convergence Zone (ITCZ) and the Congo Air Boundary (CAB) across the equator (Nicholson, 1996; Mutai and Ward, 2000). The mean annual surface temperature fluctuates between 22 and 25°C, and the mean annual rainfall reaches about 900 mm yr^{-1} near Chibwera and 1,100 mm yr^{-1} near Kanyamukali, with a mean annual evaporation varying from 1,600 to 1,900 mm yr^{-1} (Bessems *et al.*, 2008).

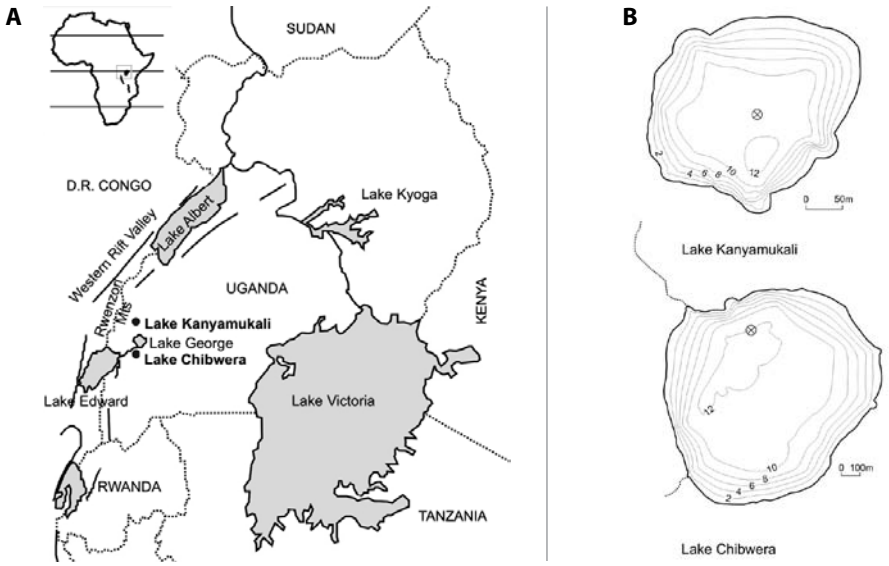

Fig. 4.1a-b. (a) Location map of the study lakes in western Uganda, situated in the western branch of the East African Rift System. (b) Bathymetric maps, based on echosounding, of Lake Kanyamukali in 2001 and Lake Chibwera in 2002 (modified from Bessems *et al.*, 2008).

Lake Chibwera (0°09'S, 30°09E, and 971 m a.s.l.) is a medium-sized maar crater lake (0.76 km^2) situated in the Bunyaruguru lake district, on the floor of the Rift Valley south of Lake George (Bessems *et al.*, 2008) (Fig. 4.1a-b). With a maximum depth of 12.6 m (Fig. 4.1b), the lake is currently fresh (surface water salinity: 472 µS/cm) and seasonally stratified, developing anoxic conditions in the lower water column (unpublished survey data, August 2008). In contrast to the saline crater lakes (e.g., L. Bagusa, L. Maseche and L. Nshenyi) in its immediate surroundings, Lake Chibwera taps into the shallow groundwater aquifer around the fresh Lake George and some ephemeral stream input, which both contribute to its water balance (Bessems *et al.*, 2008; Audenaert *et al.*, in prep.). Its catchment land cover (ca. 0.22 km^2) is characterised by *Acacia gerrardii/Themeda triandra* savannah (Krueger and Johnson, 1996; Kirabo *et al.*, 2011). The lake is nowadays fully incorporated into Queen Elizabeth National Park (QENP), a protected pristine area of ca. 2000 km^2, which encompasses a wide range of habitat types (from grassland to swamp vegetation) and mammal species (e.g., hippo, buffalo, elephant and waterbuck) (Uganda Wildlife Authority, 2009). The area currently occupied by QENP was previously a grazing area for local Basongora pastoralists, abandoned in the late 19th century as a result of cattle raiding, rinderpest and smallpox (e.g., Stanley, 1891, in Osmaston, 1998; Ofcansky, 1981; Robertshaw *et al.*, 2004). These events played an important role in the establishment of the national park in 1952 by the Protectorate administration (Blomley, 2000). The Kyambura Game Reserve, which includes Lake Chibwera and its surroundings, was added to QENP in 1965. However, until the early 1970s the area was used for licensed hunting to support the livelihoods of local communities. As a result of political upheaval from the 1970s to the 1990s, uncontrolled hunting drastically increased and subsistence farmers from the surrounding areas and migrants from southern Uganda annexed land in the south-east of the reserve. Before Uganda Wildlife Authority (UWA) started to manage the game reserve in 1996, there was no policy controlling the presence of domestic livestock, mainly goats, which graze freely in the reserve (Allen, 1994; Byaruhanga *et al.*, 2001).

Lake Kanyamukali (0°24'N, 30°14'E and 1,150 m a.s.l.) is located in the Kasenda lake district on the sub-humid shoulder of the Rift Valley north of Lake George (Bessems *et al.*, 2008) (Fig. 4.1a-b). This small maar crater lake (0.02 km^2) is fresh (surface water salinity: 958 µS/cm), and has currently a seasonally stratified water column of 10.4 m deep with near-bottom anoxia (unpublished survey data, February 2008) (Fig. 4.1b). Its steeply sloping crater walls ensure rain run-off, which helps to maintain the lake against the local negative water balance (Bessems *et al.* 2008). From the 1960s onwards, the inner and outer crater slopes of Lake Kanyamukali have been used for agriculture (Bessems *et al.*, 2008). Today, only a small part of the crater catchment itself is cultivated with crops, such as banana (3%) and maize (1%), whereas pasture land (18%), fallow land (45%) and *Eucalyptus* plantation (15%) are more abundant. The steepest portions of the catchment are overgrown with secondary forest/bush (18%) (unpublished survey data, February 2008).

At the time of a vegetation survey in the mid-20th century both lakes formed part of an extended moist *Acacia gerrardii/Themeda triandra* savannah landscape (Atlas of Uganda, 1962; Langdale-Brown *et al.*, 1994), which was grazed by both wild and domestic herbivores, and regularly burned (Langdale-Brown *et al.*, 1964; Harrington, 1974; Adlbauer, 1998) (Fig. 4.2-4.3). In Uganda, controlled burning of *Themeda* grasslands was practiced to obtain grass regrowth for forage supply, particularly in times of drought (Langdale-Brown *et al.*, 1964; Mclean, 1971; Harrington, 1974; FAO, 2009). Most of these grasslands are thought to represent fire climax vegetation (Mclean, 1971; Göhl, 1975; Edwards, 1968; Ndawula-Senyimba, 1972). Since the whole region was also heavily infected with savannah tsetse flies *Glossina* spp. (Fig. 4.3), bush clearing was used as an anti-tsetse fly measure (The Tsetse Fly Control Act, 1948; Langdale-Brown *et al.*, 1964; Harrington, 1974). To what extent these landscaping measures actually contributed to the shaping of the landscape around either of our study sites is uncertain. Nevertheless, since the 1960-70s the environmental divergence between the savannah landscape of Lake Chibwera becoming incorporated into QENP, and the savannah landscape of Lake Kanyamukali becoming subject to local human settlement, started to grow rapidly.

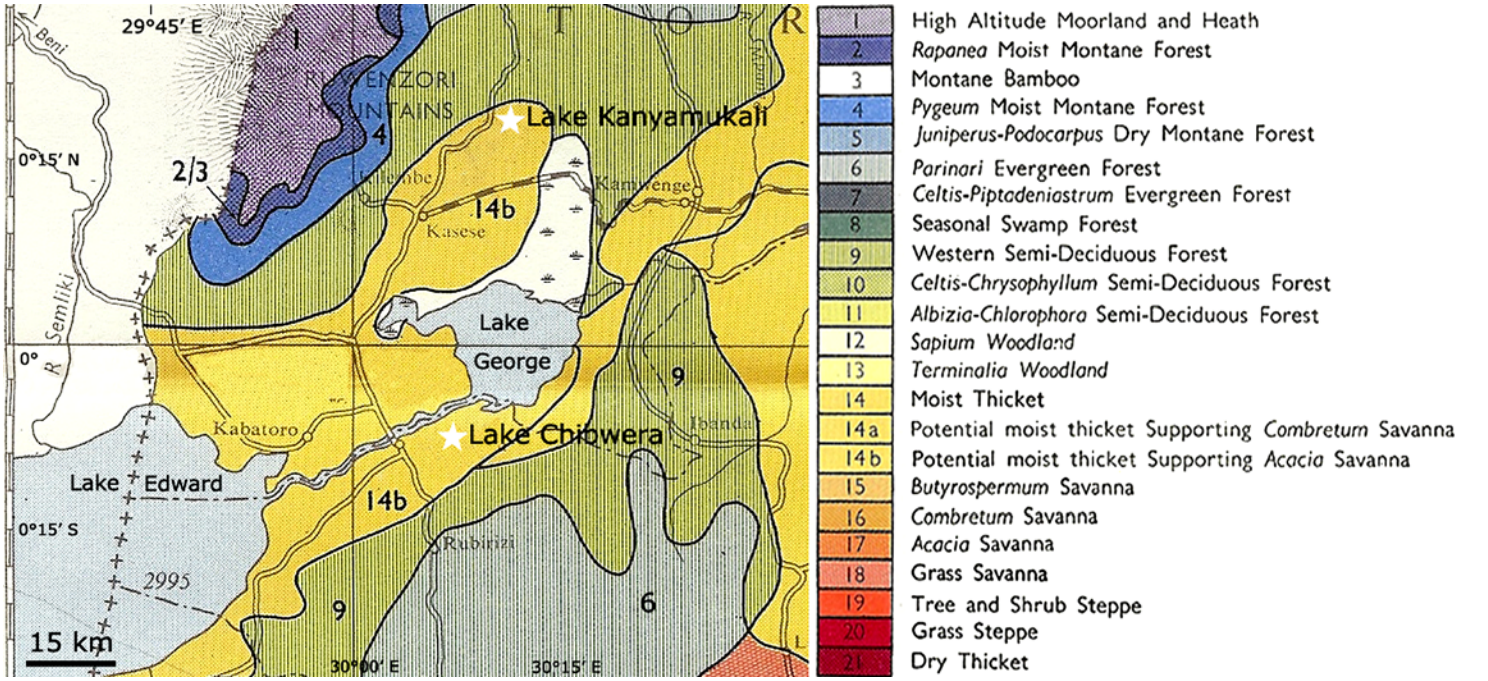

Fig. 4.2. Extract of a mid-20th century map (fieldwork conducted in 1957-1960) of the main ecological zones in the study region, based primarily on the potential distribution of climax vegetation types. Lakes Chibwera and Kanyamukali are both situated in moist *Acacia gerrardii* savannah (from Langdale-Brown *et al.*, 1964).

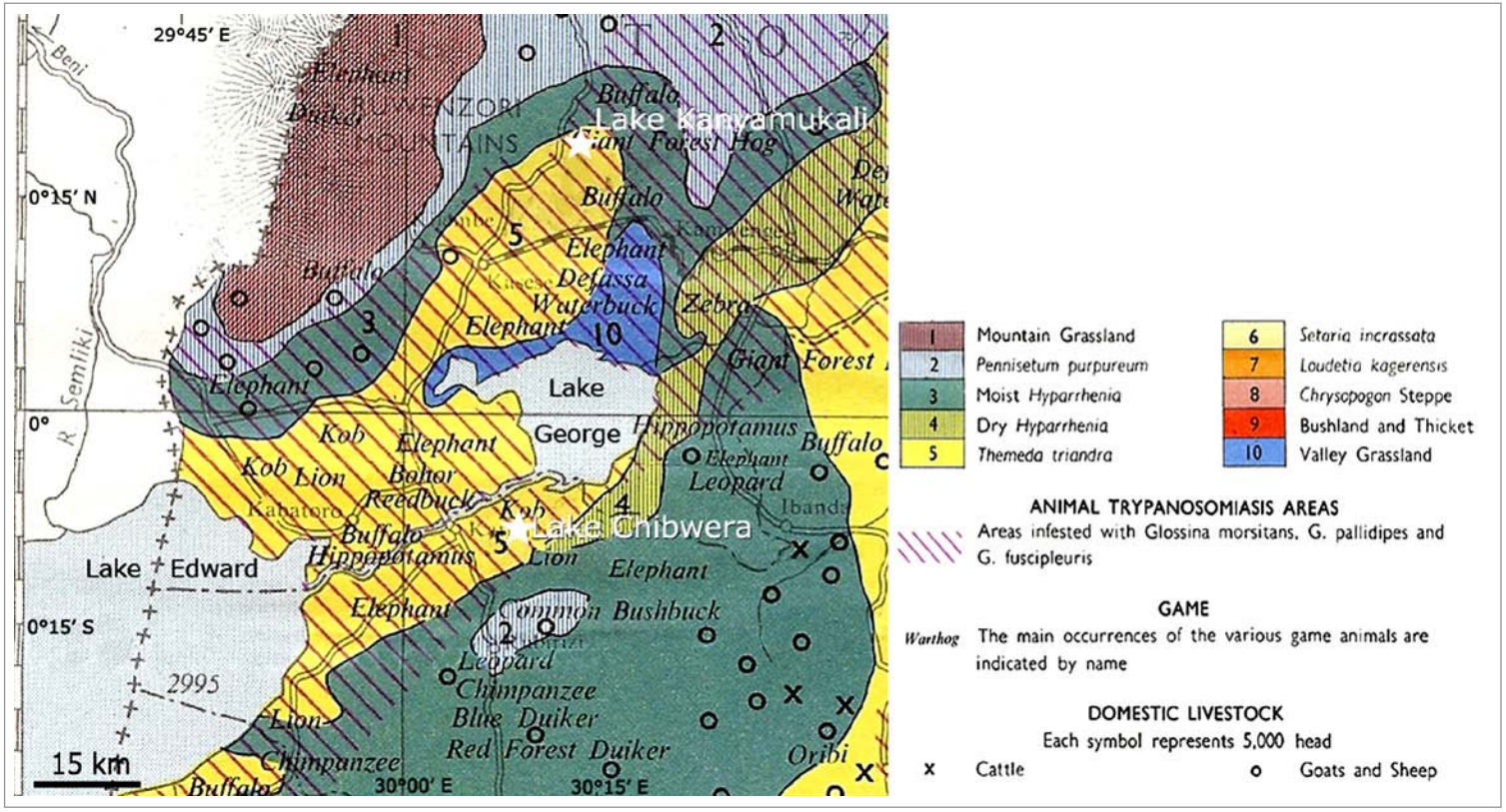

Fig. 4.3. Extract of a mid-20th century map (fieldwork conducted in 1957-1960) displaying range resources, with reference to the distribution of game species, livestock and animal trypanosomiasis. Lakes Chibwera and Kanyamukali form part of exploited *Themeda triandra* savannah, affected by trypanosomiasis (map from Langdale-Brown *et al.*, 1964; information on game species, livestock and trypanosomiasis is reproduced from the Atlas of Uganda, 1962).

4.3. Materials and methods

4.3.1. Sediment cores, lithostratigraphy and chronology

Overlapping sediment cores were collected in 2001 and 2002 from the central, deepest parts of Lake Chibwera (CHIB02-1P-I and -II) and Lake Kanyamukali (KANYA01-1P and KANYA02-1P-I and –II) using a rod-operated single-drive piston corer (Wright, 1967, 1980). The uppermost, unconsolidated sediments (~25-30 cm) near the sediment-water interface were retrieved and sectioned upright with a fixed-interval sectioning device (Verschuren, 1993) in 1-cm increments into Whirl-Pack™ bags. The deeper, more consolidated sediments were retained intact in the polycarbonate core tubes (Bessems *et al.*, 2008). Due to depletion of the uppermost, soft mud by repeated subsampling, two additional short-cores, taken at the same sampling positions, were made available to supplement the topmost sections: (i) a new recovered 30-cm sediment core from Lake Chibwera (CHIB08-1G; in 2008), and (ii) an earlier collected 52-cm sediment core from Lake Kanyamukali (KANYA00-1G; in 2000). Both short sediment cores were taken with a gravity corer, and extruded in the field in 1-cm increments.

The overlapping core sections from each lake were cross-correlated, based on the basis of bulk sediment composition and magnetic susceptibility analysis (Bessems *et al.*, 2008). The composite sequences for both lakes now include sections from several individual cores, totaling 126 cm at Chibwera and 179 cm at Kanyamukali. To accommodate the additional coring of Lake Chibwera in 2008 (CHIB08-1G), we extended the former recovered composite sequence from 2002 upward with 9 cm. The collected short core from Lake Kanyamukali (KANYA00-1G), however, completely fitted into the KANY01-1P composite sequence. To determine the chronological framework and accumulation rates for late 19th- and 20th-century sedimentation, ^{210}Pb and ^{137}Cs dating techniques were applied. Approximate sediment age at depth was calculated using the constant-rate-of-supply (CRS) model (Binford, 1990). The chronology of pre-20th century deposits is constrained by three AMS ^{14}C dates (two at Chibwera, one at Kanyamukali) on isolated terrestrial plant macrofossils to avoid the potential problem of radiocarbon reservoir effects. All radiocarbon dates were calibrated using CALIB 5.0 (in year AD; Stuiver *et al.*, 2005). To enhance age comparisons, the mid-point of the most probable 2σ age range (with a fractional probability of ≥0.1) of each ^{14}C date was used as a practical time marker (Bessems *et al.*, 2008).

Both sediment records display a broadly similar lithostratigraphy, indicating significant lake-level fluctuations due to regional climatic variability over the past ~200 years (Bessems *et al.*, 2008). The composite sequence of Lake Chibwera comprises five distinct lithostratigraphic units (Fig. 4.4). Unit 1 (117-113 cm) is characterised by a dry organic clay horizon with abundant plant fragments, reflecting a substantial lowstand of the lake. It is succeeded by a dry clay horizon with low organic content (11-16%) (Unit 2, 113-103 cm) marking an episode of (nearly) complete desiccation of the lake basin, concomitant with the late 18th to early 19th century drought (Verschuren, 2004; Verschuren and Charman, 2008). Lake sediments deposited above this desiccation horizon reflect renewed lake filling from the early 19th century onwards, starting with an initial swampy phase (Unit 3, 103-93 cm) represented by moist organic peaty clay with abundant plant fragments. This horizon is overlain by soft organic clay (Unit 4, 93-15 cm) with constant water content (~75%) and low organic matter (12-18%), reflecting a generally high lake level during the mid-19th to mid-20th century. The topmost 24-cm section (Unit 5, mid-20th century to 2008) consists of unconsolidated organic-rich clays.

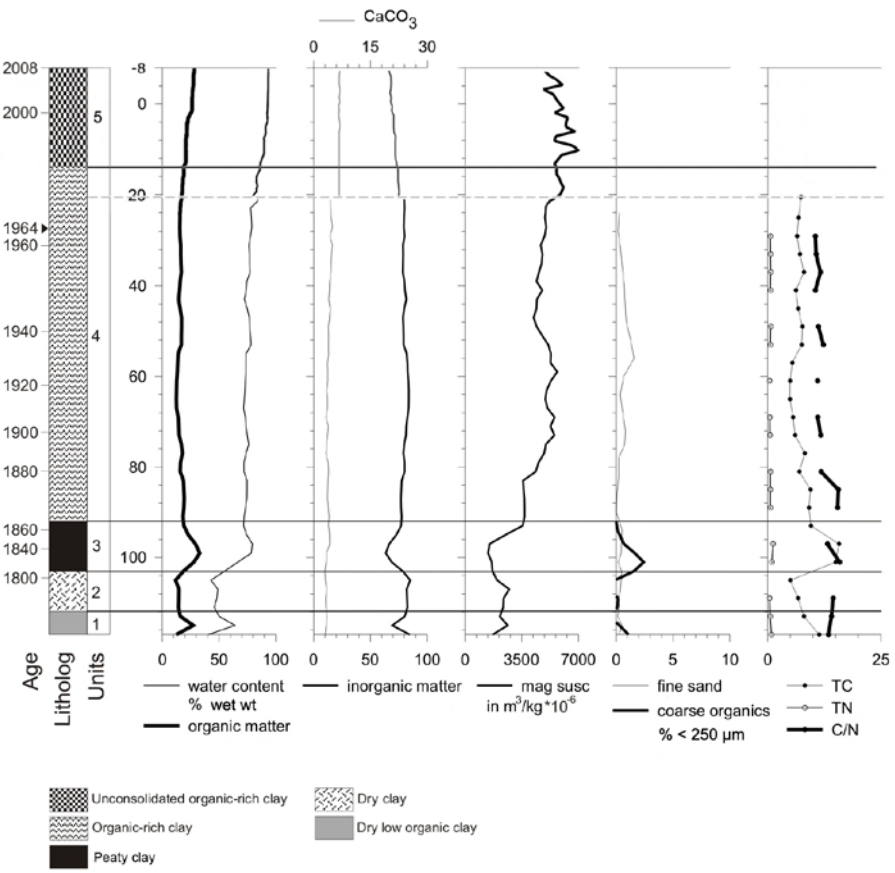

Fig. 4.4. Lithostratigraphy and composition of composite sediment sequence from Lake Chibwera (CHIB02-1P and CHIB08-1G; section boundary indicated by dashed line). Chronology based on ^{210}Pb-dating, anchored in the 1963 AD nuclear-bomb testing peak of 137Cs (arrow) (modified from Bessems *et al.*, 2008).

Based on sediment texture and composition, three lithostratigraphic units were recognised in the Kanyamukali record (Fig. 4.5). Unit 2 (179-131 cm) is composed of dry, black clay with a constant modest organic matter content (~10%), corresponding with the late 18th to early 19th century desiccation event, during which several 100 years of older deposits were oxidised and reworked. It is overlain by moist peaty clay with coarse plant remains (Unit 3, 131-114 cm), reflecting the mid-19th century swamp environment, in turn followed by homogeneous soft organic clay (Unit 4, 114-0 cm) representing the continuous lake phase after renewed filling. Based on the carbon content exceeding 15%, the lower most section of the latter unit (sub-unit 4a, 114-106 cm), however, still indicates a relative low lake level. In sub-unit 4b (106-0 cm) a sudden rise in C/N values (~25) at 32 cm, followed by more moderate values (18-20) towards the top, was probably caused by an increased uptake of carbon derived from land-use activities (e.g., clearing of natural vegetation for subsistence agriculture) within the Kanyamukali catchment in the early to mid-20th century (Bessems *et al.*, 2008). Unfortunately, ^{210}Pb dating of the Kanyamukali composite sequence was problematic because of high inter-sample variability of ^{210}Pb activity measured as ^{214}Bi (range: 7.5–23.4 dpm/g), which impeded reliable calculation of sediment age at depth (Bessems *et al.*, 2008).

