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ECOSYSTEM HISTORY OF THE BALE MOUNTAINS

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ABSTRACT: This paper presents results of the multiproxy palaeoenvironmental study of three zoogenic deposits, situated at the different altitudes in the Bale Mountains (South-central Ethiopia). Radiocarbon dating, pollen and diatom analyses were used to reconstruct the ecosystems' dynamics of the Bale Mountains during the Late Pleistocene and the Holocene. Pollen analysis revealed signals of the African Humid Period (AHP) and specified its precise time (15,000−4,600 cal yrs BP). The Weyib valley remained relatively arid from 15,000 to 8,600 cal yrs BP. A short humid period commenced at 8,500−8,000 cal yrs BP. Gradual climate aridization took place since 8,000 cal yrs BP. Diatom data show that the Sanetti plateau was relatively wet during the past 7000 years with some fluctuations in moisture. The plateau experienced more oxygenated systems after 2,500 cal yrs BP until now than before due to the creation of new lakes that indicate a humid climatic regime. The Weyib valley experienced a relatively humid period ca. 2,500 cal yrs BP. After the termination of the AHP, vegetation changes signaled the climate aridization that prevailed on more humid southern macroslope of the Bale Mountains and continued further during around 2,500 cal yrs BP, resulting in an extensive development of dry forests type of *Olea*, *Hagenia* and *Podocarpus*. Gradual climate aridity was interrupted by humid and warm period of 2,000−1,000 cal yrs BP. Noticeable human-induced environmental modification was registered on the Sanetti Plateau around 600 cal yrs BP, and around 1,000 cal yrs BP on the southern macroslope.

Key words/phrases: Bale Mountains, Climate reconstruction, Diatom, Holocene, Pollen, Radiocarbon dating.

INTRODUCTION

One of the most noteworthy highland areas in East Africa is the Bale Mountains, located in south-central Ethiopia (N 6°10′−7°10′; E 39°00′−40°00′). The Ethiopian Highlands, divided by Main Ethiopian Rift

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(MER) into two mountainous portions (north-western and south-eastern), includes the most extensive high-altitude areas throughout the African continent. The Bale mountain massif is located on the south-eastern part, and includes the highest peaks of this portion of the Ethiopian Highlands (4337 m a.s.l. (Mt. Tullu Dimtu)). It is a major center of flora and fauna endemicity (Hillman, 1986). Approximately 1300 species of flowering plants are known to inhabit the Bale Mountains, about 160 of which are endemic to Ethiopia, and 23 – only to Bale. The central part of the Bale Mountains is the Sanetti Plateau, the largest piece of Afroalpine habitat in the world with an average elevation over 4000 m a.s.l. The Plateau, covered by Afroalpine vegetation has remained a unique habitat to the rare and endangered animals such as Ethiopian wolf (*Canis simensis*), giant mole rat (*Tachyoryctes macrocephalus*), blue-winged goose (*Cyanochen cyanoptera*), etc. The Bale Mountains National Park was founded in 1970 in order to conserve the unique biodiversity of this region (Hillman, 1988; Stephens *et al*., 2001).

The Bale Mountains is characterized by pronounced altitudinal zonation inherent to all high mountains which is reflected in the vegetation structure. Study of vegetation history of such areas is very promising for past climate reconstruction. The dynamic balance of high-mountainous plant formations is so unstable that even relatively minor climate changes cause upward/downward shifts of the vegetation belts. Detection of offset of vegetation zones in the past could help draw the conclusion about the climate change (Zelikson and Gubonina, 1985).

Since the mid-Holocene, ecosystems are under significant anthropogenic pressure around the globe, especially in East Africa. This has constrained the complete and adequate interpretation of the palaeoecological data and reconstruction of native ecosystem’s history. Although palaeoecological records signalled change in the ecosystems of the Bale Mountains in the past, it is unclear whether the recent anthropogenic influences are more significant than in the past. Palaeoecological evidence suggested that anthropogenic impacts have caused little change in the ecosystems up to ca. 2000 years BP due to the low population density in these areas (Bonnefille and Hamilton, 1986; Miehe and Miehe, 1994). However, adequate evidence of the human impact is still lacking and the vegetation and climate history of these areas are poorly understood. Few archaeological investigations conducted at low altitudes of the Bale Mountains revealed the changes in the early Palaeolithic Period (Clark and Williams, 1978). However, the report has not been well complemented with sufficient amount of reliable historical data and a few of previous palaeo-reconstructions failed to precisely address the question.