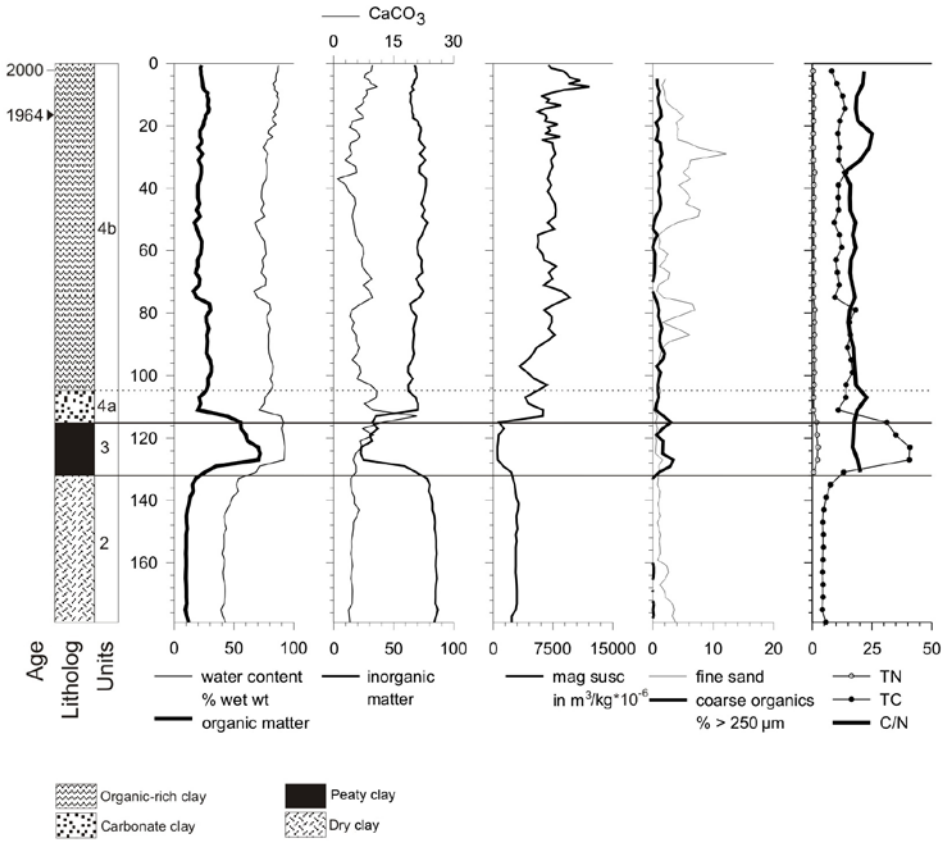

Fig. 4.5. Lithostratigraphy and composition of composite sediment sequence from Lake Kanyamukali (KANYA01-1P/02-1P; KANYA00-1G overlaps with KANY01-1P). Chronology based on ^{210}Pb-dating, anchored in the 1963 AD nuclear-bomb testing peak of 137Cs (arrow) (modified from Bessems *et al.*, 2008).

4.3.2. Non-pollen palynomorph analysis

Sediment samples of 1 ml volume were prepared following standard pollen-analytical procedures (Faegri *et al.* 1989). The samples were boiled in 10% KOH and, successively, in 10% Na pyrophosphate, dehydrated with 96% acetic acid and treated with an acetolysis mixture (1:9) of H_2SO_4 and acetic anhydride, heated to 100 °C in a water bath (for ~10 min). Samples were then subjected to treatments with 96% ethanol, a heavy liquid bromoformethanol mixture (specific gravity 2), and 96% alcohol. The microfossil samples were then put in glycerine and dried overnight in an oven at 40 °C, before being finally mounted on microscope slides.

In total, 33 samples of the Chibwera record were analyzed at ~4-cm intervals (totaling 126 cm). Due to strong variation in the sediment accumulation rate (SAR) through the Kanyamukali record (Bessems *et al.*, 2008), the lowermost samples were spaced evenly at 8-cm intervals (15 samples, 157-37 cm, ~high SAR), and the uppermost samples at 2-4-cm intervals (11 samples, 37-0 cm, ~low SAR) to increase the time resolution. Since the basal clays (179-131 cm) represent prolonged exposure to sub-aerial erosion (Bessems *et al.*, 2008), only the uppermost part of this horizon (i.e.

157-131 cm) was sub-sampled for microfossil analysis. For routine scanning and counting of NPPs an Olympus CX 31 light microscope was used at 400x and 1000x magnification. NPP identifications were based on comparison with descriptions and illustrations in published reference papers (Gelorini *et al.*, 2011; van Geel *et al.*, 2011), and the modern NPP reference collection at Ghent University. To reduce bias from potentially overrepresented NPP types (e.g., *Coniochaeta* spp., fern and moss spores, see Gelorini *et al.*, 2011; van Geel *et al.*, 2011), in each sample ca. 400 NPPs were counted as well as the total number of pollen grains (range: 277-1904; mean value: 897) encountered simultaneously. If the pollen abundances was too low (<100 specimens) compared to the NPP abundances (exceeding 400-500 specimens), counting of NPPs (range: 329-1694; mean value: 481) continued until ca. 200 pollen grains were encountered to ensure statistical robustness of the results. The abundances of individual NPP taxa were expressed as percentages relative to a non-local pollen sum (i.e., excluding aquatics) and plotted using TILIA 2.0.b.5 (Grimm, 1995) implemented by TGview 2.0.2 (Grimm, 2004). NPP-assemblage zones were defined, using a stratigraphically constrained incremental sum of squares cluster analysis (*CONISS, Grimm, 1987*), applied to all observed taxa of fungal spores, interpreted to mainly originate from terrestrial fungi growing within the crater basin (*ex situ*), including the desiccated lake bottom (*in situ*) during drystand episodes.

4.4. Results

4.4.1. Lake Chibwera

CONISS stratigraphic zonation of NPP assemblages in the sediment record of Lake Chibwera defines five non-pollen assemblage zones (NPAZ, Ch-1 to Ch-5), with Ch-2 and Ch-5 subdivided into two distinct sub-zones (Fig. 4.6). The NPP abundances varied from 27 to 203% of the non-local pollen sum, with the highest values (>125%) observed in zone Ch-1 and Ch-2a and lowest values (<50%) in zone Ch-4.

Zone Ch-1 (117-103 cm, late 18th century) corresponds stratigraphically with the dry, mostly low-organic clays deposited under (near-) drystand conditions during regional climatic drought (Unit 1-2, Fig. 4.4). The NPP assemblage of this zone is dominated by the genus of saprotrophic fungi *Coniochaeta*, which can live on diverse substrates, mostly submerged wood, dung and soil and Poaceae (Crane and Shearer, 1995; Asgari *et al.*, 2007). Among other saprotrophic Ascomycota known to inhabit dung (Krug *et al.*, 2004), *Cercophora* type and *Sordaria* spp. (UG-1180 and cf. UG-1180) occur regularly, whereas *Apiosordaria* type, *Delitschia* spp., *Sordaria* type and *Sporormiella* type are present in very low numbers only. Other fungal taxa such as *Brachydesmiella* sp., *Brachysporium* spp., cf. *Podosporium rigidum*, *Meliola* sp. and UG-1109 are also less pronounced in this zone. The presence of UG-1109 and *Glomus* sp. in zone Ch-1 is consistent with desiccated lake conditions. UG-1109 is morphologically similar to the European HdV-200, which typically occurs in relatively dry microhabitats e.g., on standing culms of helophytes (*Phragmites*, *Equisetum* and *Carex*) or plant remains on the temporarily desiccated bottoms of pools (van Geel *et al.*, 1989). Presence of *Glomus* sp., a subterranean endomycorrhizal fungus hosted on a wide range of plants (Gerdemann 1968, Gerdemann and Trappe, 1974), appears to suggest the occurrence of erosion processes causing runoff of soil and plant roots, colonised by *Glomus*, into the lake (Andersen *et al.*, 1984; van Geel *et al.*, 1989). Some *Glomus* species, such as the cosmopolitan *G. mosseae*, are particularly found in agricultural fields (Rosendahl *et al.*, 2009). HdV-1048 reaches its maximum values at the very base of the sediment record. Cf. *Lasiodiplodia theobromae* is also present, but at similar levels as higher up and throughout the entire Chibwera record. The low relative abundance of the green alga *Botryococcus* (grouping possibly two unknown species) may reflect their preference for clear epilimnia, but they are known to be tolerant for high turbidity and low nutrient too (Reynolds *et al.*, 2002; Streble and Krauter, 2002). *Botryococcus* also appears to successfully compete with other algae in shallow waters, experiencing low rainfalls (Batten and Grenfell, 1996), and in slightly acidic waters (pH<6.0) (Round, 1975). At present, the significance of *Botryococcus* is yet difficult to explain and seems heterogenuous. It is known that its palaeoecological indicator value may suggest specific (or extreme) environmental conditions, in absence of other chlorococcal green

algae, such as *Pediastrum* (Jankovská and Komárek, 2000). *Typha* and probably most of the Cyperaceae pollen (including *Carex, Cyperus, Cladium and Eleocharis)* originate from littoral emergent vegetation (Napper, 1971; Lye, 2001; Hoenselaar *et al.*, 2010) which colonised the lake basin in this lowstand phase (Fig. 4.7), although some Cyperaceae are known to occur in the savannah proper (Lye, 2001; Hoenselaar *et al.*, 2010) which surrounded the lake. Undifferentiated ferns (monoletes) only slightly occur throughout the entire record, and temporarily disappear in the following sub-zone Ch-2a and in zone Ch-4.

Sub-zone Ch-2a (103-95 cm, early to mid-19th century) is stratigraphically related to the moist peaty clay horizon (Unit 3, Fig. 4.4) representing a temporary swampy phase characterizing renewed lake filling from the early 19th century onwards. The NPP assemblage of this sub-zone shows an abrupt, temporary increase of *Brachysporium* spp., *Glomus* sp., and *Botryococcus* spp. Among *Sordaria* morphotypes, UG-1180 becomes more abundant, whereas cf. UG-1180 and *Sordaria* type decrease in abundance. Other fungal types which become more apparent are UG-1173, UG-1176 and Xylariaceae, whereas notable decreases in the abundance of *Coniochaeta* spp., *Delitschia* spp., *Sordaria* spp. (cf. UG-1180), *Sordaria* type and undifferentiated ferns (monoletes) are observed.

Sub-zone Ch-2b (95-78 cm, second half 19th century until ~1880) is stratigraphically associated with the lower one-fourth of Unit 4 (Fig. 4.4) representing true lacustrine conditions with fluctuating lake level. The NPP assemblage is typified by a marked decrease in *Cercophora* type, *Sordaria* spp. (UG-1180), *Brachysporium* spp. and *Botryococcus* spp. Percentage values of *Coniochaeta* spp. are strongly fluctuating, but start at very high levels similar to those in Ch-1 and show a general decreasing trend towards the top of the zone and further beyond the zone boundary. *Delitschia* spp. reaches in this zone the highest values from the entire record. Cf. *Savoryella lignicola*, HdV-1048, UG-1173 and UG-1176, however, persist in low abundances through this interval, whereas *Curvularia* sp., *Tetraploa aristata*, UG-1294 and UG-1360 are recorded for the first time.

Zone Ch-3 (78-58 cm, ~1880 to ~1920) corresponds stratigraphically with the next one-fourth of Unit 4 (Fig. 4.4), also representing lacustrine conditions with fluctuating lake level. The NPP assemblage of Ch-3 is characterised by gradually decreasing abundances of *Coniochaeta* spp., *Sordaria* spp. (UG-1180)*, Delitschia* spp., *Brachysporium* spp., UG-1294 and *Botryococcus* spp. towards the top of the zone. A contrasting pattern is shown by *Curvularia* sp., UG-1176, *Rosellinia* sp. and Xylariaceae, which are slightly increasing in the upper section of the zone. Here, UG-1284 and UG-1115 also briefly occur.

Zone Ch-4 (58-15 cm, ~1920 to late 20th century) is stratigraphically situated in the upper two-fourth of Unit 4 (Fig. 4.4). *Coniochaeta* spp. and *Botryococcus* spp. display their lowest percentage values throughout the entire record, showing a marked expansion towards the top of the zone. *Glomus* spp. and HdV-1048 are almost entirely absent, but feebly reappear upon the end. *Brachysporium* spp., *Sordaria* spp. (UG-1180) and undifferentiated ferns (monoletes) (near-)completely disappear in this zone. In contrast to the fluctuating patterns of most abundant fungal taxa, such as *Cercophora* sp., cf. *Lasiodiplodia theobromae,* UG-1173 and UG-1176, through this zone, *Curvularia* sp. is more consistently present. The green alga *Pediastrum boryanum* cf. var. *forcipatum* and the unassigned NPP type UG-1114 record their first distinct presence in the Chibwera sediment sequence. The only marked presence of UG-1292 throughout the Chibwera record is near the top of this interval.

Zone Ch-5 (15-(-9) cm, late 20th century-2000) corresponds stratigraphically with the uncompacted organic muds of Unit 5 (Fig. 4.4). Most notable in sub-zone Ch-5a (15-(-2) cm, late 20th century-2008) are high increases in *Botryococcus* spp. and *Pediastrum boryanum* cf. var. *forcipatum*. In this NPP assemblage *Coniochaeta* spp. show a slight reduction towards half of the zone, followed by a slight increase upon the top. *Sordaria* spp. (UG-1180), cf. *Podosporium rigidum* and *Brachysporium* spp. reappear in low abundances after being (near-)completely absent in the previous zone Ch-4. The rare fungal type UG-1106 is only in this sub-zone commonly recorded.

Sub-zone Ch-5b (-2-(-9) cm, ~2000-2008) is marked by high abundances of *Botryococcus* spp., whereas *Pediastrum boryanum* cf. var. *forcipatum* is significantly decreasing. Cf. *Podosporium rigidum* is now absent; *Brachysporium* spp. and UG-1106 being only present in the uppermost level of the sub-zone. Also contributing to this NPP assemblage

are *Cercophora* type, UG-1072, UG-1109 and cf. Xylariaceae/Sordariaceae/Coniochaetaceae, which occur in very low abundances.

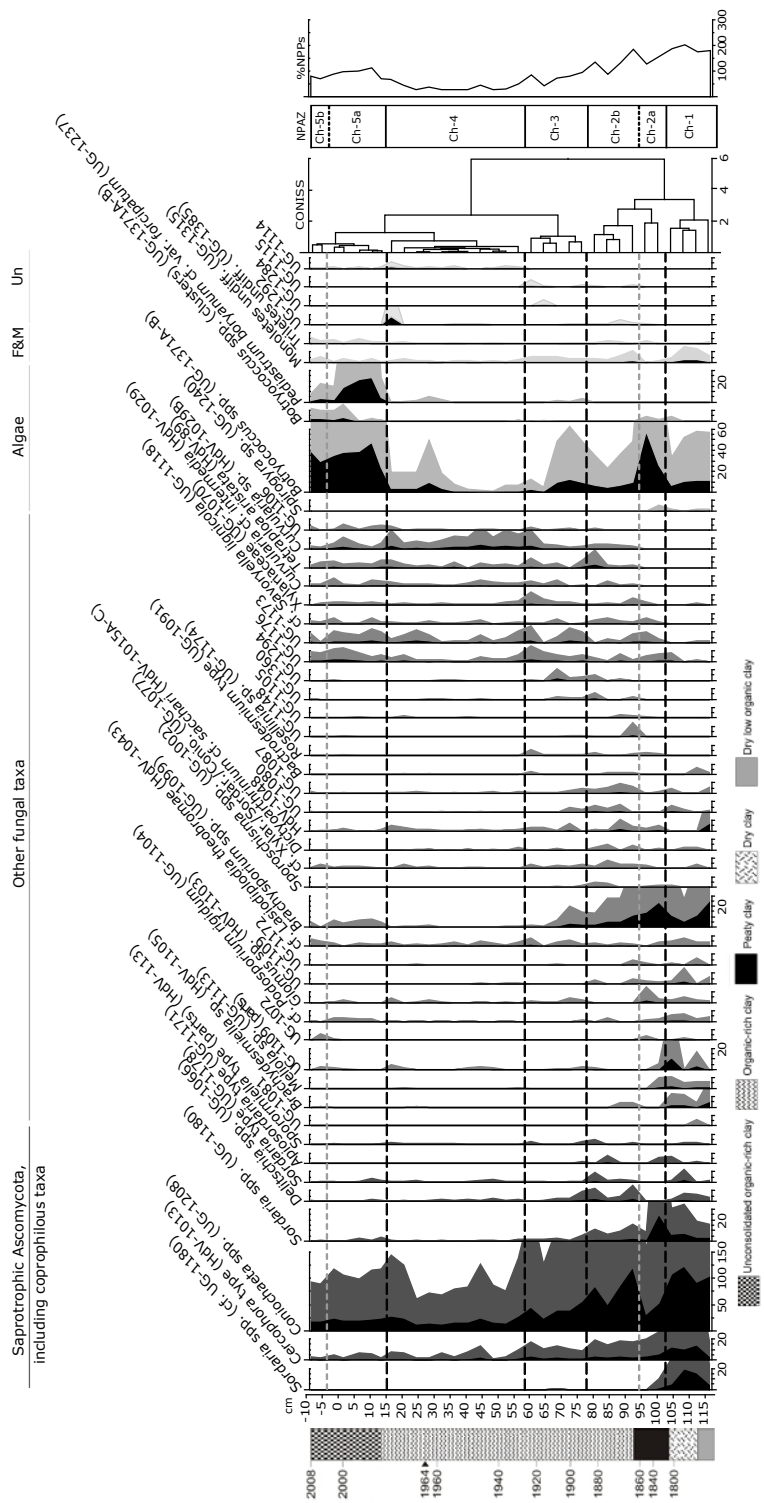

Fig. 4.6. Stratigraphic distribution and zonation of the principal NPP types (taxa with maximum value >1%) in the sediment record of Lake Chibwera. Taxon abundances and NPP sum (%NPPs) per level are expressed as percentages of the non-local pollen sum (exaggeration curves x5, in grey); NPP morphotypes are arranged into groups: saprotrophic Ascomycota including coprophilous taxa, other fungal taxa, algae, ferns and mosses (*F&M*) and unknown microfossils (*Un*).

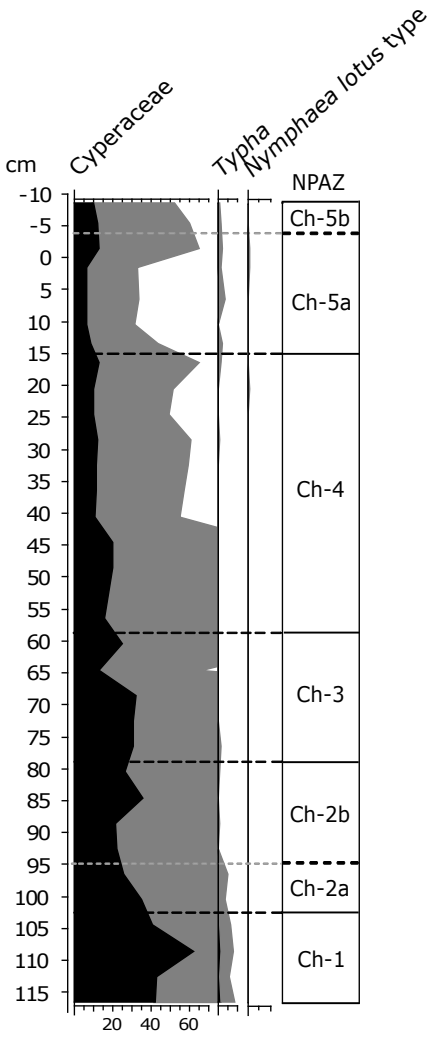

Fig. 4.7. Aquatic pollen taxa expressed as percentages of the non-local pollen sum (Exaggeration curves x5, in grey). Zone boundaries of the non-pollen assemblages (NPAZ, Fig. 4.6) are given for reference.

4.4.2. Lake Kanyamukali

In the sediment record of Lake Kanyamukali, CONISS defines five major non-pollen assemblage zones (NPAZ, K-1 to K-5), with K-5 subdivided into two distinct sub-zones (Fig. 4.8). The NPP abundances varied from 22 to 777% of the non-local pollen sum, with compared to all other zones extreme high values (>700%) reached in zone K-2.

Zone K-1 (156-145 cm, 18th century) corresponds stratigraphically with the dry clays representing the (nearly) desiccated, ephemeral or shallow lake conditions during regional climatic drought prior to the early 19th century (Unit 2, Fig. 4.5). This temporary stage of terrestrialization is also reflected in high abundances of emergent littoral (Cyperaceae and *Typha*) and floating plants (*Nymphaea lotus* type, which includes *N. lotus* and *N. nouchali*) (Fig. 4.9). *Nymphaea* species are typically present in shallow waters and littoral zones, remaining below the 2 m water level (Verdcourt, 1989). The NPP assemblage of zone K-1 is characterised by high percentage values of the fungal spore UG-1109, undifferentiated ferns (monoletes) and *Botryococcus* cf. *neglectus.* All these taxa may benefit from these shallow aquatic conditions (van Geel *et al.*, 1989; Batten and Grenfell, 1996; Verdcourt 1999, 2001). Also notable in this interval is the strong presence of

Coniochaeta spp. and *Cercophora* type, which are commonly recorded in the Kanyamukali sediment sequence. Some unknown microfossils (UG-1311, UG-1319 and UG-1324) are exclusively recovered from zone K-1. Since also *Glomus* sp. reaches its highest abundance in this zone, this combined signature may reflect an increase in soil instability and erosion during this drier period.

Zone K-2 (145-128 cm, late 18th century up to earliest 19th century) is stratigraphically related to the dry clays, deposited and reworked during the regional climatic drought in the late 18th century, and the transition into the peaty deposits representing swampy conditions during theearly 19th century renewed lake filling (Unit 2-3, Fig. 4.5). In this phase, a more swampy vegetation (Cyperaceae, *Nymphaea lotus* type and *Typha*) colonises the shallow lake basin. Zone K-2 is marked by a strong rise in UG-1109, *Cercophora* type and *Coniochaeta* spp. Simultaneously, peak percentage values are also observed in other saprotrophic fungi, including coprophilous taxa (e.g., *Apiosordaria* type, *Chaetomium* sp., *Delitschia* spp., *Sordaria* spp. (cf. UG-1180) and cf. *Sordaria* sp.) and other fungal taxa (e.g., *Savoryella curvispora*, UG-1072, UG-1073 and UG-1360). The number of undifferentiated ferns (monoletes) and *Botryococcus* cf. *neglectus* are gradually declining.

Zone K-3 (128-112 cm, ~early to mid-19th century) is stratigraphically associated with the unit of peaty clay (Unit 3, Fig. 4.5) representing swampy aquatic habitat at the start of early 19th-century lake filling, during which *Nymphaea* entirely disappears, and Cyperaceae show a marked decrease, but *Typha* remains strong. In the NPP assemblage strong reductions are observed in the percentage values of *Coniochaeta* spp., *Sordaria* spp. (cf. UG-1180) and UG-1109. Other NPP taxa such as *Cercophora* type, *Delitschia* spp. and *Botryococcus* cf. *neglectus*, which were also common to abundant in Zone K-1 and K-2, are now nearly absent. Simultaneously, increases in *Tetraploa aristata*, UG-1173 and UG-1176 occur through this interval, whereas undifferentiated ferns are increasing, albeit only temporarily, in the uppermost part.

Zone K-4 (112-47 cm, ~mid 19th century-early 20th century) corresponds stratigraphically with the unit of homogeneous organic clay (Unit 4, Fig. 4.5), of which the lowermost section (Unit 4a) still indicates relative low lake level and the uppermost section (Unit 4b) represents renewed continuous lake filling. Cyperaceae now consistently occur in strongly reduced abundances towards the top (zone K-5b) of the Kanyamukali record, emphasizing local wetter conditions. This is also markedly shown by *Nymphaea lotus* type, which only reappears in the lowermost part of zone K-4, and (near-) completely disappears, together with *Typha*, in the uppermost part and the following section K-5. The NPP assemblage of K-4 is characterised by an increase of *Coniochaeta* spp., *Sordaria* spp. (cf. UG-1180), *Sordaria* type and *Delitschia* spp. *Chaetomium* sp. is only recorded once in this zone, after its continuous presence in zones K-1 and K-2. Other fungal taxa, such as *Tetraploa aristata*, *Brachysporium* spp., UG-1173, UG-1176 and UG-1274, are more or less consistently present but in very small numbers. *Botryococcus* cf. *neglectus* occurs sporadically and is mainly concentrated in the lower half of this zone. Parts of epidermis of *Nymphaea* cf. *nouchali* are restricted to this zone and exclusively preserved contrary to Zone K-1, in which only pollen of *Nymphaea lotus* type (including *N. lotus* and *N. nouchali*) are recorded. It appears that fragile organic material, such as tissue of submerged aquatic plants, was more heavily exposed to oxidation and erosion in the catchment during the late 18th drought than during this wetter period of fully lacustrine conditions. At the top of this interval, *Filinia* sp. makes a single brief appearance.

Zone K-5 (47-0 cm, early 20th century until 2001) corresponds stratigraphically with the organic clay deposited during the continuous lake phase (Unit 4b, Fig. 4.5). It is typified by a decrease of *Coniochaeta* spp. and *Sordaria* spp. (cf. UG-1180) in the lower half of the section, followed by slightly higher percent abundances towards the top. Although *Glomus* sp. was (near-)completely absent since its continuous presence in zone K-1, it reappears in very small numbers in the uppermost section of zone K-5. *Tetraploa aristata*, cf. *Lasiodiplodia theobromae* and *Curvularia* cf. *intermedia* disappear throughout much of this zone, but are then more consistently observed towards the top. *Brachysporium* spp. now displays slightly higher percentage values. The fungal types UG-1200 and UG-1106 are only recovered from the topmost level. Undifferentiated ferns and coenobia of algae are almost absent.

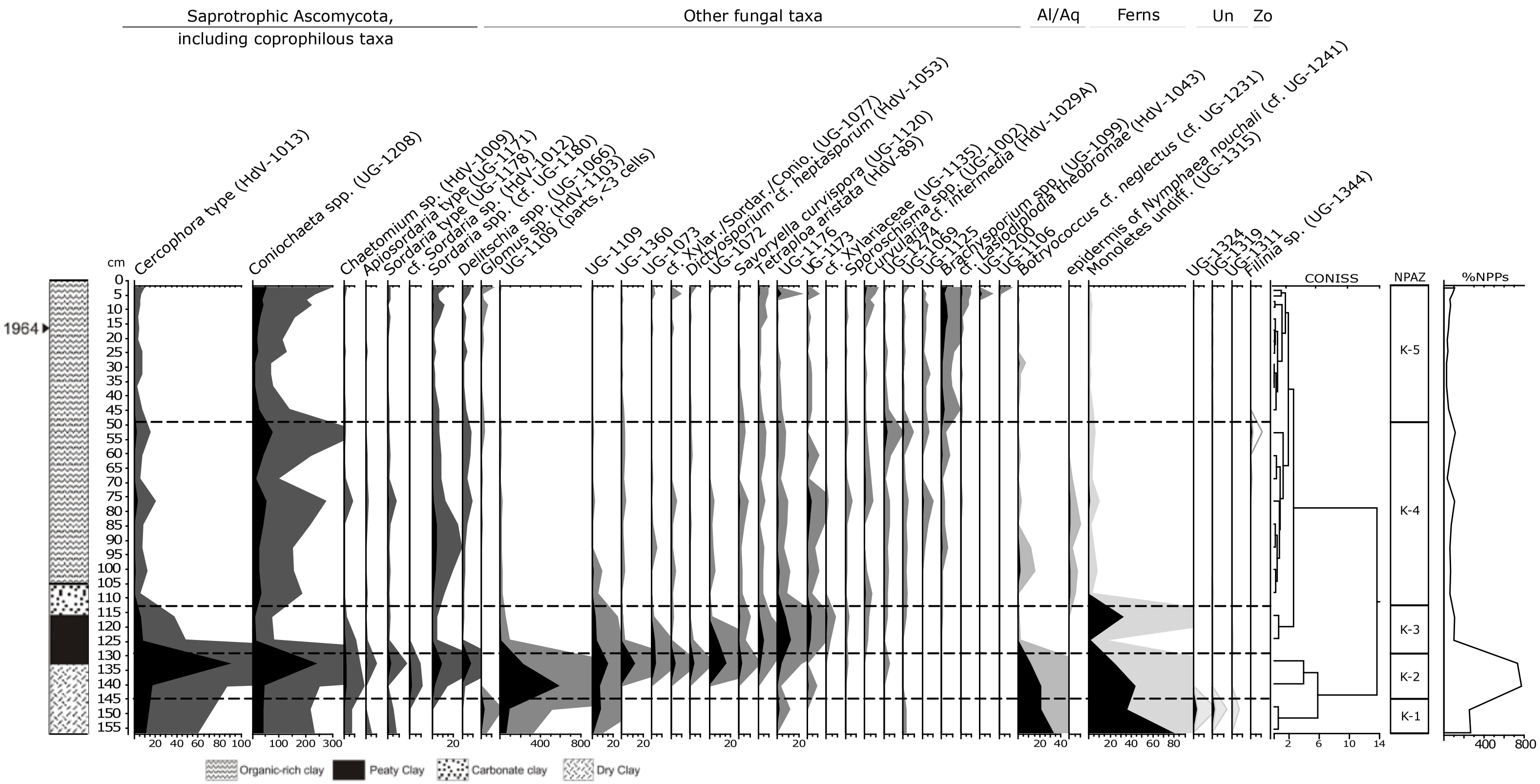

Fig. 4.8. Stratigraphic distribution and zonation of the principal NPPs (taxa with maximum value >1%) from the sediment record of Lake Kanyamukali. Taxon abundances and NPP sum (%NPPs) per level are expressed as percentages of the non-local pollen sum (exaggeration curves x5, in grey); NPP morphotypes are arranged into groups: saprotrophic Ascomycota including coprophilous taxa, other fungal taxa, algae and aquatic plant remains (*Al/Aq*), ferns, unknown microfossils (*Un*) and zoological remains (*Zo*).

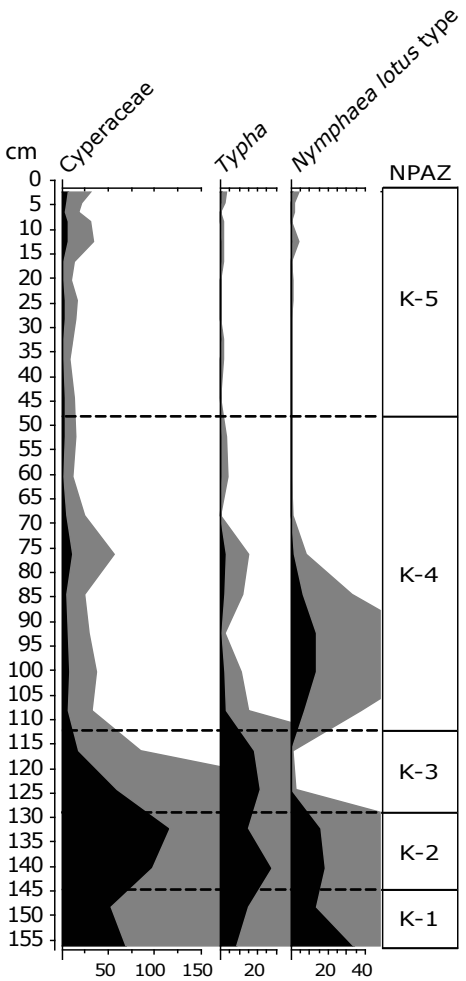

Fig. 4.9. Aquatic pollen taxa expressed as percentages of the non-local pollen sum (Exaggeration curves x5, in grey). Zone boundaries of the non-pollen assemblages (NPAZ, Fig. 4.8) are given for reference.

4.5. Discussion

4.5.1. Environmental similarities and differences between Lakes Chibwera and Kanyamukali

Lakes Chibwera and Kanyamukali have experienced similar major environmental trends during the past 200 years. Given the proximity of these lakes, the similar natural landscape in which they are located, and based on multi-proxy data collected previously (e.g., Bessems *et al.*, 2008; Audenaert *et al.*, in prep.; Ssemmanda, unpublished CLANIMAE data), they were expected to share a common climatic and environmental history.

During the late 18th-century regional drought, shallow lake conditions provided excellent for habitat for fungi and emergent (ferns, Cyperaceae and *Typha*) and floating (*Nymphaea*) littoral vegetation to flourish and spread in both lake basins. Especially in the small, nearly desiccated Lake Kanyamukali (0.02 km^2) a large portion of the lake area was occupied by emergent littoral vegetation, probably also colonizing the deeper part of the basin. This is mainly indicated by the high abundance of aquatic pollen and spore taxa, besides the high amounts of the fungal type UG-1109, which seems strongly related to the presence of macrophytes (Van Geel *et al.*, 1989). In the medium-sized Lake Chibwera (0.76

km^2) the littoral zone seemed less expanded to the relatively larger profundal zone of the lake basin. The observed diverging response between both lakes is possibly due to topographic and lake morphometric differences: Chibwera is a low-rimmed crater lake, which is more subjected to wind erosion, whereas Kanyamukali is characterised by a smaller and more strongly concave lake floor, sheltered from wind. These specific physical properties of Kanyamukali may promote higher water transparency (Audenaert *et al.*, in prep.). However, relatively higher surface runoff during this drought episode at Kanyamukali is suggested by more abundant *Glomus* spores. In Lake Chibwera, large numbers of *Brachysporium* may also suggest the presence of decaying wood and bark in the shallow lake basin (Ellis, 1971, 1976).

The desiccation event is significantly reflected in the taphonomic and preservation bias of the plant and animal microfossil assemblages in the dry clay horizons of both sediment records. Because of stronger effects of drought and erosion, the microfossil records yielded low concentrations of chironomid fossils, poorly preserved diatoms (Audenaert *et al.*, in prep.) and strongly degraded fossil pollen. Unexpectedly, these findings sharply contrast with high abundances of well preserved, intact NPPs (see also %NPPs, Figs. 4.6 and 4.8). This may indicate that (i) the specific chitinous (e.g., fungal spores, Peter, 2002) and polysaccharidic (e.g., chlorococcal algae, Domozych, 2006) composition of some NPP groups is possibly less susceptible to subaerial oxidation and mechanical forces, and/or (ii) the abundant NPPs are mainly of strictly local origin, deposited in situ in these ephemeral lakes. The higher values of %NPPs in the lowermost desiccated horizon at Kanyamukali suggest that the local desiccation impact was more pronounced than at Chibwera. Nevertheless, in the sediment records of both lakes high %NPPs values seem to clearly display the period(s), in which the lake level was at the lowest.

The major local habitat changes during the late 18th-early 19th-century lowstand are also remarkably shown in the fungal spore record of both lakes. The accumulation of appropriate substrates (mainly plant and wood remains) in the lake basins promoted the in situ growth of saprotrophic fungi, of which most fungal spores were deposited closely to their source area. This is mainly implied by very high amounts of spores of saprotrophic Ascomycota, of which most represented genera (e.g., *Cercophora* (as part of *Lasiosphaeria*), *Coniochaeta*, *Apiosordaria* and *Chaetomium*) are commonly hosted on dead wood and plant debris besides dung (Hanlin, 1990; Romero *et al.*, 1999; Asgari *et al.*, 2007; Mukerji, 2010), and only few genera (e.g., *Sordaria*, *Podospora, Delitschia* and *Sporormiella*) inhabitat dung obligately (Ahmed and Cain, 1972; Bell, 1983; Krug *et al.*, 2004). Some of these genera (e.g., *Cercophora* and *Coniochaeta*) may also include species typically occurring on submerged wood (e.g., *Cercophora aquatica*, Chaudhary *et al.*, 2007, and *Coniochaeta renispora*, Crane and Shearer, 1995). Given their association with different substrates, the ecological indicator value of most of these saprotrophs is more complex and ambiguous than their (non-obligate) affinity with dung, regularly suggested in palaeoecological studies (e.g., Willemsen *et al.*, 1996; van Geel *et al.*, 2003; López Sáez and López Merino, 2007; Mazier *et al.*, 2009), would suggest. Furthermore, proper identification of these fungi is strongly impeded by the difficulty of taxonomic discrimination. For instance, some saprotrophic fungi, such as the obligate coprophilous genus *Podospora* and occassionally dung-inhabited taxa *Cercophora*, *Schizothecium* and *Zopfiella*, may produce morphologically similar ascospores (Bell, 1983; Khan and Krug, 1989), and are therefore here grouped in a single morphotype*, Cercophora* type (HdV-1013, Gelorini *et al.*, 2011; van Geel *et al.*, 2011). Some of these fungi are only distinguishable from one another by molecular phylogenetic analysis (e.g., Chang *et al.*, 2010). Consequently, in the sediment records of Lakes Chibwera and Kanyamukali only three types of ascomycete spores, *Sordaria* spp. (UG-1180), *Delitschia* spp. (UG-1066) and *Sporormiella* type (HdV-113, including *Sporormiella* and *Sporormia*, van Geel *et al.*, 2011; see also Davis and Shafer, 2006), are likely to be, at least predominantly, indicative of the local presence of significant amounts of dung, and subsequently, indicators for wild or domestic herbivore density. This concurs with the results of a modern calibration study of fungal spores in the Lake Baringo catchment (Kenya; Kiage and Liu 2009), where *Sporormiella* type, *Chaetomium* type and *Sordaria* type (no distinction between our three types) were found to be most strongly associated with livestock keeping. Correspondence analysis of 56 types of modern NPPs (of which 13 are supposedly dung-related Ascomycota) at 31 sites in the Basque region of France also revealed a strong linkage of *Sporormiella* type (HdV-113) and *Sordaria* spp. (HdV-55A-B) with cattle grazing (Cugny *et al.*, 2010). Considering the obligate affiliation of these fungal spore types with herbivore dung, we

suggest that the sediment records of Chibwera and Kanyamukali show evidence of high local population density of wild and/or domestic herbivores during the late 18th-early 19th century lowstand. Presumably, both shallow lake basins were intensely visited by animals to drink and bath in these times of water shortage.

During the early/mid-19th century both lakes experienced a renewed lake filling. Most saprotrophic fungi (particularly *Coniochaeta* spp. and *Cercophora* type) retreated to the peripheral portions of the catchments. This significantly affected the spore influx in the lakes and moderated their abundance in both NPP records. In Lake Kanyamukali, long-lasting shallow conditions allowed abundant submerged macrophyte growth, which over time produced a substantial package of peat. High quantities of *Typha* pollen indicate that there is still a dense reed fringe, occupying a significant part of the lake. *Typha* is also known to be more tolerant to higher and less fluctuating lake levels (Brinson *et al.*, 1981; Osborne, 2000). The fungal types UG-1173 and UG-1176 seem to be favored by these local peaty, moist conditions. A sudden reduction in the coprophilous *Sordaria* spp. (cf. UG-1180) suggest that the density of herbivores in the lake area of Kanyamukali was reduced during that period, in contrast to what happened in Chibwera. In Lake Chibwera, the swampy conditions were less developed, because of more rapid lake filling, indicated by a relatively smaller amount of emergent littoral vegetation and more pronounced turnover from benthic-epiphytic to planktonic diatom dominance (Audenaert *et al.*, in prep.). High amounts of *Brachysporium*, however, may still indicate the presence of decaying wood or plant remains in the lake water.

From the mid-19th century, climatic conditions became briefly wetter, resulting in continuous filling of both lakes and provoking a retreat of emergent littoral vegetation to near-shore areas. At Kanyamukali, the water level probably started to increase more rapidly, given its high-rimmed morphometry, capturing rain run-off and accumulating sediment (cf. high SAR) more continuously. In contrast to Chibwera, where the dung-related signal almost completely disappeared, at Kanyamukali large herbivore mammals continued to use the lake area for grazing and drinking.

Historically documented episodes of decade-scale rainfall variability are strikingly recorded in both sediment sequences. Despite the chronological uncertainty of the records, a distinct climatic correlation (after the early-19th century) between *Coniochaeta* spp. and moisture change was observed, however its sensitivity to humidity changes was more apparent in the record of Lake Kanyamukali. Here, episodes of marked increases appears to correspond with episodes of Lake Victoria highstands during ~1870-1900 AD and ~1960-1990 AD (Nicholson, 1998; Tate *et al.*, 2004), whereas decreases seem to coincide with the overall slightly drier mid-19th century and the period ~1900-1960 AD. At Chibwera, however, a less clear response of *Coniochaeta* to these rainfall anomalies is shown across the record, broadly displaying the ~30 years wetter periods of the late 19th and late 20th century and the more prolonged dry period in the early/mid-20th century, particularly punctuating a short period of increased aridity in the 1940s-50s (Nicholson, 1986, 1989, 1996). This strong correlation between *Coniochaeta* and moisture changes agrees with the palaeoecological results from Van Geel *et al.* (2011), showing a positive correlation between *Coniochaeta* cf. *ligniaria* (here included in *Coniochaeta* spp.) and a proxy indicator of moisture balance in the fungal record of the 25,000 year sediment sequence of Lake Challa (southeastern Kenya). Also at Kuahuqiao, an early Neolithic site in the lower Yangtze region of east China, the occurrence of *Coniochaeta* (C. *xylariispora* and *C.* cf. *ligniaria*) in the sediment record seemed indicative for early Holocene hydrological changes in the swamp environment (Innes *et al.*, 2009). Apart from more local-specific, heterogeneous habitat changes (e.g., accumulation of dung and/or organic matter during severe lowstands), the distribution of *Coniochaeta* in fossil lake-sediment records may thus be strongly related to local and regional moisture changes at longer and shorter time scales. Along with the less abundant fungal taxa *Tetraploa aristata* and *Curvularia* cf. *intermedia*, *Coniochaeta* is probably hosted on plants which prefer moist conditions.

In the early/mid-20th century, during a relatively dry period, a marked decline in the abundance of *Botryococcus* occurred at Chibwera. Conversely, the wetter episode from ~1960-1990 AD significantly enhanced blooms of *Botryococcus* and *Pediastrum boryanum* cf. var. *forcipatum,* colonizing the lake until at present. Unfortunately, it is yet unclear if nearby human activity may have altered the nutrient cycling of Chibwera, particularly in the past 30 years. The recovered cultivated pollen taxa (including cereals, Cupressaceae, eucalyptus and pine) in the Chibwera sediment

sequence are more likely transported over long distance by wind into the protected reserve, however Cupressaceae locally occur. Probably, they were planted by people visiting the Nsere Lodge, a permanent camping site located near the lake shore in the 1980s-1990s. At Kanyamukali, intensified grazing and subsistence farming in the lake catchment commenced in the mid-20th century with the establishment of human settlements near the lake. These agricultural activities are mainly reflected in a slight increase of coprophilous taxa (*Sordaria* and *Delitschia*) in the uppermost section of the Kanyamukali record. The simultaneous occurrence of *Glomus* sp. throughout that period probably marks the first evidence of soil erosion and land degradation, caused by crop cultivation and tree plantation on the crater slopes. This is also indicated by cultivated pollen types (including cereals, eucalyptus and pine), which record their first consistent presence from ~1964 AD.