Moreover, despite the great importance of these territories for reconstruction of climate and anthropogenic impacts on the ecosystems of the African highlands, vegetation and climate history of the Bale Mountains is still largely unexplored. While a large number of research based on the study of lake sediments was carried out in the Great Rift Valley, situated at much lower altitudes (Gasse and Street, 1978; Chalié and Gasse, 2002; Dagnachew Legesse *et al*., 2002; Foerster *et al*., 2012; and others), there are only a few studies devoted to ecosystems and environmental conditions of the Bale Mountains during the late Pleistocene and Holocene (Hamilton, 1982; Mohammed and Bonnefille, 1998; Umer *et al*., 2007). This is largely attributed to the absence or low availability of deposits suitable for reconstruction. There are very few appropriate lake sediments (Umer *et al*., 2007), while peat bogs found in these territories are often characterized by poor preservation (Hamilton, 1982; Mohammed and Bonnefille, 1998). An alternative source for palaeoecological information could be zoogenic deposits that accumulate in long-term animal shelters: caves and various rocky niches. As a result of animal activities, stratum of dung, bones, hair, feathers and plant remains is continuously formed at the bottom of these shelters (Savinetsky *et al*., 2012). Continuity of sedimentation process makes such deposit an important source of information for palaeoecological reconstructions. In particular, using this deposit type, we investigated the ecosystem history of the Bale Mountains during the Late Pleistocene-Holocene.

MATERIALS AND METHODS

Sampling sites

This study investigated the zoogenic deposits from three rock shelters found in the Bale Mountains on the territory of the Bale Mountains National Park (Fig. 1, Table 1). The samples were taken during the Joint Ethiopian-Russian Biological Expedition (JERBE) fieldworks.

The Konteh rock shelter is situated on the Sanetti plateau. Niche is located at the foot of a rock cliff on the northern shore of a small shallow alpine lake. Konteh is positioned in the Afroalpine vegetation belt. This vegetation type is characterized by pulvinated dwarf shrubs of the *Helichrysum* species (Asteraceae) which are co-dominant with the firm bunchgrasses (*Festuca richardii*, *Pentaschistis pictigluma*, *Agrostis quinqueseta* etc. (Poaceae)). One of the notable plant species here is the giant lobelia (*Lobelia* *rhynchopetalum*) which is endemic to Ethiopia.

There is a dung deposit, formed, presumably, of the rock hyrax (*Procavia capensis*) within the Konteh niche. The deposit thickness is about 20 cm. It has been sampled in 2007 to carry out radiocarbon analysis. The samples were 3–4 cm thick. Four samples were collected for radiocarbon dating. Seven samples were taken for diatom analysis. The deposit has been re-sampled in 2012 to conduct the spore-pollen analysis. These samples were 1 cm thick. In total 20 samples were selected for spore-pollen analysis.

The Fincha Habera rock shelter is situated in the Weyib river valley along a small stream called Wella. The site lies at the Northern grasslands, pushing the upper limit for tree growth at the boundary between the ericoid and Afroalpine vegetation belts. Areas are scrubby with wormwood (*Artemisia afra*, *Artemisia schimperi*), everlasting (*Helichrysum* sp. (especially *H. splendidum*), lady's mantle (*Alchemilla haumannii*). The region is mainly covered with grasses (principally *Festuca richardii*) with restricted patches of *Erica trimera*. As in other mountains in Ethiopia and throughout East Africa, the ericoid vegetation has been strongly modified by human and fire resulting in changes in the structure of the vegetation which subsequently and more importantly, gave rise to large-scale replacement of ericoid communities by herbaceous vegetation (Wesche *et al*., 2000).