4.5.2. The linkage with pastoralism: a critical evaluation

In our dataset, only three ascomycete spore types (*Sordaria* spp., *Delitschia* spp. and *Sporormiella* type) can be classified as being predominantly coprophilous. Although some coprophilous species included in other saprotrophic fungal types (such as *Cercophora* type, *Chaetomium* type and *Coniochaeta* spp.) may be cryptically present in both sediment records, their stratigraphic distribution suggests dominant control by non-dung related factors. Nevertheless, obligate coprophilous taxa represent a relatively significant proportion of the fungal spore assemblage in the lowermost horizons of both lakes. At Chibwera, a high abundance of spores is observed in the dry clay phase, whereas at Kanyamukali most of these spores occur at the transition to the peat accumulation. This indicates that both lakes were frequently used by wild/domestic animals during that period. The high proportion of spores at Chibwera during the late 18th century drought suggests that water is probably more permanently available, whereas at Kanyamukali the lake at least more periodically (nearly) desiccated. Here, herbivores were attracted more consistently when the lake start to gradually refill from the early 19th century. It is, however, yet unclear if these dung peaks can be associated with cattle herding or trans-humant pastoralism, since no direct linkage with local human activities can be made, because of absence of archaeological sites and sufficiently detailed palaeoenvironmental data. These coprophilous spore types can also not typically be associated with specific herbivore species. Only at the species level, few taxa may be strongly associated with specific animals (Lundqvist, 1972; Parker, 1979; Caretta *et al.*, 1998). Also variable food intake (Kruys and Ericson, 2008) and other environmental factors, such as temperature, nutrient availability and other dung-inhabiting species may influence species composition on dung substrates (Ebersohn and Eicker, 1997). Since both lakes are located in a savannah area inhabited by wild mammals, the dung concentration could result from the local aggregation of wild herbivores due to dry conditions (Ekblom and Gillson, 2010). However, the location of Lake Kanyamukali near an ancient cattle trail and/or trading route may suggest that this lake is more frequently visited by pastoralists, herding their cattle to suitable grazing areas. In contrast, Lake Chibwera is located in an area with large freshwater resources (such as L. George), which are more likely to be exploited by humans to water their cattle. The discrepancy between the amount of coprophilous spores in both lakes becomes more apparant from the mid-19th century until the present, and may shed light on anthropogenic signals in the sediment records. At Kanyamukali, a low signal of dung influx continuously persists, whereas at Chibwera, it totally disappears. Although there is no reason to believe that wild animals may have left the Chibwera area, a relatively higher population density of herbivores is consistently recorded at Kanyamukali. This may, however, strengthen our hypothesis that Kanyamukali was permanently visited by cattle herds. Furthermore, a decrease in the abundances of dung spores during the early/mid-20th century may be due to the prolonged sleeping sickness epidemic in the area (Tse Tse Berrang-Ford *et al.*, 2006), affecting both wild and domestic animals. During that period, the area was heavily subjected to protective measures, and subsequently abandoned by humans. From the mid-20th century, a human settlement was established near Kanyamukali, resulting in agricultural activities (grazing and crop cultivation) in the crater area, marked by a slight increase of herbivore dung spores (*Sordaria* spp. and *Delitschia* spp.).

4.6. Conclusion

The study of paired fossil non-pollen palynomorph records of two small, relatively shallow crater lakes in western Uganda allowed us to separate the individualistic environmental responses of both lakes to regional short-term rainfall variability and local human impact over the past 200 years. The NPP assemblages of Lakes Chibwera and Kanyamukali clearly showed distinct decade-scale episodes of lake-level fluctuations, and major moisture changes in the lake catchments. Moreover, the marked presence of some obligate coprophilous Ascomycota, *Sordaria* spp. and *Delitschia* spp., predominantly growing on herbivore dung, also suggested intense usage of the lakes by wild/domestic herbivores during severe lowstands in the late 18th-early 19th century. The dung signal in the sediment record of Chibwera disappeared from the early/mid-19th century despite its location in a savanna area inhabited by wild mammals (elephant, hippo, waterbuck..), suggesting that their use of the lake does not suffice to be recorded, unless the lake was almost dry and coprophilous fungal spores were deposited on the central lake floor. However, evidence of high impact of herbivores persisted at Kanyamukali, and further increased with intensifying human activity in recent decades. We therefore surmise that Lake Kanymukali was more frequently and consistently visited and used by pastoralists, herding their cattle to watering places and grazing areas. The current location of Lake Kanyamukali near the main road Kasese-Fort Portal, arisen from an ancient cattle trail and/or trading route, may underscore its stronger historical linkage with transhumant pastoralism. From the mid-20th century, its catchment area was also intensively used for crop cultivation and grazing, mainly indicated by the presence of coprophilous Ascomycota, *Sordaria* spp. and *Delischia* spp., and *Glomus* spp., an endomycorrhizal fungus, associated with increasing soil erosion and land degradation.

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General discussion and conclusion

As a final reflection on this PhD research, the overall significance of our results for palaeoecology and particularly African palaeoecology are discussed in a scientific framework where boundaries of time and space are metaphorically fading. Present and past are confronted with one another to provide a take-home message on future perspectives of non-pollen palynomorph (NPP) analysis in African palaeoecology. Our assessment of the diversity and palaeoecological significance of NPP assemblages in East African lake sediments proved challenging, but revealed a fascinating palaeoecological microcosmos ready for further exploration.

Non-pollen palynomorphs in East African lake sediments: a new palaeoecological microcosmos

Confronting present and past: a perfect match between modern and fossil diversity?

To evaluate if modern (present-day, until ~10 years ago) NPP assemblages recovered from recently deposited (surface) lake sediments are an appropriate reference to study fossil NPPs extracted from ancient lake sediments, we first need to compare both major datasets (modern vs. fossil) consistently. Previous paired studies of modern and fossil NPPs in terrestrial sediment archives (e.g., Prager *et al.*, 2006; Yeloff *et al.*, 2007; Cugny *et al.*, 2010) suggested that these NPP assemblages are often difficult to reconcile. For instance, in Alder wood peats in NE Germany (Barthelmes *et al.*, 2006; Prager *et al.*, 2006) only 12% of overall NPP taxon richness was shared between modern and fossil datasets. Similarly in the fossil record of a peat bog from the Iraty Massif in France, Cugny *et al.* (2010) detected only few of the modern NPPs (mainly from saprotrophic ascomycetes, including dung-inhabiting taxa) trapped on moss polsters nearby. Both studies concluded that the discrepancy in richness and composition between modern and fossil datasets could be attributed mainly to (i) sampling of different substrate types, which may host specific autochthonous NPPs, and (ii) taphonomic processes which may cause selective degradation and preservation of different fossil NPPs. Moreover, the abundance of NPPs in subsoils and sediment archives is strongly determined by differences in NPP dispersal to the site (various transport vectors and distance from the source area), NPP-specific characteristics (such as production variability between taxa and biotic groups) and environmental conditions (vegetation, moisture balance and disturbance).

Given that most of the NPPs encountered in the surface sediments of our 24 calibration lake basins[1] (for an overview of those basins, see Chapter 3) were recorded only rarely (278 out of 302 NPP taxa represent <0.5% of the total ~12,400 specimens counted; i.e. Chapter 3 only includes fungal spores), the strength of this exploratory research was the rigorous discrimination and inventarisation of 302 distinguishable NPP morphotypes. In contrast, overall taxon richness in a comparable number of fossil NPP assemblages (33 and 26 samples, respectively) extracted from the sediment records of Lakes Chibwera and Kanyamukali was significantly lower, totaling 167 and 156 morphotypes, respectively (Fig. i)[2]. We suggest that the high taxon richness of our modern NPP dataset can be mainly attributed to the environmental heterogeneity of the 24 lake basins selected for our calibration study rather than to degradation of NPPs after incorporation in the sediment record. Research on the preservation of palynomorphs in lake sediments (Davis, 1968, 1973; Davis, 1969; Wilmshurst and McGlone, 2005a) have shown that those types of pollen and spores

1 For an overview of the 24 calibration lakes, see Fig. 3.1, Chapter 3.

2 Because van Geel et al. (2011) focused on a subset of well-defined NPP types in the fossil record of Challa, it was not feasible to assess the total NPP richness recovered from that study site, hence the NPP data from Lake Challa are not included in this analysis.

which are most susceptible to detoriation, are already completely destroyed before they are actually incorporated into the lake sediment. However, the harsh pollen preparation method also strongly affects thin-walled fungal spores and silicious microfossils (e.g., diatoms and dinoflagellates). Nevertheless, our results demonstrate a remarkable coherence in rarefacted richness (*EF159*, i.e. at constant sample size of 159 individuals) of fungal spores between our 24 modern assemblages, which vary from 12 to 38 morphotypes (mean: 24) per lake site, and the fossil assemblages (Fig. ii), which range from 15 to 31 morphotypes (mean: 24) and 6 to 31 morphotypes (mean: 20) per sampled level in the sediment sequences of Lakes Chibwera and Kanyamukali, respectively. This similarity in overall fungal spore rarefacted richness seems to dispel a predominant effect of post-depositional decay on fungal spore richness. However, in fossil records, the magnitude of changes through time in local (micro-) habitats and catchment land cover, linked to past climate variation, are probably more decisive than preservation conditions to explain the contrast in overall fungal spore richness between an individual fossil record and the collection of reference sites represented by surface-sediment samples. This is exemplified by the effect of local habitat change on *EF159* in the fossil records of Lakes Chibwera and Kanyamukali, showing the lowest richness values (<20 taxa) in zones Ch-1 and K-1, i.e. coeval with the late 18th-early 19th-century drought episode, when both lakes (periodically) nearly desiccated. However, *EF159* appears not to be affected by late 20th-century human impact, as reflected by its correlation with the percentage sum of recorded cultivated pollen taxa. The relationship between fungal spore richness and the presence of cultivated (and other) pollen types is most probably complicated by environmental processes, such as dispersal mechanisms, pollen versus spore production rates, host specificity etc. For instance, at Lake Chibwera the cultivated pollen types (except for Cupressaceae, which also occur in natural vegetation) are more likely transported over long distance by wind into the protected reserve, making evidence for possible correlation inadequate. The evenness of fungal spore diversity ($E_{1/D}$) is consistently low in both 24 modern assemblages, ranging from 0.04 to 0.26 (mean: 0.08), and the fossil assemblages, varying from 0.05 to 0.14 (mean: 0.08) and 0.04 to 0.35 (mean: 0.10) per sampled level in the sediment records of Lakes Chibwera and Kanyamukali, respectively. However, diversity evenness peaked at values of 0.13-0.14 in zone Ch-2a at Chibwera, and values of 0.28 and 0.35 in zone K-3 at Kanyamukali, when the local environment was characterised by swampy conditions and %*Coniochaeta* spp. was at its lowest. The latter may have affected evenness, as has also been suggested in our modern study (see Chapter 3), however since its negative correlation with evenness is mostly limited to the peat horizon, we suggest that local habitat changes had a stronger effect on evenness than the varying percent abundance of the over-dominant *Coniochaeta*.

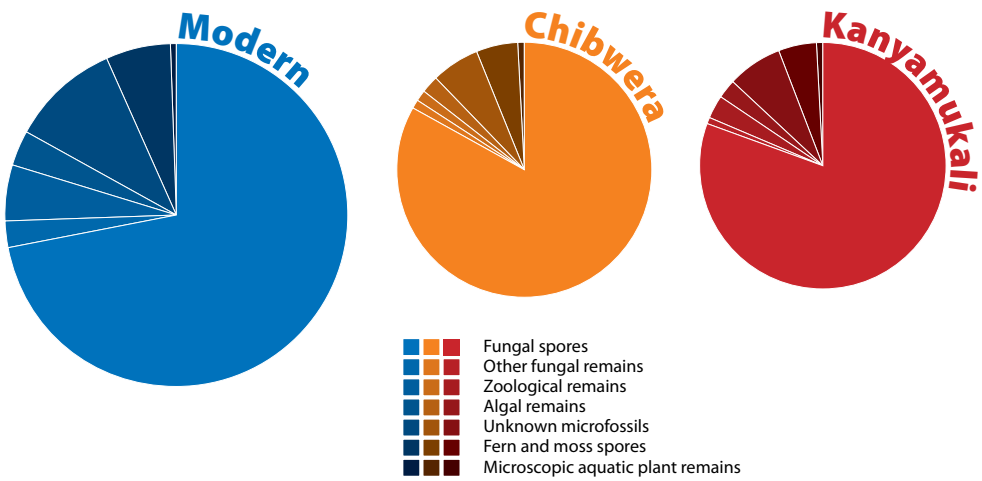

Fig. i. Overall taxon richness per NPP group, recorded in the modern assemblages of 24 Ugandan crater lakes (N=302 morphotypes) and in the fossil assemblages of Lakes Chibwera (N=167) and Kanyamukali (N=156).

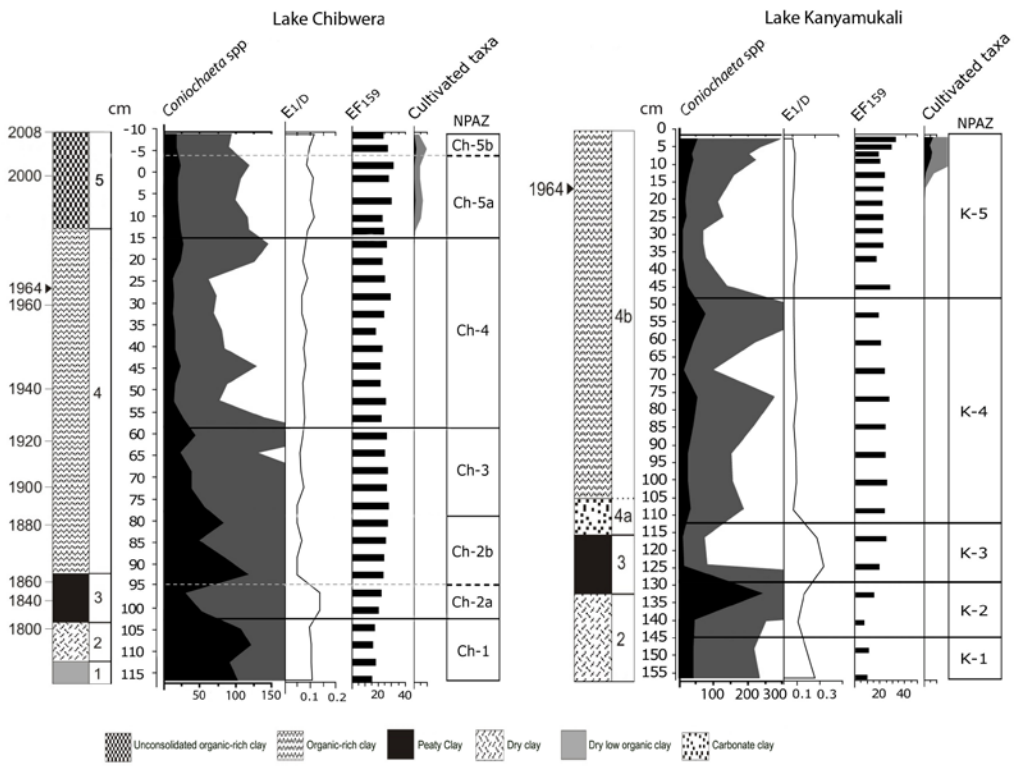

Fig. ii. Evenness ($E_{1/D}$) and rarefacted richness (EF_{159}), calculated for the fungal spore types, recorded in Lake Chibwera and Kanyamukali. *Coniochaeta* spp. and cultivated taxa (i.e. including cereals, Cupressaceae, *Eucalyptus* and *Pinus*) are expressed as percentages of the non-local pollen sum (Exaggeration curves x5, in grey scale). Zone boundaries of the non-pollen assemblages (NPAZ) are given for reference.

Further, respectively 142 (85%) and 137 (86%) of all morphotypes recovered from the Chibwera and Kanyamukali records are represented in the modern samples ('cf.' morphotypes included). Among the 34 morphotypes that are not represented, 10 (29%) were present in both sediment sequences. This high degree of coherence contrasts with the results of all other paired studies of modern and fossil NPPs (cited above), where coherence is much lower. This is probably due to an advantageous combination of research conditions in our study, namely (i) the high environmental heterogeneity among calibration sites, thus covering much of the overall NPP diversity in Ugandan lake sediments, (ii) the rich environmental history recorded in the sediment sequences of Lake Chibwera and Kanymukali, promoting fossil NPP diversity, (iii) importantly, the similar sedimentary conditions represented in surface-sediment samples and older lake deposits (e.g., Wilmshurst and McGlone, 2005b), demonstrating the appropriateness of the former as modern analogues for the latter, and (iv) the allochthonous origin of most NPPs deposited in lake sediments (see infra), which reduces bias from strictly autochthonous taxa occurring at peat sites and in moss polsters (e.g., Prentice, 1985; Sugita, 1993; Wilmshurst and McGlone, 2005b; Prager *et al.* 2006; Cugny *et al.*, 2010).

Similar to the modern dataset, the two fossil datasets were dominated by fungal spores, fern and moss spores, zygospores and colonies/coenobia from algae, and unknown microfossils (Fig. i). The other fungal remains (cleistothecia and/or sporangia) and zoological remains (mainly oocytes and cysts from aquatic invertebrates), however, appeared affected

by slight richness loss compared to the modern dataset (Fig. i). These findings are partially consistent with the results of Prager *et al.* (2006), in which fungal, invertebrate and microscopic vascular plant remains were better represented in modern surface samples than in fossil samples. A possible hypothesis for this richness loss is the lower production rate of these types (e.g., sporangia, cysts, oocytes, epiderms etc.), originating from mainly local source organisms (e.g., (semi-) aquatic fungi, aquatic invertebrates and aquatic plants). As a result, these specific types may be more susceptible to differential deposition and hence generate a more patchy representation in NPP assemblages, similar to the situation of pollen from insect-pollinated plants in pollen assemblages.

Fungal spores of *Coniochaeta* are remarkably ubiquitous in both our modern and two fossil datasets, representing respectively 50% (modern; total NPP sum: 12,392), 47% (Lake Chibwera, total NPP sum: 14,140 NPP) and 45% (Lake Kanyamukali, total NPP sum: 14,257) of all counted NPPs. A relatively high abundance of *Coniochaeta* cf. *ligniaria* is also generally reported in Lake Challa (21%, total NPP sum: 16,403), however a significantly higher mean value is shown from ca. 8000 cal. BP until the present (38%, NPP sub-sum: 6023). Given the heterogeneous ecological preference of this fungal genus, which can grow on various substrates (e.g., submerged wood, dung and plant material), its true palaeoecological significance is yet unclear. However, on both long (millennial) and short (decadal-to-century) time scales, its palaeoecological signature appears to be affected by climate-driven changes in humidity (van Geel *et al.*, 2011; Innes *et al.*, 2009; Ekblom and Gillson, 2010; Chapter 4).

On the origin of non-pollen palynomorphs in lake sediments

One of the more challenging tasks we faced during this research was to work with as-yet unidentified microfossils, of which the source origin was mainly unknown or uncertain. However, as shown in Fig. iii even mycologists studying modern fungi are mostly unaware of the habitat associations of fungi in lakes. In their review on fungi in lake ecosystems, Wurzbacher *et al.* (2010) metaphorically stated that searching the literature for fungal occurrence or activity in lakes is like fishing in these lakes using the wrong bait. Indeed, until recently, mycological research on lake ecosystems only focused on specific groups of fungi, such as yeasts and aquatic hyphomycetes (e.g., Sparrow, 1960; Jones, 1976; Canter-Lund and Lund, 1995; Gleason *et al.*, 2008). Most ecological niches of fungi in and around lakes remain largely unexplored (Wurzbacher *et al.*, 2010; Wong *et al.*, 1998), particularly in the tropics. Lakes are, nevertheless, highly structured into different zones, each zone harboring specific animal, plant, algal and fungal communities (Smol *et al.*, 2001a-b; Birks and Birks, 2006). Wurzbacher *et al.* (2010) emphasised the importance to distinguish between the littoral zone, which is a hot spot for all kinds of fungi, and the pelagic zone which harbors only highly specialised species or serves as a medium for the dispersal of fungal spores. However, none of the more common fungal spore types in our fossil datasets of Lake Chibwera and Kanyamukali showed a significant correlation with the distinguishable pollen types of aquatic plants (Cyperaceae, *Typha* and *Nymphaea*), present in the littoral zones of our study lakes (see Chapter 4). This may suggest that (i) fungal spores from littoral species are mostly deposited within the littoral zone, which still needs to be assessed, or (ii) most thick-walled fungal morphotypes that we recovered from the lake sediments are of allochthonous origin, i.e., mainly derived from terrestrial fungi living in the lake catchments. We surmise that the thick-walled fungal spores are introduced into the lake via soil runoff, inflowing streams, rainwater and wind. It is generally known that pollen and spores in lake sediments derive from many sources (eroded soils, river bank and littoral sediments, aerial deposition, rain-out and surface runoff) with relative importance depending on local catchment conditions, and that they mainly contain non-local species (Wilmshurst and McGlone, 2005b). On the other hand, some of the non-fungal NPP groups we recorded are strictly autochthonous, such as the remains of algae, aquatic invertebrates and aquatic plants, of which the habitats are strongly linked to the aquatic environment. We assume that the major part of aerial deposed fungal spores are not surviving since they are hyaline and thin-walled. The thick-walled and pigmented spores that are mainly present in the sediment are more likely to be produced in the direct envirnoment. Moreover, during lake lowstands local

communities of (coprophilous) fungi on in situ deposited substrates (such as dung, dead plant material and submerged wood) may also colonise the temporally exposed parts of the lake floor (see Chapter 4).

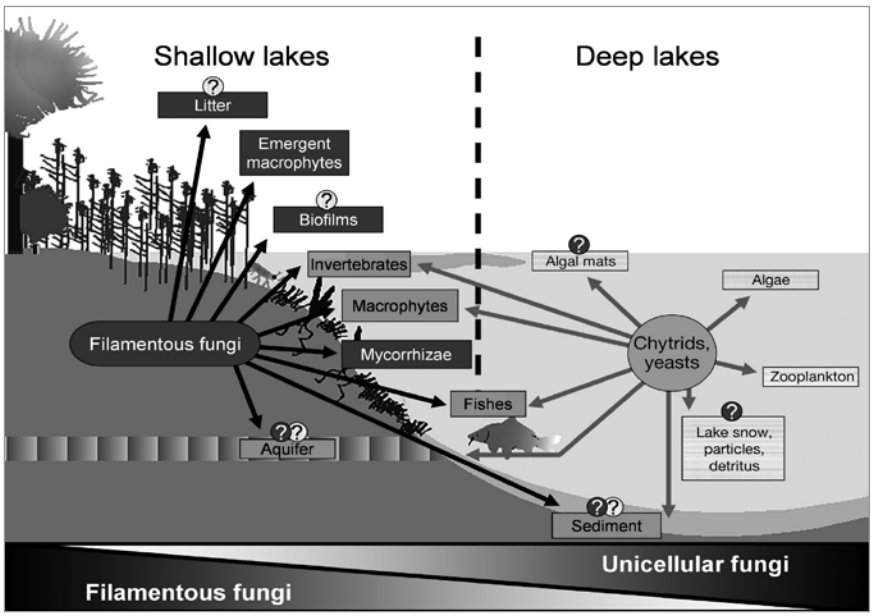

Fig. iii. Schematic representation of the knowledge gaps (question marks) in the habitat specificity of mycoflora from shallow and deep lake ecosystems, and the possible interactions between fungi and lake elements, as shown by Wurzbacher *et al.* (2010). At present, we are one step closer to the removal of a 'downtrodden' (cf. sediment) question mark.

On the issue of habitat specificity, our work made a reasonable contribution to the understanding of the origin of NPPs in lake sediments, but we cannot deny that we are still in the exploratory phase. Proper insight in NPP transport from their source habitat to their final burial site is imperative to further constrain the significance of NPPs for palaeoecological research.

Implications for climate and human-impact history

In the three fossil NPP records studied in this PhD thesis, the abundance of *Coniochaeta* was strongly associated with moisture changes through time. In Lake Challa, a major turnover of fungal taxa was most apparent from ca. 16,500 cal. yr BP (e.g., *Curvularia*) and from the transition of the Late Glacial to the Holocene (ca. 11,500 cal. yr BP) (e.g., *Tetraploa aristata*, *Dictyoarthrinium* cf. *sacchari*, cf. *Byssothecium*, types HdV-1032 and HdV-1033). The sediment sequences of Lakes Chibwera and Kanyamukali, however, reflected decade-scale rainfall variability over the past 200 years i.e. coeval with periods of drier and wetter episodes also recorded in the lake-level and/or water chemistry changes of other climate-sensitive tropical African lakes (e.g., Verschuren, 2000; Ssemmanda *et al.*, 2005; Bessems *et al.*, 2008; Ryves *et al.*, 2011). Particularly, the signature of the late 18th century climatic anomaly of severe drought was indicated in our data, supporting the hypothesis (Nicholson, 1998; Verschuren, 2004) that this event was widespread over equatorial East Africa, caused by continental-scale climate forcing (Bessems *et al.*, 2008).

Some distinctly individualistic signals of local human activity were particularly observed at Kanyamukali, mainly suggested by the continuous presence of obligate coprophilous fungal taxa, such as *Sordaria* and *Delitschia*. In Chibwera, evidence of large herbivore presence was (nearly) completely absent from the mid-19th century, although there is no reason to believe that wild animals left the Chibwera area. This discrepancy between both lakes may underscore the hypothesis that Kanyamukali was permanently visited by cattle herds. Given its current location near the main road Kasese-Fort Portal, arisen from an ancient cattle trail and/or trading route, its relationship with transhumant pastoralism seems more consistently present. Our data suggest that obligately coprophilous fungi, such as *Sordaria*, *Sporormiella* and *Delitschia*, may be potential human indicators in palaeoenvironmental records, when related to anthropogenic signals derived from other palaeoecological or historical proxies.

Future African NPP research will certainly benefit from a modern calibration study, based on multivariate analysis, applied separately on major aquatic and terrestrial groups of NPPs and relevant site characteristics, to assess the ecological indicator value of the most common NPP taxa. An ecologically indicative linkage between modern and fossil NPP types seems very promising, as has already been demonstrated for sediment archives outside Africa (e.g., Blackford and Innes, 2006; Prager *et al.*, 2006; Cugny *et al.*, 2010; Montoya *et al.*, 2010). However, a succesful quantitative linkage between modern and fossil NPP assemblages has proved to be a difficult task so far (Prager *et al.*, 2006; Cugny *et al.*, 2010), mainly complicated by (i) taxonomic smoothing (i.e., one fossil type may group different modern species, genera or a whole family, occupying various ecological niches), (ii) differential representation (e.g., differential production, dispersal, and preservation may lead to taxa being overrepresented, underrepresented, or even absent) (e.g., Jackson and Williams, 2004; Prager *et al.*, 2006), and (iii) taphonomical processes (e.g., modern assemblages may represent a snapshot of current environmental conditions, whereas, due to compaction and bioturbation, fossil assemblages may assemble environmental conditions over longer time) (e.g., Blackford and Innes, 2006; Prager *et al.*, 2006). Furthermore, an actuo-ecological mycological study of fresh dung from the most common herbivores (cow, donkey, sheep, goats, hippo, elephant, antelope) in the lake regions may reveal a possible dung preference of specific (non-)obligate coprophilous fungi, and may possibly enhance identification of yet unknown (non-)obligate coprophilous fungal spores, included in our modern dataset.

Integrating non-pollen palynomorph analysis in African palaeoecology: the missing link?

As we have now reached the coda of this PhD thesis, it seems appropriate to make a final plea for routine application of non-pollen palynomorph analysis in African palaeoecology. With this exploratory research, we certainly did not intend to establish a novel comprehensive proxy which closes all knowledge gaps left by other traditional palaeoenvironmental proxies. We hope to have demonstrated that non-pollen palynomorph analysis is, indeed, a promising tool to help elucidate impacts of past climate change and human activity on African ecosystems and to help unravel the precise relationships between land-use impacts and climatic variability. In tropical Africa there is a much greater need for a well-constrained palaeoenvironmental framework than, for example, northwest Europe, because written sources and archaeological information documenting on the history of indigenous African people from before the 20th century are scarce. In turn, the long-term perspective offered by palaeoecology on the natural dynamics and carrying capacity of African ecosystems - which are extremely vulnerable to human impact and climate change - has enormous value for the creation of sound strategies in sustainable development.

However, like all other palaeoenvironmental proxies, NPP analysis is just a means to an end, and its potential will only be fully revealed in the context of a multi-proxy, quantitative approach. In a joint venture with other landscape-related proxies (e.g., pollen, charcoal, phytoliths), and in conjunction with in-lake proxies (e.g., diatoms, chironomids, ostracoda),

NPP analysis can make a significant contribution to interpretive palaeolimnological research. High-quality lake-sediment archives appear very reliable for the study of fossil NPPs, capable to tackle most of the deficiencies associated with other archive types (such as peat, moss polsters and subsoil sediments; see supra). Lake surface sediments and ancient lake sediments form good counterparts to assess the goodness of fit between modern and fossil assemblages (i.e. modern analogue analysis); both are very rich in animal and plant microfossils, reflecting local and extra-local environmental conditions.

During the past 30 years, NPP analysis has assumed an increasingly prominent role in palaeoecological research worldwide. Until the 1990s, most research was concentrated in Europe, the cradle of NPP analysis, but today its dia'spora' goes well beyond this continent. Palynologists, the chief curators of NPP microfossils, have raised this former sub-discipline of palynology to a higher level; a decent discipline in its own right (e.g., van Geel, 2006; Haas, 2010). With the presented work, we are on the verge of introducing this updated discipline to tropical Africa, formerly a virtually white spot on the map of NPP research. Most previous studies on fossil African NPPs (e.g., Lejju *et al.*, 2005; Mumbi *et al.*, 2008) near exclusively referred to European studies, with their specifically European ecological and contextual properties. Along with the parallel effort by van Geel *et al.* (2011), this study has tried to create a tropical framework for NPP analysis in order to validate modern and fossil NPP assemblages in African sediment records more accurately. At present, we are just one small step beyond their discovery in tropical contexts to hopefully make a giant leap towards their routine application in African palaeoecology.

General conclusion

Studies of high-quality palaeoenvironmental records progressively improve documentation of past climate variability in East Africa, but evidence on the exact timing and relative magnitude of indigenous (pre-20th century) anthropogenic activity in the region is, unfortunately, still highly fragmentary and ambiguous. New and improved palaeoenvironmental proxies of human impact may, however, pave the way to a better understanding of climate-human-ecosystem interactions in tropical Africa. High-resolution, high-quality lake-sediment records offer the opportunity to undertake multi-proxy palaeolimnological studies in order to separate the palaeoecological signature of human impact more clearly from those of natural climate variability. We combined taxonomical, ecological and palaeoecological studies of tropical non-pollen palynomorphs (NPPs) to explore the potential value of these microfossils for African palaeoecology, and developed a novel tool to help unravel the relationships between climate change, human impact and natural ecosystems in tropical Africa. This structured research strategy shed light on important methodological, taphonomical and interpretative issues. Overall, our results indicate that high-quality lake-sediment records are highly appropriate archives for the study of fossil non-pollen palynomorphs, and avoid some problems of taphonomy and calibration associated with other archive types (peat, moss polsters, subsoil sediment). As such, we created new promising perspectives for NPP analysis as a full-fledged research discipline, and for its contribution to African palaeoecology in particular.

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Samenvatting

In tropisch Afrika wordt het paleoecologisch onderzoek naar de menselijke invloed op het landschap sterk bemoeilijkt door overheersende signalen van korte- en lange-termijn klimatologische processen, die de landschappelijke signatuur van de mens deels overschaduwen en zelfs compleet onzichtbaar maken. Nochtans is een beter inzicht in de relatieve omvang van historische, menselijke verstoring van cruciaal belang om de natuurlijke veerkracht en het herstelvermogen van ecosystemen te bepalen. Sinds de industriële revolutie (eind 18de eeuw) kampen heel wat tropische gebieden namelijk met een exponentiële bevolkingsgroei, wat een ingrijpende invloed heeft op de water- en voedselbevoorradingen met o.a. verlies aan habitats en biodiversiteit, vervuiling, erosie en overexploitatie van natuurlijke ecosystemen tot gevolg.

In dit onderzoek wordt een nieuwe paleoecologische methode voor tropisch Afrika ontwikkeld met als doelstelling het landschappelijke signaal van menselijke verstoring beter van klimatologisch gerelateerde milieu-effecten te kunnen onderscheiden. Aan de hand van non-pollen palynomorfen (NPP) assemblages (bestaande uit voornamelijk sporen van fungi, sporen van varens en mossen, zygosporen en coenobia/koloniën van groenwieren (orde Chlorococcales) en resten van aquatische invertebraten, enz…) uit sedimentarchieven van kratermeren in Oost-Afrika, wordt het potentieel van deze organismen voor toepassing in Afrikaanse, paleoecologische studies nagegaan. Het onderzoek van non-pollen palynomorfen is reeds decennia lang ingeburgerd in palynologisch onderzoek wereldwijd, maar de toepassing in een Afrikaanse context bleef tot nog toe beperkt tot een extrapolatie van de meest courante, Europese NPP morfotypes, met hun specifieke ecologie en contextuele omstandigheden, gelinkt aan het milieu van meer gematigde gebieden.

Op basis van het actualiteitsprincipe hanteren we een multidisciplinaire onderzoeksstrategie, waarbij zowel hedendaagse als fossiele NPP assemblages worden aangewend om inzicht te krijgen in de potentiële, ecologische indicatorwaarde van deze organismen. In *Hoofdstuk 1* wordt de taxonomische diversiteit van NPPs in een boorkern uit het Challa-meer nabij Mt. Kilimanjaro (zuidoost Kenya) onderzocht. Het sedimentarchief, dat de klimaatsgeschiedenis van equatoriaal Oost-Afrika over de afgelopen 25000 jaar omvat, herbergt in totaal 65 welomschreven NPP types (voornamelijk sporen van fungi), waarvan sommigen sterke associaties vertonen met het verloop van temperatuur, neerslagvariabiliteit, specifieke vegetatie types en biomen van tropisch Afrikaanse vegetatie. Hoofdzakelijk sterk gewijzigde klimatologische omstandigheden op de overgang van het laatglaciaal naar het holoceen (ca. 11,500 cal. yr BP) blijken een invloed te hebben op de verbreiding van bepaalde fungi, zoals bijv. *Curvularia*, *Coniochaeta cf. ligniaria*, *Acrodyctis*, *Tetraploa aristata*, cf. *Byssothecium* and de types HdV-1032 and HdV-1033.

Als aanvulling op de diversiteit van de meest courante NPP types, ontdekt in de boorkern van het Challa-meer, zijn ook moderne microfossielen geëxploreerd in de oppervlaktesedimenten van 20 kratermeren in West-Oeganda, langs een landschappelijke gradiënt van natuurlijke vegetatie (bijv. savanna, tropische loofbossen en regenwouden) tot sterk antropogeen verstoorde milieus (bijv. akkerbouw, veeteelt and plantages), en specifieke limnologische karakteristieken (morfometrie, waterchemie en aquatische produktiviteit van de meren). Dit leverde een totaal van 265 verschillende NPP morfotypes op, waarvan 28% kon worden geïdentificeerd aan de hand van primaire taxonomische literatuur. *Hoofdstuk 2* is dan ook opgevat als een eerste kennismaking met deze Ugandese microfossielen onder de vorm van een identificatie-atlas/gids voor paleoecologen, waarbij 187 NPP types uit 20 kalibratiemeren taxonomisch worden beschreven en geïllustreerd aan de hand van foto's. De geïdentificeerde morfotaxa zijn tevens vergezeld van de nodige tropische, ecologische informatie.

Predictiemodellen hebben aangetoond dat tegen het jaar 2100 de tropen voornamelijk te kampen zullen hebben met een significant biodiversiteitsverlies, hoofdzakelijk veroorzaakt door intensief landgebruik. Voor een dataset van 24 kalibratiemeren gaan we na of agrarische activiteiten in de kraterbekkens een invloed kunnen hebben op de diversiteit van sporen van fungi in oppervlaktesedimenten (*Hoofdstuk 3*). Het diversiteitsonderzoek van fungi op macro-schaal (de locale en regionale distributie doorheen het landschap) is namelijk zeer tijdrovend door een aantal methodologische

beperkingen (i.v.m. de immense soortenrijkdom, bemonsteringsstrategie, seizoenale aanwezigheid en cultivering). Het onderzoek van sporen van fungi in oppervlaktesedimenten en sedimentarchieven van (krater)meren kan mogelijk (i) een uitkomst bieden voor deze methodologische beperkingen door een meer omvattende, landschappelijke steekproef van de fungi-diversiteit te bewerkstelligen, (ii) een licht werpen op de effecten van menselijke verstoring op de fungi-diversiteit, (iii) verschuivingen in diversiteit in het verleden nagaan, en (iv) als een proxy worden gebruikt om menselijke impact op het landschap (en meer specifiek op fungi) in het verleden te dedecteren. Op basis van het gebruik van biodiversiteits-indexen, gecombineerd met statistische analyse (modelselectie), komt tot uiting dat de morfotyperijkdom (richness) negatief wordt beïnvloed door menselijke impact (de omvang van agrarische activiteit) in de kraterbekkens, en dat de verdeling van de individuen over de soorten (evenness) het meest evenwichtig blijkt te zijn in kraterbekkens van grote omvang met een stabiele, natuurlijke vegetatie. Deze link met stabiliteit in biomassa is echter louter suggestief, aangezien alle datasets sterk gedomineerd worden door hoge abundanties van *Coniochaeta*, wat mogelijk een vertekend beeld van de werkelijke correlaties kan opleveren. Alleszins kan indirect de stressrespons van fungi op menselijke landschappelijke verstoring worden aangetoond.

In *Hoofdstuk 4* worden de fossiele NPP assemblages uit de 200 jaar oude sedimentarchieven van het huidige, relatief onverstoorde Chibwera-meer en het menselijk verstoorde Kanyamukali-meer (West-Oeganda) onderzocht en met elkaar vergeleken. Op die manier kunnen specifieke, lokale habitatverschillen worden gereconstrueerd en signalen van de historische, menselijke invloed op het landschap worden geëxtraheerd. Beide studies blijken hoofdzakelijk een sterk gelijklopend signaal op te vangen van de regionale neerslagvariabiliteit, wat resulteert in veranderingen in de vochtbalans en fluctuaties in de meerniveaus. Zoals in de boorkern van het Challa-meer is de respons van *Coniochaeta* spp. zeer sterk gelinkt aan klimatologische veranderingen. Tijdens de droogte van de late 18de-vroege 19de eeuw was het waterniveau van beide meren aanzienlijk gedaald, waardoor een groot aantal herbivoren (wild en/of gedomesticeerd) beide meerbekkens frequent gingen gebruiken als drinkpoel. Dit wordt aangetoond door hoge abundanties van de vrijwel obligaat coprofiele schimmelsporen *Sordaria* en *Delitschia*, die hoofdzakelijk leven op uitwerpselen van planteneters. Gedurende de 19de en de 20ste eeuw, tijdens de permanente stijging van het waterniveau in beide meren en het verplaatsen van de drinklocatie naar de rand van het meer, wordt het signaal sterk afgezwakt, voornamelijk in het Chibwera-meer, waar het weliswaar compleet wegvalt. In het Kanyamukali-meer blijft het signaal van een hogere populatiedichtheid van herbivoren echter aanwezig tot de dag van vandaag. Gezien het vrijwel zeker is dat (kuddes van) wilde dieren beide meren bleven bezoeken gedurende de afgelopen 200 jaar, kan de hogere frequentie van coprofiele sporen in het Kanyamukali-meer mogelijk verklaard worden door pastoralisten, die hun veekuddes naar geschikte graaslanden leidden en lieten drinken in het Kanyamukali-meer. De locatie van dit meer in de directe nabijheid van de belangrijke hoofdas Kasese-Fort Portal, voortvloeiend uit een oude handels- en of veeroute, geeft een sterke aanwijzing in die richting. Vanaf ca. 1960 vestigt er zich ook een permanente nederzetting, met intensifiëring van begrazing, het telen van graangewassen en exploitatie van eucalyptus en den in het kraterbekken van Kanyamukali tot gevolg. Ook deze agrarische activiteiten komen enigszins tot uiting in een lichte stijging van coprofiele taxa en het voorkomen van *Glomus*, een endomycorrhiza schimmel, die vaak geassocieerd wordt met toenemende erosie en landdegradatie.

Dit onderzoek heeft aangetoond dat NPP analyse veelbelovende perspectieven biedt in het Afrikaanse, paleoecologische onderzoeksveld. Met deze studie hebben we een eerste licht kunnen werpen op belangrijke methodologische, tafonomische en interpretatieve kwesties binnen het NPP onderzoek in het algemeen en binnen de Afrikaanse paleoecologie in het bijzonder. Tevens blijken sedimentarchieven van meren zeer geschikt te zijn voor moderne en fossiele NPP studies. Een grootschalige toepassing van deze paleoecologische methode, gecombineerd met een multi-proxy benadering, zal zeker in de toekomst vruchten afwerpen bij het ontrafelen van de complexe, historische interacties tussen klimaat, mens en natuurlijke ecosystemen in tropisch Afrika.

Appendices

Appendix I. Raw NPP data from the surface samples of 25 western Uganda crater lakes.

Modern	Identification	Tax group	Kanyamukali	Murusi	Wankenzi	Mwengenyi	Kikorongo	Chibwera	Murabyo	Nkugute	Kako	Nyantonde	Katanda	Kitere	Mahuhura
UG-1231	*Botryococcus* cf. *neglectus*	A/C	136	4	1	34		303	71	41	58	7	1	17	3
UG-1233	*Coelastrum reticulatum*	A/C								112					
UG-1235	*Pediastrum angulosum*	A/C													
UG-1236	*Pediastrum boryanum* var. *brevicorne*	A/C				1							78		5
UG-1237	*Pediastrum boryanum* cf. var. *forcipatum*	A/C				3		107		2					
UG-1239	*Scenedesmus* sp.	A/C													
UG-1240	*Spirogyra* sp.(rugulate)	A/C			1				3						
UG-1305	*Scenedesmus* sp. (spines)	A/C													
UG-1313	*Spirogyra* sp.(reticulate)	A/C													
UG-1359	*Pediastrum duplex*	A/C													
UG-1241	Epidermis of *Nymphaea nouchali*	AP													3
UG-1002	*Sporoschisma* spp.	F	1	1	2	1			2	4	4		2	1	2
HdV-1005	*Brachydesmiella* sp.	F	1			2		1	3					1	
HdV-1008	cf. *Valsaria* sp.	F													
HdV-1009	*Chaetomium* sp.	F	1												
HdV-1015A-C	*Dictyoarthrinium* cf. *sacchari*	F													
HdV-1018A	*Spegazzinia tessarthra*	F						1	1	2			1	1	
HdV-1018B	*Spegazzinia tessarthra*	F						1					1	1	
HdV-1022	*Clasterosporium* sp.	F					1		3				1		
HdV-1023	*Spegazzinia intermedia*	F													
HdV-1025	*Diplocladiella* cf. *scalaroides*	F													
HdV-1026	*Peziza/Scutellinia* sp.	F			1										
HdV-1027	*Munkovalsaria donacina*	F													
UG-1370		F													
HdV-1029A	*Curvularia* cf. *intermedia*	F	1	5	2	1		3		2	3	1	1		1
HdV-1029B	*Curvularia* sp. *(* assymmetric)	F													
HdV-1030	cf. *Byssothecium* sp.	F							1						
HdV-1032		F						1							
HdV-1035A	*Paraphaeosphaeria* cf. *michotii*	F													
HdV-1043	cf. *Lasiodiplodia theobromae*	F	14	3	23	2		2	5	2	7		3	3	
HdV-1048		F	2		6								3	4	4
HdV-1049	cf. *Mitteriella ziziphina*	F			2										
HdV-1052	Xylariaceae	F				1		1	4			2	1	1	
HdV-1053	*Dictyosporium* cf. *heptasporum*	F	4	1	3	2		1	4	2		3	6		1
HdV-1058A		F		2											
UG-1065	Xylariaceae	F			1									2	1
UG-1066	*Delitschia* spp.	F	5	4	15	6		1	1	16	17	2	2	1	10
UG-1068		F	5		5			1		47	39	4	1	4	4
UG-1069		F									1				
UG-1070	Xylariaceae	F		10	9		1		7	2		1	1	2	2
UG-1071	cf. *Amphirosellinia* sp.	F	2		5										
UG-1072		F			6			1		6				2	3
UG-1073		F	2		17	1	1			29	2			1	
UG-1075		F								2			1		
UG-1076		F			1			1				4			
UG-1077	cf. Xylariaceae/Sordariaceae/Coniochaetaceae	F		4	6				4		3	2			
UG-1078	*Sporidesmium* spp.	F	1	1	1			1	5			1		1	3
UG-1079	*Urocystis* sp.	F	4	1							1				
UG-1080		F	9					1							1