The Fincha Habera rock shelter contains sediments of, presumably, rock hyrax dung, and possibly, other animals. Deposit thickness is 86 cm (10–96 cm). Zero was situated at the 10 cm from sediment surface. The deposit has been sampled in 2008 and 17 samples were collected for pollen, diatom analysis and radiocarbon dating. The thickness of samples was about 3–4 cm.

The Katcha rock shelter is located on the southern macroslope of the Bale Mountains called Harenna forest (Harenna Escarpment), the largest cloud forest in Ethiopia. It is divided into distinct vegetation belts in climb. The Katcha niche is situated at the base of a rocky outcrop in an extensive bamboo belt.

The deposit is formed by faeces of wild animals, presumably, bats and ungulates. Deposit thickness is 107 cm. Zero was situated at the 25 cm from sediment surface. Deposit was sampled in 2012 and 37 samples were collected for radiocarbon dating. Thickness of these samples was 3–4 cm. For the pollen analysis, the samples were taken with 1–2 cm interval. A total of 19 samples at different depths were investigated.

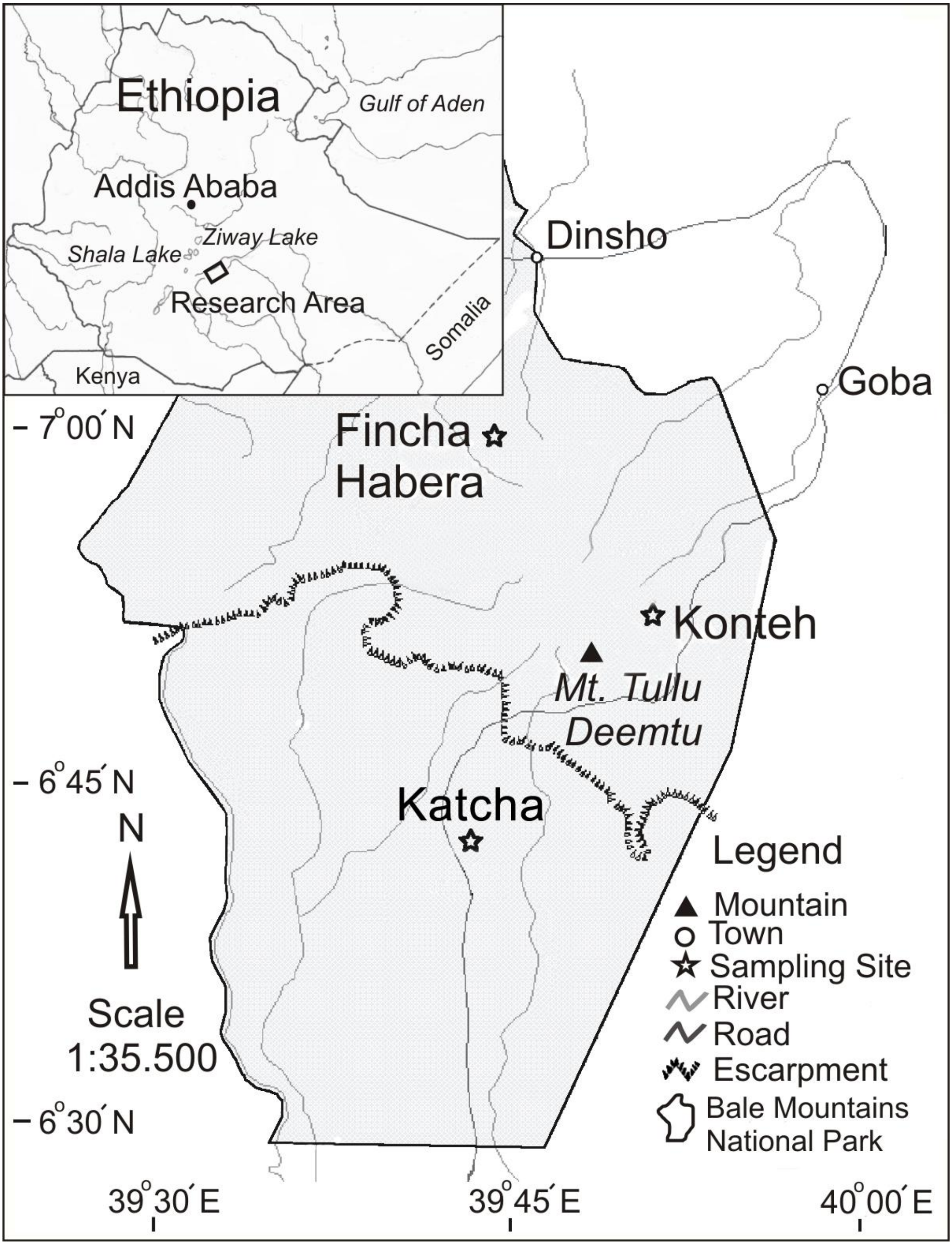

Fig. 1. Map of the study region with sampling sites.

Table 1. Location and brief description of the studied rock shelters.

Geographical coordinates		Length, m	Height, m	Depth, m	Entrance direction	Elevation a.s.l., m
N	**E**					
Konteh						
06º51′	039º53′	2,7	1,2	2,8	South-eastward	4110
Fincha Habera						
07º01′	039º44′	70	3	30	Eastward	3430
Katcha						
06º43′	039º44′	4,6	4,4	5,3	Eastward	2700

Radiocarbon dating

We used the method of radiocarbon dating to determine the deposits’ age. Plant remains and, mainly, charcoals served as dating material. Dates were derived using conventional liquid scintillation techniques in the Laboratory of Historical Ecology (A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences (RAS). Correct timing of historical events can be conducted only with adequate age-depth models. For constructing age-depth model of the deposits, the Bchron 3.1 program (Parnell *et al*., 2008) was used. In total, eighteen dates were obtained.

Diatom analysis

Diatom analysis was carried out for two studied zoogenic deposits - Konteh and Fincha Habera. Samples were prepared and analyzed at Addis Ababa University laboratories. About 1 gm of soil was resampled for diatom extraction. Samples were cleaned and processed for microscopic observations according to Battarbee (1986). 30% H_2O_2 was used for removing organic matter from the silica wall of diatoms. Blanco *et al.