Modern	Identification	Tax group	Nyarayabana	Mubiro	Kyogo	Bagusa	Bugwagi	Ibamba	Nyungu	Kisibendi	Kigezi	Mirambi	Kanyanchu	Katinda
UG-1231	*Botryococcus* cf. *neglectus*	A/C			55									5
UG-1233	*Coelastrum reticulatum*	A/C												
UG-1235	*Pediastrum angulosum*	A/C			29			2						
UG-1236	*Pediastrum boryanum* var. *brevicorne*	A/C			31									
UG-1237	*Pediastrum boryanum* cf. var. *forcipatum*	A/C												
UG-1239	*Scenedesmus* sp.	A/C			6									
UG-1240	*Spirogyra* sp.(rugulate)	A/C						4						
UG-1305	*Scenedesmus* sp. (spines)	A/C									1			
UG-1313	*Spirogyra* sp.(reticulate)	A/C								2				
UG-1359	*Pediastrum duplex*	A/C											6	
UG-1241	Epidermis of *Nymphaea nouchali*	AP			55								99	
UG-1002	*Sporoschisma* spp.	F		4			1	1	4	1	11			
HdV-1005	*Brachydesmiella* sp.	F	5	2							38		1	7
HdV-1008	cf. *Valsaria* sp.	F											1	
HdV-1009	*Chaetomium* sp.	F								6	10			9
HdV-1015A-C	*Dictyoarthrinium* cf. *sacchari*	F									2	1	1	8
HdV-1018A	*Spegazzinia tessarthra*	F	1		1	1								1
HdV-1018B	*Spegazzinia tessarthra*	F						1		1				2
HdV-1022	*Clasterosporium* sp.	F					1				1			1
HdV-1023	*Spegazzinia intermedia*	F											1	1
HdV-1025	*Diplocladiella* cf. *scalaroides*	F								1	2			
HdV-1026	*Peziza/Scutellinia* sp.	F											26	29
HdV-1027	*Munkovalsaria donacina*	F												2
UG-1370		F								1	9		8	
HdV-1029A	*Curvularia* cf. *intermedia*	F	4				1	1	4	4	5	4		5
HdV-1029B	*Curvularia* sp. *(* assymmetric)	F								1	3	3	1	11
HdV-1030	cf. *Byssothecium* sp.	F										1		
HdV-1032		F									1		1	
HdV-1035A	*Paraphaeosphaeria* cf. *michotii*	F											1	
HdV-1043	cf. *Lasiodiplodia theobromae*	F	2		1		1		3	10	44	5	6	18
HdV-1048		F					4					1		5
HdV-1049	cf. *Mitteriella ziziphina*	F											4	
HdV-1052	Xylariaceae	F		1			2							
HdV-1053	*Dictyosporium* cf. *heptasporum*	F			1		1	4			3			3
HdV-1058A		F												3
UG-1065	Xylariaceae	F												
UG-1066	*Delitschia* spp.	F	2	1			7	2	3	1	39		1	10
UG-1068		F	5				26	1	2		136			1
UG-1069		F									13	1		5
UG-1070	Xylariaceae	F		1	1	1	1	1		12			27	
UG-1071	cf. *Amphirosellinia* sp.	F										1		1
UG-1072		F	1				9		4		13	1		7
UG-1073		F					5		41	1	9	8	1	8
UG-1075		F			1						2			
UG-1076		F		2										
UG-1077	cf. Xylariaceae/Sordariaceae/Coniochaetaceae	F			3			2		4	5	2	14	7
UG-1078	*Sporidesmium* spp.	F		1	1		2							1
UG-1079	*Urocystis* sp.	F									1			
UG-1080		F					9		2		7			6

Modern	Identification	Tax group	Kanyamukali	Murusi	Wankenzi	Mwengenyi	Kikorongo	Chibwera	Murabyo	Nkugute	Kako	Nyantonde	Katanda	Kitere	Mahuhura
UG-1081		F		1										1	
UG-1082		F	1						1		1				
UG-1083		F	1						1	3	3		1		
UG-1084		F			1					1	2				4
UG-1085		F													
UG-1086		F													
UG-1087		F	15										1	4	1
UG-1088		F		2											
UG-1089		F	1						1						
UG-1090	*Sporidesmium* cf. *macrurum*	F	2	3		3			1						
UG-1091	*Bactrodesmium* type	F	3	2	10	4		1	8	5			8	7	4
UG-1092		F							2			1			
HdV-1093	*Gelasinospora* cf. *cratophora*	F			1		1	2		2		2			
UG-1094		F													
UG-1095		F			2										
UG-1096		F	2	1											
UG-1097		F													
UG-1098		F	3							3					
UG-1099	*Brachysporium* spp.	F	42	3	9	15	1	10	56	1		4	16	21	54
UG-1100		F	1												
UG-1101		F	7							1					
UG-1103	*Glomus* sp.	F	3		1	4	1		1	2			5	1	4
UG-1104	cf. *Podosporium rigidum*	F		3				3	2	1		2		2	
UG-1105		F			1				2						
UG-1106		F		3	2	7		1	3			4	4		
UG-1107		F													
UG-1108		F												1	1
UG-1109		F	4		1			1		1					3
UG-1110		F		4	4								1		3
UG-1111		F						1					1		
UG-1112	*Phaeosphaeria* type	F		3	5										
UG-1113	*Meliola* sp.	F				2		1	1						2
UG-1116		F	1												
UG-1117		F		1											
UG-1118	cf. *Savoryella lignicola*	F			7			2							
UG-1119		F			1										
UG-1120	*Savoryella curvispora*	F		2	6								1		
UG-1121		F			1										
UG-1122	cf. *Cookeina* sp.	F			5										
UG-1123		F			1				1						
UG-1124		F			1										
UG-1125		F							4						
UG-1126		F							3						
UG-1127		F				2		1							
UG-1128	cf. *Kretzschmaria clavus/K. cetrarioides*	F		1											
UG-1129		F							1						
HdV-113	*Sporormiella* type (parts)	F		1			1						1		
UG-1131		F													
UG-1132		F				1									

Modern	Identification	Tax group	Nyarayabana	Mubiro	Kyogo	Bagusa	Bugwagi	Ibamba	Nyungu	Kisibendi	Kigezi	Mirambi	Kanyanchu	Katinda
UG-1081		F												
UG-1082		F			2									
UG-1083		F												
UG-1084		F							2					
UG-1085		F		1		1	1						1	
UG-1086		F					1							
UG-1087		F	1				4		1					1
UG-1088		F						1			1			
UG-1089		F	2										1	
UG-1090	*Sporidesmium* cf. *macrurum*	F								2		1	1	1
UG-1091	*Bactrodesmium* type	F	5	1		1	1						1	1
UG-1092		F	4											
HdV-1093	*Gelasinospora* cf. *cratophora*	F					1	2			2			2
UG-1094		F							1					
UG-1095		F												
UG-1096		F												
UG-1097		F						2						
UG-1098		F						4			2	1		
UG-1099	*Brachysporium* spp.	F	13	2			2			1	1		5	
UG-1100		F												
UG-1101		F												
UG-1103	*Glomus* sp.	F	5				3			2	3	2		4
UG-1104	cf. *Podosporium rigidum*	F		2		1		2		2			1	
UG-1105		F						1			7			
UG-1106		F		1			1			4			4	4
UG-1107		F						3						
UG-1108		F												
UG-1109		F	2			19	3	3					1	
UG-1110		F											1	
UG-1111		F	2											1
UG-1112	*Phaeosphaeria* type	F									2		1	2
UG-1113	*Meliola* sp.	F								1		2	1	
UG-1116		F												
UG-1117		F												
UG-1118	cf. *Savoryella lignicola*	F											1	
UG-1119		F												
UG-1120	*Savoryella curvispora*	F								5	17	4	1	
UG-1121		F								1			3	3
UG-1122	cf. *Cookeina* sp.	F												
UG-1123		F												
UG-1124		F												
UG-1125		F								3	3		3	3
UG-1126		F		2						5				
UG-1127		F		1	1									
UG-1128	cf. *Kretzschmaria clavus/K. cetrarioides*	F												
UG-1129		F		1			2							
HdV-113	*Sporormiella* type (parts)	F												2
UG-1131		F				1								
UG-1132		F												

Modern	Identification	Tax group	Kanyamukali	Murusi	Wankenzi	Mwengenyi	Kikorongo	Chibwera	Murabyo	Nkugute	Kako	Nyantonde	Katanda	Kitere	Mahuhura
UG-1133		F				1									
UG-1134		F													4
UG-1135	cf. Xylariaceae	F													
UG-1136		F	2								2				
UG-1137	*Meliola* sp.	F													
UG-1138		F				1				1				1	
UG-1139	*Gelasinospora* sp.	F								1					
UG-1140		F						3							
UG-1141		F		1											
UG-1142		F		2											
UG-1143		F		1											
UG-1144		F		1											
UG-1145	cf. *Fusarium* sp.	F	1	1	2	1						1	1		1
UG-1146		F		1											
UG-1147		F													1
UG-1148		F						1					15		2
UG-1149		F						1							
UG-1150		F													
UG-1151		F	8			2			6				6	1	13
UG-1152		F	1												
UG-1153		F		2				1		41			1	1	
UG-1155		F	1								1				2
UG-1157	*Rosellinia* sp.	F												1	
UG-1158		F													
UG-1159		F									2				
UG-1161		F													
UG-1162		F								1	1				
UG-1163		F													
UG-1164		F													
UG-1165		F													
UG-1166		F													
UG-1167		F									1				
UG-1168		F			1										
HdV-1351	*Gelasinospora* cf. *dictyophora*	F													
UG-1170		F			2										
UG-1171	*Apiosordaria* type	F	1		2					1					
UG-1172		F	2					1							1
UG-1173		F		2	5		2	1	12	1			4		
UG-1174	*Rosellinia* sp.	F		2	11	1		2	5	1			1		3
UG-1176		F		3	8		1	3	14	1	2	5		1	
UG-1177		F													
UG-1179		F	1												
HdV-1013	*Cercophora* type	F	2	1	22	3		2	8	6	4	3	3		1
UG-1180	*Sordaria* spp.	F	6		6	2	3	3		7	1	3	1	5	4
UG-1178	*Sordaria* type	F	3	6	1		1				3		2	2	1
UG-1183	cf. *Cercophora* sp.	F													
UG-1182		F			3					1					
UG-1184		F			1										
UG-1185		F		5	3				4						

Modern	Identification	Tax group	Nyarayabana	Mubiro	Kyogo	Bagusa	Bugwagi	Ibamba	Nyungu	Kisibendi	Kigezi	Mirambi	Kanyanchu	Katinda
UG-1133		F												
UG-1134		F												
UG-1135	cf. Xylariaceae	F			2					2				
UG-1136		F												
UG-1137	*Meliola* sp.	F				1							1	
UG-1138		F	1			1								
UG-1139	*Gelasinospora* sp.	F												
UG-1140		F	4			2								
UG-1141		F					1							
UG-1142		F												
UG-1143		F												
UG-1144		F								1				
UG-1145	cf. *Fusarium* sp.	F					1	1		1	2			
UG-1146		F												
UG-1147		F			1	1								
UG-1148		F												
UG-1149		F												
UG-1150		F		2										
UG-1151		F	3										1	
UG-1152		F												
UG-1153		F												
UG-1155		F					6					2		
UG-1157	*Rosellinia* sp.	F	2											
UG-1158		F	2											
UG-1159		F			2						1			
UG-1161		F									3			
UG-1162		F												
UG-1163		F									1			
UG-1164		F			1									
UG-1165		F									2			
UG-1166		F			1									
UG-1167		F												
UG-1168		F												
HdV-1351	*Gelasinospora* cf. *dictyophora*	F									1			
UG-1170		F								1				
UG-1171	*Apiosordaria* type	F				1	1							
UG-1172		F											1	
UG-1173		F		4		2				7		1	14	
UG-1174	*Rosellinia* sp.	F			1								4	
UG-1176		F			4	1				19	15	3	9	20
UG-1177		F			1					1				
UG-1179		F												
HdV-1013	*Cercophora* type	F	1	2		31	4	5	1	4	50	6	4	5
UG-1180	*Sordaria* spp.	F	4	2	1		3	1		1		2	1	
UG-1178	*Sordaria* type	F	2			1		1	4		13	1		8
UG-1183	cf. *Cercophora* sp.	F						1						
UG-1182		F												
UG-1184		F												
UG-1185		F							1					

Modern	Identification	Tax group	Kanyamukali	Murusi	Wankenzi	Mwengenyi	Kikorongo	Chibwera	Murabyo	Nkugute	Kako	Nyantonde	Katanda	Kitere	Mahuhura
UG-1186		F												1	
UG-1187		F	1												
UG-1188		F	1		1					2					1
UG-1189		F													
UG-1190		F													1
UG-1191		F							1						
UG-1192		F				1						4			
UG-1193		F												1	
UG-1194		F							7						
UG-1195		F							3						
UG-1196		F		1								1			
UG-1197		F		1											
UG-1199		F											1		
UG-1200		F	1		1	1								1	
UG-1202		F										1			
UG-1203		F			3										
UG-1204		F											1		2
UG-1205		F											1		
UG-1206	cf. *Acroconidiellina loudetiae*	F							1						
UG-1208	*Coniochaeta* spp.	F	577	281	366	99	188	185	316	371	247	221	224	161	263
UG-1209		F				1			1						
UG-1210		F		1					2						
UG-1211		F							1						
UG-1212		F			1										
UG-1213		F			1										
UG-1215		F			1										
UG-1216	*Diporotheca* sp.	F			2										
UG-1217		F			4										
UG-1218		F			1										
UG-1230		F				1									
UG-1238		F													
HdV-1245	*Diporotheca* sp.	F	7		3	3				2		1		1	6
UG-1250	*Curvularia* cf. *comoriensis*	F	1	1				6							
UG-1251		F			1	1									
UG-1252		F			2	1									
UG-1262	*Canalisporium* spp.	F			2				4			2		1	4
UG-1268	*Canalisporium variabile*	F			2			1							
UG-1269		F		1											
UG-1274		F			31	20		6	13	21	22	8	18	6	2
UG-1275		F													
UG-1276		F	1						1		1				
UG-1277		F	22	6								14	4	1	2
UG-1278		F			2										
UG-1279		F			1				5			2	2		
UG-1281		F			2										
UG-1282		F										1			1
UG-1283		F													
UG-1285	cf. *Ascodesmis* sp.	F						1							
UG-1289		F							1						

Modern	Identification	Tax group	Nyarayabana	Mubiro	Kyogo	Bagusa	Bugwagi	Ibamba	Nyungu	Kisibendi	Kigezi	Mirambi	Kanyanchu	Katinda
UG-1186		F								1				
UG-1187		F	1					2					1	
UG-1188		F					3							
UG-1189		F					2							
UG-1190		F												
UG-1191		F												
UG-1192		F												
UG-1193		F												
UG-1194		F												
UG-1195		F												
UG-1196		F												
UG-1197		F					2	1			3			
UG-1199		F							1		2			
UG-1200		F	1	1		2								
UG-1202		F												
UG-1203		F												
UG-1204		F	2											
UG-1205		F									4			
UG-1206	cf. *Acroconidiellina loudetiae*	F				1								
UG-1208	*Coniochaeta* spp.	F	203	153	185	185	344	174	237	87	507	170	40	414
UG-1209		F												
UG-1210		F												
UG-1211		F				1								
UG-1212		F												
UG-1213		F												
UG-1215		F												
UG-1216	*Diporotheca* sp.	F												
UG-1217		F												
UG-1218		F					1							
UG-1230		F	1											
UG-1238		F									2			
HdV-1245	*Diporotheca* sp.	F	1				1					1		
UG-1250	*Curvularia* cf. *comoriensis*	F												
UG-1251		F												
UG-1252		F											1	
UG-1262	*Canalisporium* spp.	F				3								
UG-1268	*Canalisporium variabile*	F												
UG-1269		F												
UG-1274		F	4	4	4	9	21	5	7	2	22	5		2
UG-1275		F									1			
UG-1276		F												
UG-1277		F	1	2			1	9			1			
UG-1278		F												
UG-1279		F			4									
UG-1281		F												
UG-1282		F							1		4			
UG-1283		F									6			
UG-1285	cf. *Ascodesmis* sp.	F												
UG-1289		F												

Modern	Identification	Tax group	Kanyamukali	Murusi	Wankenzi	Mwengenyi	Kikorongo	Chibwera	Murabyo	Nkugute	Kako	Nyantonde	Katanda	Kitere	Mahuhura
UG-1291	*Glomus* type	F													
UG-1293		F				1									
UG-1294		F			1										
UG-1297		F													
UG-1304		F								1					
UG-1314		F			1										1
UG-1320		F			6					16		1			
UG-1323		F													
UG-1325		F													
UG-1328		F													
UG-1329	cf. Xylariaceae	F					1								
UG-1330		F					1		1						
UG-1331		F										2			
UG-1332		F	2		2	1					1		1	1	
UG-1333		F	1										1		
UG-1334		F													1
UG-1336		F							1						
UG-1338		F											1		
UG-1339		F											1		
UG-1340		F													1
UG-1341		F													1
UG-1342		F													
UG-1343	cf. *Cirrenalia* sp.	F													
UG-1345		F				2									
UG-1349		F													
UG-1350		F													
UG-1357		F													
UG-1352		F				1						2			
UG-1356		F													
UG-1354		F													
UG-1355		F													
HdV-89	*Tetraploa aristata*	F	3	5	12	7		4	2	4		4	6	3	5
UG-1358		F													
UG-1242	*Dryopteris* subg. *Dryopteris*	F/M	1					1	2						
UG-1243	cf. *Asplenium* sp.	F/M	4	1		6		4	2	1		1		1	8
UG-1246	*Isoetes* type	F/M						2	57	11	2	2		2	1
UG-1247		F/M			2										
UG-1248		F/M			1										1
UG-1249	cf. *Ctenitis/Lastreopsis* sp.	F/M			4										
UG-1253	Polypodiaceae	F/M		1	1				3	2	1	1	1		
UG-1254	*Phaeoceros* cf. *carolianus*	F/M							1	13	3		1		
UG-1255	*Ophioglossum* subg. *Ophioglossum*	F/M						2							
UG-1257		F/M							1						
UG-1258		F/M								7	2				
UG-1259	*Pteridium aquilinum*	F/M	1			1	2	4	5						2
UG-1260	*Coniogramme africana* type	F/M	3	2	8	3		2	10	19	8	3	1		1
UG-1261	cf. *Pteris/Actiniopteris* sp.	F/M					1	1	2		4	1			
UG-1263	cf. *Grammitis* sp.	F/M			5					1					
UG-1264	*Pteris* sp.	F/M										2			

Modern	Identification	Tax group	Nyarayabana	Mubiro	Kyogo	Bagusa	Bugwagi	Ibamba	Nyungu	Kisibendi	Kigezi	Mirambi	Kanyanchu	Katinda
UG-1291	*Glomus* type	F					1				1			
UG-1293		F												
UG-1294		F												
UG-1297		F									1			
UG-1304		F												
UG-1314		F	2											
UG-1320		F					1	1						
UG-1323		F								4				
UG-1325		F								2				
UG-1328		F											1	
UG-1329	cf. Xylariaceae	F												
UG-1330		F												
UG-1331		F												
UG-1332		F	1								2			
UG-1333		F												
UG-1334		F												1
UG-1336		F												
UG-1338		F												
UG-1339		F												
UG-1340		F												
UG-1341		F												
UG-1342		F	1											
UG-1343	cf. *Cirrenalia* sp.	F			1									
UG-1345		F												
UG-1349		F										5		
UG-1350		F										1		2
UG-1357		F												1
UG-1352		F												
UG-1356		F												1
UG-1354		F												1
UG-1355		F												1
HdV-89	*Tetraploa aristata*	F	13	13	1	1	4	4		9	9	10	3	4
UG-1358		F								1			7	
UG-1242	*Dryopteris* subg. *Dryopteris*	F/M		1									1	
UG-1243	cf. *Asplenium* sp.	F/M	5	1			18	12		8			2	
UG-1246	*Isoetes* type	F/M	1	1	1		7			2				
UG-1247		F/M												
UG-1248		F/M												
UG-1249	cf. *Ctenitis/Lastreopsis* sp.	F/M												
UG-1253	Polypodiaceae	F/M			3	1	2	4					5	2
UG-1254	*Phaeoceros* cf. *carolianus*	F/M						4			1			
UG-1255	*Ophioglossum* subg. *Ophioglossum*	F/M												
UG-1257		F/M												
UG-1258		F/M												
UG-1259	*Pteridium aquilinum*	F/M	6			2	6	1	4		4	2	1	1
UG-1260	*Coniogramme africana* type	F/M			6	1	13	2	3					
UG-1261	cf. *Pteris/Actiniopteris* sp.	F/M						1						1
UG-1263	cf. *Grammitis* sp.	F/M												
UG-1264	*Pteris* sp.	F/M												

Modern	Identification	Tax group	Kanyamukali	Murusi	Wankenzi	Mwengenyi	Kikorongo	Chibwera	Murabyo	Nkugute	Kako	Nyantonde	Katanda	Kitere	Mahuhura
UG-1315	monoletes undiff.	F/M	2	10	44	4	3	4	27	13	17	11	5	6	12
UG-1316	*Asplenium* type	F/M			7								11		
UG-1347		F/M													
UG-1266		OF			7										
UG-1267		OF			1										
UG-1270		OF			11										1
UG-1271		OF	7							1			2	2	4
UG-1273		OF	1												
UG-1318		OF						2	1				1		1
UG-1327		OF			1										
UG-1114		U						1					1		
UG-1115		U									1				
UG-1130		U													
UG-1154		U													
UG-1160		U													
UG-1181		U													
UG-1201		U													1
UG-1226		U	1												
UG-1232		U						1							
UG-1234		U													
UG-1280		U		2											
UG-1284		U						2							
UG-1286		U													
UG-1287		U	1												
UG-1292		U													
UG-1296		U									1				
UG-1298		U													
UG-1299		U													
UG-1300		U								1			1		1
UG-1301		U													
UG-1303		U										11			
UG-1306		U	2												
UG-1307		U								26	7				
UG-1308		U													
UG-1309		U			5										
UG-1310		U									1				
UG-1311		U			21										3
UG-1312		U							1						
UG-1319		U					4			10	9		14	2	
UG-1324		U													
UG-1346		U													
UG-1219	Claws - Ephydridae parapods	Z	1												
UG-1220	Culicidae larval mouthparts	Z													
UG-1221	tropical oocyte	Z							1						1
UG-1222	tropical oocyte	Z													
UG-1223	tropical oocyte	Z	2	1		1			20	1		3	3	3	1
UG-1224	tropical oocyte	Z							9						
UG-1225	tropical cyst	Z							1						
UG-1227	head insecta	Z													1
UG-1228	femur insecta	Z										1			
UG-1229	tropical cyst	Z	1	1				2	2						2
UG-1288		Z	1												
UG-1321	animal hair	Z				2									
UG-1326		Z	1												
UG-1335		Z													
UG-1344	*Filinia* resting egg	Z													
UG-1348	Mentum Chironomidae	Z							1			1	1		
Total NPPs			**948**	**409**	**800**	**260**	**214**	**699**	**757**	**874**	**485**	**353**	**479**	**284**	**484**
Indeterminata	Pollen/NPPs indeterminata	Ind	46	12	42	19	14	14	27	17	7	17	7	7	11
Total Pollen+aquatics			**520**	**530**	**505**	**557**	**580**	**522**	**503**	**530**	**564**	**499**	**534**	**548**	**531**
Lycopodium marker			**1000**	**1193**	**589**	**177**	**8603**	**1264**	**1245**	**1181**	**626**	**1945**	**537**	**341**	**747**

Modern	Identification	Tax group	Nyarayabana	Mubiro	Kyogo	Bagusa	Bugwagi	Ibamba	Nyungu	Kisibendi	Kigezi	Mirambi	Kanyanchu	Katinda
UG-1315	monoletes undiff.	F/M	7	6	18	12	14	132	2	31	5	4		
UG-1316	*Asplenium* type	F/M								5		1		3
UG-1347		F/M							3					
UG-1266		OF												
UG-1267		OF	1											
UG-1270		OF					2							
UG-1271		OF												
UG-1273		OF												
UG-1318		OF		1										
UG-1327		OF												
UG-1114		U												
UG-1115		U	3											5
UG-1130		U	5				1						1	1
UG-1154		U									1			
UG-1160		U									28			
UG-1181		U									3			1
UG-1201		U												
UG-1226		U												
UG-1232		U												
UG-1234		U			9									
UG-1280		U												
UG-1284		U												
UG-1286		U						15						1
UG-1287		U												
UG-1292		U						1			1		4	
UG-1296		U	1						1					
UG-1298		U									8			
UG-1299		U							2					
UG-1300		U												
UG-1301		U									1			
UG-1303		U												
UG-1306		U	2								2		1	1
UG-1307		U									10			
UG-1308		U	1											
UG-1309		U			6									
UG-1310		U							7		24			
UG-1311		U					1				2			3
UG-1312		U												
UG-1319		U	3		6	9					10			
UG-1324		U								6			1	
UG-1346		U					3							
UG-1219	Claws - Ephydridae parapods	Z				2								
UG-1220	Culicidae larval mouthparts	Z				1								
UG-1221	tropical oocyte	Z	2		2		1							
UG-1222	tropical oocyte	Z			2									
UG-1223	tropical oocyte	Z	2		21	1	14					2	3	
UG-1224	tropical oocyte	Z			1									
UG-1225	tropical cyst	Z												
UG-1227	head insecta	Z												
UG-1228	femur insecta	Z												
UG-1229	tropical cyst	Z												
UG-1288		Z												
UG-1321	animal hair	Z												
UG-1326		Z												
UG-1335		Z										10	4	
UG-1344	*Filinia* resting egg	Z										19	2	2
UG-1348	Mentum Chironomidae	Z		2										
Total NPPs			**343**	**218**	**472**	**297**	**568**	**414**	**341**	**266**	**1146**	**283**	**338**	**661**
Indeterminata	Pollen/NPPs indeterminata	Ind	15	16	12	9	26	24	6	29	35	12	27	28
Total Pollen+aquatics			**524**	**528**	**263**	**428**	**507**	**533**	**86**	**636**	**466**	**520**	**944**	**541**
Lycopodium marker			**935**	**1183**	**5981**	**2382**	**1506**	**2583**	**4932**	**7115**	**330**	**2046**	**66**	**337**

Appendix II. Raw NPP data from the sediment record of Lake Chibwera (western Uganda).

L. Chibwera	Identification		-8.5	-5.5	-1.5	1.5	6.5	10.5	13.5	16.5	20.5	24.5	28.5	32.5	36.5	40.5	44.5	48.5	52.5
UG-1237	*Pediastrum boryanum* cf. var. *forcipatum*	A/C	9	22	15	59	98	105	28		1	4	14	7					
UG-1240	*Spirogyra* sp. (rugulate)	A/C																	
UG-1371A-B	*Botryococcus* sp.	A/C	223	182	179	158	178	210	143	26	28	60	118	57	22	9	4	2	19
UG-1371A-B (large cluster)	*Botryococcus* sp.	A/C	14	13	10	13	0	2	1	0	0	0	0	0	0	0	0	0	0
HdV-130	*Spirogyra* sp. (smooth)	A/C																	
UG-1241	epidermis of *Nymphaea nouchali*	AP			1														
HdV-1001	*Caryospora* sp.	F																	
UG-1002	*Sporoschisma* spp.	F								1					1				1
HdV-1005	*Brachydesmiella* sp.	F		1								1							
HdV-1009	*Chaetomium* sp.	F	3		1	2	2	1					1		1		2		
HdV-1012	cf. *Sordaria* sp.	F																	2
HdV-1013	*Cercophora* type	F	4	3	5	2	6	5	3	11	10	8	4	21	10	22	26	5	10
HdV-1014	*Rosellinia* type	F							1	1									
HdV-1015A-C	*Dictyoarthrinium* cf. *sacchari*	F										1	1			1		1	
cf. HdV-1015	*Dictyoarthrinium* cf. *sacchari*	F																	
HdV-1018A	*Spegazzinia tessarthra*	F				1													1
HdV-1018B	*Spegazzinia tessarthra*	F		1			2	2	1				1	1					1
HdV-1022	*Clasterosporium* sp.	F		2	1	2			1	2						1	1		
HdV-1023	*Spegazzinia intermedia*	F								1			1						
HdV-1025	*Diplocladiella* cf. *scalaroides*	F											1						
HdV-1028		F											1						
UG-1370		F			2					5	1								
HdV-1029A	*Curvularia* cf. *intermedia*	F	3	3	8	2	1	5	6	6	3	7	5	5	5	8	11	13	8
HdV-1029B	*Curvularia* sp. (assymmetric)	F	3	2	6	9	4	1	6	24	8	23	13	26	37	32	42	33	52
HdV-1030	cf. *Byssothecium* sp.	F			1														
HdV-1032		F								4									
HdV-1040	*Isthomospora spinosa*	F																	
HdV-1043	cf. *Lasiodiplodia theobromae*	F	8	6	3		3	2	2	5	2	6	3	6	11	4	9	9	3
HdV-1048		F		1	1	2			2	7	5	6	3	1	2	3	4	2	3
HdV-1047	*Rhytidospora* cf. *tetraspora*	F			1														
HdV-1049	cf. *Mitteriella ziziphina*	F									1		1						3
HdV-1052	Xylariaceae	F				1	1						1						
HdV-1053	*Dictyosporium* cf. *heptasporum*	F	2		1	1	2	2	1	2				1			1		1
UG-1065	Xylariaceaea	F										1							
UG-1066	*Delitschia* spp.	F	1					2	1		1		1	5	3	4	2	7	3
UG-1068		F														3	1	3	5
UG-1069		F									1	1							
UG-1070	Xylariaceae	F		3	3	3	2	3	3	2	3	4	3	8	3	3	2	5	8
UG-1071	cf. *Amphirosellinia* sp.	F			1		1							1				1	
UG-1072		F		7	1								1						
UG-1073		F																	
UG-1077	cf. Xylariaceae/Sordariaceae/Coniochaetaceae	F	2	5	1	2	2	1	1		7	4	5	1	1	4	2		
UG-1078	*Sporidesmium* spp.	F										2						1	
UG-1080		F	1											1			1		
UG-1081		F																	
UG-1082		F								2	1								
UG-1083		F																	1
UG-1084		F									1					2	1		
UG-1085		F							1										
UG-1087		F	2			1				1	1	5	2	1	2	1	1	5	1
UG-1089		F										1							
UG-1090	*Sporidesmium* cf. *macrurum*	F					1												
UG-1091	*Bactrodesmium* type	F									1		2		1				

L. Chibwera	Identification		56.5	60.5	64.5	68.5	72.5	76.5	80.5	84.5	88.5	92.5	96.5	100.5	104.5	108.5	112.5	116.5
UG-1237	*Pediastrum boryanum* cf. var. *forcipatum*	A/C				2	1	3										
UG-1240	*Spirogyra* sp. (rugulate)	A/C												3	1		1	1
UG-1371A-B	*Botryococcus* sp.	A/C	12	13	10	57	63	43	26	23	23	22	200	67	15	21	27	28
UG-1371A-B (large cluster)	*Botryococcus* sp.	A/C	1	0	1	0	0	0	0	0	0	0	3	1	2	0	0	0
HdV-130	*Spirogyra* sp. (smooth)	A/C																1
UG-1241	epidermis of *Nymphaea nouchali*	AP																
HdV-1001	*Caryospora* sp.	F				1												
UG-1002	*Sporoschisma* spp.	F				1		2	4	4			1	1	1			
HdV-1005	*Brachydesmiella* sp.	F									3	2			6	5	2	14
HdV-1009	*Chaetomium* sp.	F		2			2	1	1		3	1	1	1	1			
HdV-1012	cf. *Sordaria* sp.	F																
HdV-1013	*Cercophora* type	F	17	18	21	16	11	8	14	14	12	8	14	14	28	22	34	9
HdV-1014	*Rosellinia* type	F																
HdV-1015A-C	*Dictyoarthrinium* cf. *sacchari*	F	4			2			2	5		2		1		1	1	
cf. HdV-1015	*Dictyoarthrinium* cf. *sacchari*	F			2	3	1											
HdV-1018A	*Spegazzinia tessarthra*	F																
HdV-1018B	*Spegazzinia tessarthra*	F	1						2	1	1							
HdV-1022	*Clasterosporium* sp.	F	1	1	2						2	1	1					
HdV-1023	*Spegazzinia intermedia*	F																
HdV-1025	*Diplocladiella* cf. *scalaroides*	F						1										
HdV-1028		F																
UG-1370		F																
HdV-1029A	*Curvularia* cf. *intermedia*	F	6	5	5	7		1		5	1	1						
HdV-1029B	*Curvularia* sp. *(*assymmetric)	F	24	18	8	4	2	2	3	4	2	1						
HdV-1030	cf. *Byssothecium* sp.	F						1										
HdV-1032		F											1					
HdV-1040	*Isthomospora spinosa*	F					1											
HdV-1043	cf. *Lasiodiplodia theobromae*	F	6	8	1	5	6	2	2	1	2	1		2	2	3	2	2
HdV-1048		F	2	4	6	1	7		1	1	7	2	2	3				19
HdV-1047	*Rhytidospora* cf. *tetraspora*	F									1					1		
HdV-1049	cf. *Mitteriella ziziphina*	F									1						1	
HdV-1052	Xylariaceae	F			1	2			1									
HdV-1053	*Dictyosporium* cf. *heptasporum*	F					4	1	2	4	1	1						
UG-1065	Xylariaceaea	F			1					1			1					
UG-1066	*Delitschia* spp.	F	3		1	3	3	8	9	3	3	7			1	3	3	2
UG-1068		F		1				2		4	2	1	1			1		
UG-1069		F					1	1	2		1							
UG-1070	Xylariaceae	F	7	13	12	4	3	1	1	2	1	3	2				1	
UG-1071	cf. *Amphirosellinia* sp.	F		1							1							
UG-1072		F											3			1		
UG-1073		F												1				
UG-1077	cf. Xylariaceae/Sordariaceae/Coniochaetaceae	F		4	3	4	2	4	2	8	3	2	2				2	
UG-1078	*Sporidesmium* spp.	F										2					2	
UG-1080		F					5	2	5	4	5				3	1		1
UG-1081		F															3	
UG-1082		F	2		2					1	1							
UG-1083		F																
UG-1084		F																
UG-1085		F			2	2												
UG-1087		F	3	1	2	1	3	4	3	6	6	3		1	2			3
UG-1089		F						1				1		2	2			
UG-1090	*Sporidesmium* cf. *macrurum*	F	1	1	1	3												
UG-1091	*Bactrodesmium* type	F		3						2	1	1					3	1

L. Chibwera	Identification		-8.5	-5.5	-1.5	1.5	6.5	10.5	13.5	16.5	20.5	24.5	28.5	32.5	36.5	40.5	44.5	48.5	52.5
HdV-1093	*Gelasinospora* cf. *cratophora*	F		2	2	1							2						
UG-1095		F	1																
UG-1097		F																	
UG-1098		F																	
UG-1099	*Brachysporium* spp.	F	6		7	3	6	7	6		1	3	5	1	1	1		2	2
HdV-1103	*Glomus* sp.	F			1	2				6		2	5	1			2		2
UG-1104	cf. *Podosporium rigidum*	F	1		3	3	2	2		1		2		3		2			1
UG-1105		F					1				3					3			2
UG-1106		F	4		1	5	1	3	5	5		2	1	1			1	1	
UG-1108		F		1															
UG-1109		F															1		3
UG-1109 (parts <3 cells)		F		3	2	1				6	3					5	5	4	
UG-1110		F																	
UG-1111		F								4	1	1		5	4	3	2	1	
UG-1112	*Phaeosphaeria* type	F		4	2	2		1	2	4				1	1		1	1	
UG-1113	*Meliola* sp.	F									1								
UG-1118	cf. *Savoryella lignicola*	F	3	3	6	1	1	5	2	3	1	4	7	3	2	7	8		2
UG-1120	*Savoryella curvispora*	F		1															
UG-1123		F																1	
UG-1125		F		1		2			2	1				1	1	1	1		1
UG-1126		F	1	1									1			1			1
UG-1127		F			1														
UG-1128	cf. *Kretzschmaria clavus/K. cetrarioides*	F			1													1	
HdV-113	*Sporormiella* type (parts)	F			1				1	3	2	3	3	4	3	2	1		
UG-1135	cf. Xylariaceae	F																	
UG-1137	*Meliola* sp.	F										1							
UG-1138		F																	
UG-1142		F							1										
UG-1144		F										1							
UG-1145	cf. *Fusarium* sp.	F														2			
UG-1147		F																1	
UG-1148		F				1													1
UG-1150		F								1								1	1
UG-1153		F																	
UG-1155		F												1	1			1	1
UG-1162		F																	
cf. UG-1162		F								2									
UG-1165		F			1														
UG-1170		F																	
UG-1171	*Apiosordaria* type	F											1						
UG-1172		F										2	1	1					
UG-1173		F	10	1	12	8	7	12	13	5	11	40	18	2	5	5	15	7	14
UG-1174	*Rosellinia* sp.	F				1						1	1	1		1			
UG-1176		F	11	10	13	11	8	4	8	5	10	7	4	6	3	3	10	8	9
UG-1177		F																	
UG-1178	*Sordaria* type	F		1	1		1	3	2	1	1	7	1		1	2	4	10	3
UG-1180	*Sordaria* spp.	F		1			2	1	4	1		2		2			2	3	
cf. UG-1180		F																	
UG-1184		F		1			1			1				1					
UG-1185		F																	
UG-1186		F		1							1								
UG-1187		F																	2
UG-1188		F																	1
UG-1197		F		3					1										
UG-1200		F												1					
UG-1204		F			1														
UG-1206	cf. *Acroconidiellina loudetiae*	F	1				1									2			
UG-1208	*Coniochaeta* spp.	F	105	110	121	89	91	103	141	197	187	192	173	212	238	237	247	267	218
UG-1209		F																	
UG-1210		F					1					1	1						
UG-1211		F					1												
HdV-1245	*Diporotheca* sp.	F							1								1		1

L. Chibwera	Identification		56.5	60.5	64.5	68.5	72.5	76.5	80.5	84.5	88.5	92.5	96.5	100.5	104.5	108.5	112.5	116.5
HdV-1093	*Gelasinospora* cf. *cratophora*	F									1	1			1	2		
UG-1095		F																
UG-1097		F		1														
UG-1098		F		1					1									
UG-1099	*Brachysporium* spp.	F	2	2	3	8	20	13	10	27	18	26	49	62	27	11	28	62
HdV-1103	*Glomus* sp.	F		2	1	1	4	2					10	2	1	2	1	1
UG-1104	cf. *Podosporium rigidum*	F						1		3			1	1	3	3	1	2
UG-1105		F			1						2	1	1					
UG-1106		F		3		1	2		1									
UG-1108		F																
UG-1109		F	1						3			2	2	1	1	6		3
UG-1109 (parts <3 cells)		F				1	1	2	1					3	26		8	
UG-1110		F																2
UG-1111		F	1															
UG-1112	*Phaeosphaeria* type	F		1	1				1									
UG-1113	*Meliola* sp.	F	1											5	5	2	3	3
UG-1118	cf. *Savoryella lignicola*	F	4	1	3	6		1	3	6	2	1	4	1				
UG-1120	*Savoryella curvispora*	F		1	1		3		3			1	1					
UG-1123		F	3	2	3	1	1	1										
UG-1125		F	2	2			1		1									
UG-1126		F	3	2					1	1								
UG-1127		F		2														
UG-1128	cf. *Kretzschmaria clavus/K. cetrarioides*	F																
HdV-113	*Sporormiella* type (parts)	F		3	1			3	4			1				1	1	
UG-1135	cf. Xylariaceae	F	2			3	1											
UG-1137	*Meliola* sp.	F													1			
UG-1138		F			1	1		1	1	1							1	
UG-1142		F																
UG-1144		F	1		2	1												
UG-1145	cf. *Fusarium* sp.	F																
UG-1147		F			1								1					
UG-1148		F					1	1				6						
UG-1150		F																
UG-1153		F							1									
UG-1155		F	1		1	1	1	4	4	1	1	2						1
UG-1162		F										1						
cf. UG-1162		F																
UG-1165		F												1				
UG-1170		F											1					
UG-1171	*Apiosordaria* type	F			1			2		8	1			3	3		1	
UG-1172		F				1						2	1		1		3	
UG-1173		F	19	16		7	14	9		4	1	4	7	2			1	1
UG-1174	*Rosellinia* sp.	F		6	3	1	1	1	2			1	2	1				
UG-1176		F	12	15	18	8	5	6	3	1	5	1	4	4	4		1	
UG-1177		F		1														
UG-1178	*Sordaria* type	F	1	1	1		1	1	7	2	2	1			1	5		1
UG-1180	*Sordaria* spp.	F	3	2	4	3	1	5	8	6	6	7	6	66	14	14	9	8
cf. UG-1180		F				1								5	13	40	38	12
UG-1184		F																
UG-1185		F	1															
UG-1186		F																
UG-1187		F		1										1				1
UG-1188		F							2	1	1					2		
UG-1197		F																
UG-1200		F						1										
UG-1204		F																
UG-1206	cf. *Acroconidiellina loudetiae*	F																
UG-1208	*Coniochaeta* spp.	F	238	234	248	231	198	254	318	249	282	273	108	135	246	251	219	256
UG-1209		F		2	1													
UG-1210		F																
UG-1211		F							1									
HdV-1245	*Diporotheca* sp.	F						1	1	4	3							

L. Chibwera	Identification		-8.5	-5.5	-1.5	1.5	6.5	10.5	13.5	16.5	20.5	24.5	28.5	32.5	36.5	40.5	44.5	48.5	52.5
UG-1250	*Curvularia* cf. *comoriensis*	F			1		2	1					1			1	1		
UG-1252		F																	1
UG-1262	*Canalisporium* spp.	F									1								
UG-1274		F											1						
UG-1294		F			1									2	1				
UG-1323		F												1					
UG-1325		F					1												
cf. UG-1330		F	1																
UG-1334		F																	
UG-1341		F											1						
HdV-1351	*Gelasinospora* cf. *dictyophora*	F																1	
UG-1352		F																	
UG-1356		F			2														
UG-1357		F			1														
UG-1358		F						1				1	1	1				1	2
UG-1360		F	1										1	1			1		
HdV-1047		F										1							
HdV-89	*Tetraploa aristata*	F	3	6	6	3	4	3	9	10	5	6	6	2	16		9	6	10
UG-1363		F			1														
UG-1372		F	1																
UG-1373	*Curvularia* sp.	F		1			1												
UG-1374	*Rosellinia* sp.	F				1													
UG-1375		F								1									
UG-1376	*Curvularia* sp.	F									1							1	
UG-1378		F														1			
UG-1379	*Curvularia* sp.	F																1	
UG-1381	*Gelasinospora* sp.	F																	1
UG-1380	*Rosellinia sp.*	F																	1
UG-1383		F																	
UG-1384		F																	
UG-1243	cf. *Asplenium* sp.	F/M								2		1						1	
UG-1246	*Isoetes* type	F/M	2			2				3		1	1						1
UG-1253	Polypodiaceae	F/M													1			1	
UG-1255	*Ophioglossum* subg. *Ophioglossum*	F/M	1																
UG-1260	*Coniogramme africana* type	F/M																	
UG-1261	cf. *Pteris/Actiniopteris* sp.	F/M									2				1			1	
UG-1315	Monoletes undiff.	F/M	3	7	1	3	1	3	1	2	6	7	4	1	6	4	2	6	2
UG-1385	Triletes undiff. (smooth)	F/M	6	3	4	1	4	2	2	1	3	1			3	1		3	1
UG-1377		F/M									1								
cf UG-1266		OF										1							
cf. UG-1267		OF		1															
UG-1114		U	1	1	1		1		2	8	3	3	4	2	8			1	8
UG-1115		U								1				2	1				
UG-1154		U				3	3					1							
UG-1284		U																	
UG-1292		U								53			1		3	4	2	1	
UG-1296		U								1				1					3
UG-1300		U																	
UG-1307		U																1	
UG-1319		U		1															
UG-1382		U																	
UG-1221	tropical oocyte	Z					1												
UG-1223	tropical oocyte	Z	1	2	1					3									
Indeterminata	Non-pollen palynomorphs		10	20	15	6	14	11	18	25	10	22	15	16	5	16	13	9	9
Total NPPs			**448**	**437**	**451**	**407**	**459**	**503**	**422**	**456**	**329**	**450**	**442**	**418**	**404**	**401**	**439**	**430**	**426**
Total pollen+aquatics			628	695	583	450	496	472	650	778	826	1724	1348	1742	1666	1583	1179	1858	1708
Conversion factor (aquatics)			0.10	0.11	0.12	0.07	0.07	0.06	0.09	0.12	0.10	0.09	0.11	0.11	0.10	0.10	0.17	0.17	0.15
Aquatics			61	77	71	30	36	29	56	93	80	157	149	187	174	160	202	317	264
Pollen sum			**567**	**618**	**512**	**420**	**460**	**443**	**594**	**685**	**746**	**1567**	**1199**	**1555**	**1492**	**1423**	**977**	**1541**	**1444**

L. Chibwera	Identification		56.5	60.5	64.5	68.5	72.5	76.5	80.5	84.5	88.5	92.5	96.5	100.5	104.5	108.5	112.5	116.5
UG-1250	*Curvularia* cf. *comoriensis*	F			1													
UG-1252		F																
UG-1262	*Canalisporium* spp.	F				2	3	1	2	1	1							
UG-1274		F				1	4		3	1		2						
UG-1294		F		1		13	3	3	4		1							
UG-1323		F																
UG-1325		F																
cf. UG-1330		F																
UG-1334		F												1				
UG-1341		F						4										
HdV-1351	*Gelasinospora* cf. *dictyophora*	F						1		1	1							
UG-1352		F												1				
UG-1356		F																
UG-1357		F																
UG-1358		F																
UG-1360		F				3	2	1	5			1						
HdV-1047		F		1														
HdV-89	*Tetraploa aristata*	F	3	9	5	5		6	12	2	1	1						
UG-1363		F																
UG-1372		F																
UG-1373	*Curvularia* sp.	F																
UG-1374	*Rosellinia* sp.	F																
UG-1375		F																
UG-1376	*Curvularia* sp.	F																
UG-1378		F																
UG-1379	*Curvularia* sp.	F																
UG-1381	*Gelasinospora* sp.	F			1													
UG-1380	*Rosellinia sp.*	F																
UG-1383		F												1	1			
UG-1384		F															1	1
UG-1243	cf. *Asplenium* sp.	F/M																
UG-1246	*Isoetes* type	F/M	1		1		2								1	1		
UG-1253	Polypodiaceae	F/M							1							1		
UG-1255	*Ophioglossum* subg. *Ophioglossum*	F/M																
UG-1260	*Coniogramme africana* type	F/M						1			1			2	1			
UG-1261	cf. *Pteris/Actiniopteris* sp.	F/M				1			1							1		1
UG-1315	Monoletes undiff.	F/M	4	6	11	6	4	3	3	3	4	5		1	2	6	6	3
UG-1385	Triletes undiff. (smooth)	F/M					1	1	1	3	1		2					1
UG-1377		F/M																
cf UG-1266		OF																
cf. UG-1267		OF																
UG-1114		U	2															
UG-1115		U		7	2			2	1			1						
UG-1154		U																
UG-1284		U			12													
UG-1292		U	1				1	1	1	1	3	1	1					
UG-1296		U		4	2		3			2								
UG-1300		U			1													
UG-1307		U						1				2						
UG-1319		U																
UG-1382		U					5	1										
UG-1221	tropical oocyte	Z																
UG-1223	tropical oocyte	Z											1	1	1	1		
Indeterminata	Non-pollen palynomorphs		26	8	6	4	5	3	4	7	7	11	3	6	7	3	3	
Total NPPs			**422**	**430**	**418**	**429**	**403**	**426**	**495**	**428**	**428**	**417**	**437**	**403**	**424**	**411**	**407**	**440**
Total pollen+aquatics			994	633	1113	778	656	583	470	669	392	277	435	349	323	331	338	352
Conversion factor (aquatics)			0.14	0.20	0.12	0.24	0.24	0.24	0.21	0.26	0.18	0.19	0.21	0.27	0.30	0.39	0.31	0.31
Aquatics			138	127	132	190	156	139	100	177	71	51	93	93	96	129	104	108
Pollen sum			**856**	**506**	**981**	**588**	**500**	**444**	**370**	**492**	**321**	**226**	**342**	**256**	**227**	**202**	**234**	**244**

Appendix III. Raw NPP data from the sediment record of Lake Kanyamukali (western Uganda).