* (2008) recommended sample: hydrogen peroxide ratio of 1:1 for a 6-h oxidizing reaction as optimized protocol. In doing so, successive decantation instead of centrifuging was employed. Slides were dried at room temperature overnight. Cleaned diatoms were fixed with Naphrax. Scanning electron microscope as well as light microscopes were applied for identification and counting of diatom frustules. Standard identification manuals and publications were used for diatom identification (Gasse, 1986; Krammer and Lange-Bertalot, 1988; Metzeltin and Lange-Bertalot, 1998; Kelly, 2000; Metzeltin and Lange-Bertalot, 2007; Round *et al*., 2007). At least 300 valves were counted in each sample. The diatom stratigraphy was constructed using Tilia 2.0 and Tilia Graph View (TGView 2.0.2) (Grimm, 1987). Constrained incremental sum of squares was calculated and loaded with CONISS onto the diatom diagram to analyze the diatom stratification (Grimm, 1987). During the field trips, modern diatom samples from lakes, streams and bryophyte surfaces were collected. Modern samples were collected towards comparing of fossil diatom spectra from zoogenic deposits with existent currently in various environments (Habte Debella, 2012). Seven diatom metrics were used to construct past diatom diversity using the Shannon Diversity Index (H′) over the Holocene under the premise that diatoms have an environmental optimum and tolerance limits in any given environment (Habte Debella, 2012).

Pollen analysis

Sample preparation for spore-pollen analysis was carried out according to standard techniques (Faegri and Iversen, 1975; Moore *et al.*, 1991) in the Laboratory of Historical Ecology (A.N. Severtsov Institute of Ecology and Evolution, RAS). The volume of the samples from the Fincha Habera deposit was 4 cm^3; weighed amount (1 gram (gm)) have been used for samples from the Konteh and Katcha deposits. Pollen concentrations were calculated using known numbers of “exotic” *Lycopodium clavatum* marker spores in a tablet (batch No 1031 (Konteh and Katcha) and 483216 (Fincha Habera)), added to the samples before processing (Stockmarr, 1973). Pollen and spore were counted comprised of at least 500 (1000) grains (in some cases up to 300) per sample. Identification of pollen and spores was based on published pollen atlases (Bonnefille, 1971; Reille, 1998), images from the African Pollen Database website (http://apd.sedoo.fr/pollen/interface/indexPollen.html), and the reference collection comprising approximately 70 palynotypes at the Laboratory of Historical Ecology (A.N. Severtsov Institute of Ecology and Evolution, RAS). Percentages were calculated from a sum of all pollen grains and spores. The diagrams were plotted using programs Tilia 1.7.16, Tilia 2.0 и TGView 2.0.2. Pollen zones were distinguished using stratigraphically constrained cluster analysis (CONISS) (Grimm, 1987), as well as based on the presence/absence of taxa and the concentrations of pollen and spores.