L. Kanymukali	Identification	Tax group	2.5	4.5	6.5	8.5	12.5	16.5	20.5	24.5	28.5	32.5	36.5	44.5	52.5	60.5
cf. UG-1231	*Botryococcus* cf. *neglectus*	A/C			1			1	1		24	7	6			3
HdV-130	*Spirogyra* sp. (psilate)	A/C														
HdV-131	*Spirogyra* sp. (microreticulate)	A/C														
UG-1240	*Spirogyra* sp. (rugulate)	A/C														
cf. UG-1241	epidermis of *Nymphaea nouchali*	AP														
cf. UG-1084		F		1										1		
cf. UG-1119		F		1												
cf. UG-1126		F							2							
cf. UG-1180	*Sordaria* spp.	F	10	5	9	14	14	5	2	8	4	8	8	12	5	12
HdV-1001	*Caryospora* sp.	F							1			1	1	2		
UG-1002	*Sporoschisma* spp.	F	1	1	2	1	3	1	1	3				2	2	
HdV-1005	*Brachydesmiella* sp.	F	2	3	1	2	2	2	2			1		2		1
HdV-1009	*Chaetomium* sp.	F	2	1		1		1		2	1			2	1	1
HdV-1012	cf. *Sordaria* sp.	F														
HdV-1013	*Cercophora* type	F	8	6	8	7	7	9	8	16	25	24	10	13	13	10
HdV-1014	*Rosellinia* type	F												1		
HdV-1015A-C	*Dictyoarthrinium* cf. *sacchari*	F		3					1							2
HdV-1018A	*Spegazzinia tessarthra*	F		1									1			
HdV-1018B	*Spegazzinia tessarthra*	F		1	1					2	1					1
HdV-1022	*Clasterosporium* sp.	F					2		2	2		3			2	2
HdV-1025	*Diplocladiella* cf. *scalaroides*	F	1													
HdV-1026	*Peziza/Scutellinia* sp.	F									1					
HdV-1029A	*Curvularia* cf. *intermedia*	F	11	10	7	11	9	2	1		1	4	1	1	1	5
HdV-1029B	*Curvularia* sp. *(*assymmetric)	F				1		1		2	2			1		
HdV-1030	cf. *Byssothecium* sp.	F														
HdV-1031	*Acrodictys* sp.	F	1													
HdV-1032		F	1													
HdV-1036	cf. *Brachysporium* sp.	F												1		
HdV-1040	*Isthmospora spinosa*	F					1									
HdV-1042	*Montagnula* sp.	F				1			1							
HdV-1043	cf. *Lasiodiplodia theobromae*	F	8	9	11	9	3	4	1	1	1	5	2	3		1
HdV-1045		F							1							
HdV-1047	*Rhytidospora* cf. *tetraspora*	F				1		1	1	1	1	1		2		
HdV-1048		F	3		4		1	4								
HdV-1052	Xylariaceae	F		1			1									
HdV-1053	*Dictyosporium* cf. *heptasporum*	F	4	1			1				1	1		2	1	2
HdV-1054		F					1	3	2	1						
HdV-1093	*Gelasinospora* cf. *cratiphora*	F				1										1
HdV-1103	*Glomus* sp.	F	10	1	3	7	6	3	5	2		1		3	3	
HdV-113	*Sporormiella* type (parts)	F		1												
HdV-1245	*Diporotheca* sp.	F	1		4	2	2	3			1			1		
HdV-1351	*Gelasinospora* cf. *dictyophora*	F														
HdV-89	*Tetraploa aristata*	F	8	9	11	8	16	5	7	5	5	8	4	6	6	9
UG-1065	Xylariaceaea	F							1			1		1		
UG-1066	*Delitschia* spp.	F	8	6	4	1	7	4	4	9	5	6	4	7	7	11
UG-1068		F	2	2		2	1		1							1
UG-1069		F	4	1		1	3	1	2	3	3		1	2	8	1
UG-1070	Xylariaceae	F										1				
UG-1071	cf. *Amphirosellinia* sp.	F		1										2		
UG-1072		F	3		1											
UG-1073		F	2	3				1								
UG-1076		F				2										
UG-1077	cf. Xylariaceae/Sordariaceae/Coniochaetaceae	F	1	9			1	4		1		1				
UG-1079	*Urocystis* sp.	F														

L. Kanymukali	Identification	Tax group	68.5	76.5	84.5	92.5	100.5	108.5	116.5	124.5	132.5	140.5	148.5	156.5
cf. UG-1231	*Botryococcus* cf. *neglectus*	A/C		2		17	21		1	2	26	49	49	67
HdV-130	*Spirogyra* sp. (psilate)	A/C								3				
HdV-131	*Spirogyra* sp. (microreticulate)	A/C							1					
UG-1240	*Spirogyra* sp. (rugulate)	A/C												1
cf. UG-1241	epidermis of *Nymphaea nouchali*	AP	8	5	12	4	10	10						
cf. UG-1084		F				1	1							
cf. UG-1119		F												
cf. UG-1126		F												
cf. UG-1180	*Sordaria* spp.	F	23	10	29	41	25	19	4	4	21	6		
HdV-1001	*Caryospora* sp.	F						1						
UG-1002	*Sporoschisma* spp.	F	3	5	1	2	1		3	1	1			
HdV-1005	*Brachydesmiella* sp.	F		2					1					
HdV-1009	*Chaetomium* sp.	F	3	7		1	1	1	2	10	6	8	3	3
HdV-1012	cf. *Sordaria* sp.	F									4	5		
HdV-1013	*Cercophora* type	F	13	17	10	11	17	10	35	45	192	38	33	24
HdV-1014	*Rosellinia* type	F												
HdV-1015A-C	*Dictyoarthrinium* cf. *sacchari*	F	4	2	3	3		2	2	3				
HdV-1018A	*Spegazzinia tessarthra*	F												
HdV-1018B	*Spegazzinia tessarthra*	F	1					3					1	
HdV-1022	*Clasterosporium* sp.	F						1		2				
HdV-1025	*Diplocladiella* cf. *scalaroides*	F												
HdV-1026	*Peziza/Scutellinia* sp.	F			5			1	1					
HdV-1029A	*Curvularia* cf. *intermedia*	F	16	6			2	12	3	2				
HdV-1029B	*Curvularia* sp. *(* assymmetric)	F	1	3	1		2	2						
HdV-1030	cf. *Byssothecium* sp.	F						2						
HdV-1031	*Acrodictys* sp.	F												
HdV-1032		F												
HdV-1036	cf. *Brachysporium* sp.	F												
HdV-1040	*Isthmospora spinosa*	F												
HdV-1042	*Montagnula* sp.	F					1	3		1				
HdV-1043	cf. *Lasiodiplodia theobromae*	F		1										
HdV-1045		F												
HdV-1047	*Rhytidospora* cf. *tetraspora*	F												
HdV-1048		F												
HdV-1052	Xylariaceae	F					2		1					
HdV-1053	*Dictyosporium* cf. *heptasporum*	F	1		1					3	9			
HdV-1054		F	1											
HdV-1093	*Gelasinospora* cf. *cratiphora*	F				1	2		1				1	
HdV-1103	*Glomus* sp.	F	4		1								9	2
HdV-113	*Sporormiella* type (parts)	F	2	2	1	1	1	2						
HdV-1245	*Diporotheca* sp.	F												
HdV-1351	*Gelasinospora* cf. *dictyophora*	F	1											
HdV-89	*Tetraploa aristata*	F	5	5	2	7	6	7	11	29	6			
UG-1065	Xylariaceaea	F			1									
UG-1066	*Delitschia* spp.	F	11	8	5	4	3	3	1		18	1		
UG-1068		F	2			1								
UG-1069		F	5	4	3	5	4	7	2				1	1
UG-1070	Xylariaceae	F								1	1			
UG-1071	cf. *Amphirosellinia* sp.	F							1					
UG-1072		F		4	3	5	7		2	45	34			
UG-1073		F	2		1	7			2	18	10			
UG-1076		F												
UG-1077	cf. Xylariaceae/Sordariaceae/Coniochaetaceae	F		4	2	2	6	3	2		11			
UG-1079	*Urocystis* sp.	F	1											

L. Kanymukali	Identification	Tax group	2.5	4.5	6.5	8.5	12.5	16.5	20.5	24.5	28.5	32.5	36.5	44.5	52.5	60.5
UG-1080		F	3							1	1	1			2	1
UG-1081		F		1		1									2	
UG-1082		F													1	
UG-1083		F														
UG-1084		F			1		1		1							
UG-1087		F	1		6	5	2	1	2							
UG-1091	*Bactrodesmium* type	F	2	1					1							
UG-1092		F								1						
UG-1096		F	1													
UG-1097		F		1	1		1			1				1		
UG-1098		F				2	1			1					1	1
UG-1099	*Brachysporium* spp.	F	25	20	33	36	66	52	51	26	33	29	35	32	3	11
UG-1104	cf. *Podosporium rigidum*	F	3	1		1	3	7	1	4	2	1				
UG-1105		F												1		
UG-1106		F	10	1												
UG-1107		F									1					
UG-1109		F	1					1			1				1	
UG-1109 (parts <3 cells)		F	1												8	3
UG-1113	*Meliola* sp.	F	2	1	2				1		1					
UG-1118	cf. *Savoryella lignicola*	F						1								
UG-1120	*Savoryella curvispora*	F	1	1	1					1	1	3	3	7	5	4
UG-1123		F	2													
UG-1125		F		3	3	6	7	6	6	2	14	26	10	6	5	
UG-1126		F		1								2	1	2	1	
UG-1127		F														
UG-1128	cf. *Kretzschmaria clavus/K. cetrarioides*	F	1							1						
UG-1132		F		1												
UG-1135	cf. Xylariaceae	F									1					
UG-1137	*Meliola* sp.	F						1				1	1			
UG-1140		F					2		1				3	2		
UG-1145	cf. *Fusarium* sp.	F		1								2				
UG-1147		F						1	1	2		1				
UG-1148		F	2													
UG-1150		F			1	3					2	1		2		5
UG-1151		F	3	1	1		3	1		1				4		
UG-1155		F		1	2		2			1	2	2	2	1		
UG-1157	*Rosellinia* sp.	F						1								
UG-1158		F														
UG-1159		F														
UG-1167		F														
UG-1171	*Apiosordaria* type	F								2						2
UG-1172		F		1												
UG-1173		F	3	11			5	2	4	1	10	14	14	8		15
UG-1176		F	2	23			1			1	8	5	9	6	7	9
UG-1178	*Sordaria* type	F	2	2	2		3	1						2	1	3
UG-1184		F	1	1				1						3		
UG-1185		F														
UG-1186		F		1		1										
UG-1187		F									1			1		
UG-1188		F														
UG-1197		F											1			
UG-1199		F														

L. Kanymukali	Identification	Tax group	68.5	76.5	84.5	92.5	100.5	108.5	116.5	124.5	132.5	140.5	148.5	156.5
UG-1080		F		3	1	1		2						
UG-1081		F	1					1						
UG-1082		F												1
UG-1083		F					1							
UG-1084		F												
UG-1087		F						1						
UG-1091	*Bactrodesmium* type	F												
UG-1092		F												
UG-1096		F												
UG-1097		F												
UG-1098		F												
UG-1099	*Brachysporium* spp.	F	3	2	3	9	1	1	1					
UG-1104	cf. *Podosporium rigidum*	F			1									
UG-1105		F					1	4						
UG-1106		F					1							
UG-1107		F					3	1	4					
UG-1109		F		2	1	1	13	10	22	26	33	18	20	4
UG-1109 (parts <3 cells)		F		13	9	6	23	21	47	81	491	1329	229	132
UG-1113	*Meliola* sp.	F												
UG-1118	cf. *Savoryella lignicola*	F			1	1	1							
UG-1120	*Savoryella curvispora*	F		7	6	3	3	5	10	5	8			
UG-1123		F								1				
UG-1125		F	1	8	6	3		1						
UG-1126		F												
UG-1127		F					1		1					
UG-1128	cf. *Kretzschmaria clavus/K. cetrarioides*	F												
UG-1132		F												
UG-1135	cf. Xylariaceae	F		1					8	3				
UG-1137	*Meliola* sp.	F			1									
UG-1140		F												
UG-1145	cf. *Fusarium* sp.	F												
UG-1147		F			1									
UG-1148		F												
UG-1150		F			1	2								
UG-1151		F												
UG-1155		F		3	3			1						
UG-1157	*Rosellinia* sp.	F												
UG-1158		F					1						1	
UG-1159		F		1										
UG-1167		F											2	
UG-1171	*Apiosordaria* type	F	2	2	1			2		1	4			2
UG-1172		F						2						
UG-1173		F	4	22	19	10	14	7	22	18		4		
UG-1176		F	7	8	10	9	15	16	38	61	9	1	5	
UG-1178	*Sordaria* type	F	2	6	2	1	2	1	2	1	7		2	3
UG-1184		F									2			
UG-1185		F					1				1	2	2	
UG-1186		F												
UG-1187		F		1		2								
UG-1188		F				2						1		
UG-1197		F					1							
UG-1199		F	1											

L. Kanymukali	Identification	Tax group	2.5	4.5	6.5	8.5	12.5	16.5	20.5	24.5	28.5	32.5	36.5	44.5	52.5	60.5
UG-1200		F		12												
UG-1206	cf. *Acroconidiellina loudetiae*	F														
UG-1208	*Coniochaeta* spp.	F	267	242	298	282	306	276	291	291	236	243	289	256	355	313
UG-1212		F	1													
UG-1215		F		1												
UG-1217		F									1					
UG-1250	*Curvularia* cf. *comoriensis*	F	1	1			3		2	1	1			1		
UG-1252		F	2													
UG-1261		F														
UG-1262	*Canalisporium* spp.	F								1	1			1		
UG-1274		F	2			1	3	1	4	8	6	4	8	7	16	8
UG-1277		F	1							1						
UG-1278		F				1			1							
UG-1279		F	1													
UG-1332		F											2		1	
UG-1334		F											1			
UG-1352		F	2													
UG-1353		F		2												
UG-1358		F														
UG-1360		F			1			1	1			1		3	2	3
UG-1363		F							2							
UG-1364	*Rosellinia* sp.	F					1					2				
UG-1365		F	1													
UG-1366		F	3													
UG-1368		F	1													
UG-1385	Triletes undiff. (smooth)	F/M				2	2		1		1			1		1
UG-1243	cf. *Asplenium* sp.	F/M	1		1	2	3		1	2						
UG-1246	*Isoetes* type	F/M								3	1	1				
UG-1253	Polypodiaceae	F/M				1										
UG-1259	*Pteridium aquilinum*	F/M			1											
UG-1261	cf. *Pteris/Actiniopteris* sp.	F/M														
UG-1315	Monoletes undiff.	F/M		2	3	4	3	5	6	5	5	6	5	7	5	5
UG-1316	*Asplenium* type	F/M						1		4						
UG-1270		OF	1													
UG-1114		U	1		2	1	2		1							
UG-1115		U	2													
UG-1292		U					1	1	1		1			1	1	2
UG-1296		U	1												2	
UG-1307		U														
UG-1309		U	2													
UG-1311		U														
UG-1312		U								1						
UG-1319		U				1			2			1		2		
UG-1324		U		1												
UG-1367		U	1													
UG-1221	tropical oocyte	Z	1				1									
UG-1321		Z	2													
UG-1344	*Filinia* resting egg	Z													9	
UG-1361	thecamoebae	Z									1					
UG-1369	*Arcella* sp.	Z					1									
Indeterminata	Non-pollen palynomorphs		18	25	8	7	21	14	19	12	9	11	3	12	5	17
Total NPPs			**469**	**437**	**434**	**429**	**525**	**430**	**448**	**433**	**417**	**430**	**425**	**436**	**482**	**466**
Total pollen+aquatics			496	542	775	688	1056	1065	1363	1195	1741	1792	1904	944	456	735
Conversion factor (aquatics)			0.07	0.05	0.04	0.06	0.07	0.03	0.02	0.03	0.03	0.03	0.02	0.03	0.03	0.03
Aquatics			35	26	29	42	76	31	29	39	50	45	39	25	16	22
Pollen sum			**461**	**516**	**746**	**646**	**980**	**1034**	**1334**	**1156**	**1691**	**1747**	**1865**	**919**	**440**	**713**

L. Kanymukali	Identification	Tax group	68.5	76.5	84.5	92.5	100.5	108.5	116.5	124.5	132.5	140.5	148.5	156.5
UG-1200		F												
UG-1206	cf. *Acroconidiellina loudetiae*	F					1	1						
UG-1208	*Coniochaeta* spp.	F	265	231	265	225	209	333	66	74	515	110	97	93
UG-1212		F												
UG-1215		F												
UG-1217		F												
UG-1250	*Curvularia* cf. *comoriensis*	F	4											
UG-1252		F												
UG-1261		F										1		
UG-1262	*Canalisporium* spp.	F												
UG-1274		F	4	4	6	4	6	5	3		2			
UG-1277		F												
UG-1278		F												
UG-1279		F												
UG-1332		F				1								
UG-1334		F												
UG-1352		F												
UG-1353		F			1		1			1				
UG-1358		F		1										
UG-1360		F	3	3	1	3	3		1	2	28			
UG-1363		F												
UG-1364	*Rosellinia* sp.	F												
UG-1365		F												
UG-1366		F												
UG-1368		F												
UG-1385	Triletes undiff. (smooth)	F/M									1	2	2	
UG-1243	cf. *Asplenium* sp.	F/M				1								
UG-1246	*Isoetes* type	F/M			3	1					1			
UG-1253	Polypodiaceae	F/M	2								1	1		
UG-1259	*Pteridium aquilinum*	F/M												
UG-1261	cf. *Pteris/Actiniopteris* sp.	F/M											1	
UG-1315	Monoletes undiff.	F/M	9	8	3	8	10	6	158	14	53	97	82	161
UG-1316	*Asplenium* type	F/M												
UG-1270		OF												
UG-1114		U	5	2		3	1		1		1			
UG-1115		U												
UG-1292		U	3	1		2		1	1					
UG-1296		U											2	1
UG-1307		U		2	1		1							
UG-1309		U												
UG-1311		U								1			3	
UG-1312		U												
UG-1319		U						1					6	
UG-1324		U											10	
UG-1367		U												
UG-1221		Z												
UG-1321		Z												
UG-1344	*Filinia* sp.	Z	1											
UG-1361		Z												
UG-1369	*Arcella* sp.	Z												
Indeterminata	Non-pollen palynomorphs		21	22	24	22	21	14	18	11	19	21	9	32
Total NPPs			**445**	**440**	**451**	**433**	**447**	**526**	**479**	**469**	**1515**	**1694**	**570**	**527**
Total pollen+aquatics			1434	485	700	898	842	1053	637	850	511	534	408	424
Conversion factor (aquatics)			0.05	0.14	0.12	0.17	0.19	0.15	0.26	0.45	0.60	0.59	0.45	0.53
Aquatics			66	66	85	151	161	153	167	379	305	316	184	224
Pollen sum			**1368**	**419**	**615**	**747**	**681**	**900**	**470**	**471**	**206**	**218**	**224**	**200**

Photograph by Bob Rumes

Front cover:

Rock art from the UNESCO's classified archaeological site Nyero (Uganda) - ritual symbol, used for rainmaking in the late 19th century

Fishing boy (Photograph by Pierre-Denis Plisnier)

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