RESULTS

Radiocarbon dating

Four radiocarbon dates were obtained for the Konteh deposit (Table 2). The age-depth model shows that sedimentation in the Konteh rock niche began about 7,300 years BP. The deposit accumulated evenly and very slowly. The Fincha Habera deposit has a complex stratigraphy. Sediment is divided into two levels by a layer of stones and rock debris at 57–86 cm. Perhaps, roof collapse occurred in a rocky niche, and the lower stratum (86–96 cm) was separated from the surface by stone burst. The age of this stratum could not be determined as there was no organic material convenient for dating. Ten radiocarbon dates were obtained for upper level of the Fincha Habera deposit (Table 2). The resulting age-depth model showed that the Fincha Habera deposit accumulated unevenly. Sedimentation rate was quite high between 15,000–13,000 and 9,500–6,000 years BP and notably slowed down between 13,000–9,500 and 5,000–1,500 years BP. The age of the beginning of the upper stratum (25–57 cm) sedimentation is also unknown. The small amount of organic material was an obstacle to date the layers from 51–57 cm. It is clear from the overlying dates that the age of these layers exceeds 15,000 years. Sedimentation in the Fincha Habera rock shelter terminated about 1,500 years BP. Four radiocarbon dates were carried out for the Katcha deposit (Table 2). The age-depth model shows that the age of the Katcha deposit is about 6,500 years. Sedimentation rate was relatively high 6,500–4,600 years BP, and then decreased and was comparatively low in period 4,600 years BP - present.

Table 2. Conventional radiocarbon dates of the zoogenic deposits and the results of age-depth modelling with Bchron 3.1 program (Parnell *et al*., 2008).

Lab No.	**Depth (cm)**	**Conventional radiocarbon dates (years BP)**	**Calibrated age (years BP) (median)**	**Range (years BP) (median ± 2σ)**
Konteh				
IEMAE-1398	1–3	Modern	585	270–920
IEMAE-1397	6–10	2015±185	2465	2070–2840
IEMAE-1396	10–13	3010±55	3645	3050–4185
IEMAE-1395	16–20	5800±195	7195	6355–7795
Fincha Habera				
IEMAE-1429	10–11	730±45	1685	860–2440
IEMAE-1428	11–15	2020±135	3705	2275–5235
IEMAE-1427	15–19	4820±150	6255	5585–6840
IEMAE-1430	19–22	6170±180	7320	6985–7645
IEMAE-1426	26–29	7815±185	8435	8240–8620
IEMAE-1425	32–35	7620±150	9055	8735–9485
IEMAE-1424	35–38	8170±270	11125	9720–12525
IEMAE-1423	38–41	10980±235	13370	12830–13915
IEMAE-1422	41–45	12195±245	14165	13830–14525
IEMAE-1421	48–51	12110±320	15070	14600–15985
Katcha				
IEMAE-1842	28–31	Modern	565	145–2530
IEMAE-1832	65–68	4020±60	4530	4290–4760
IEMAE-1833	80–82	4330±65	5000	4865–5450
IEMAE-1834	130–132	5630±65	6500	6210–7230

Diatom analysis

A few studies of diatom flora were conducted in Ethiopia (Telford and Lamb, 1999; Telford *et al*., 1999). The palaeolimnological study of the Bale Mountains was started in 1970's by Austrian limnologist Löffler (Löffler, 1978). However, it did not continue thereafter. All previous studies were conducted for lake sediments, but no diatom analysis of zoogenic deposits were carried out.

Overall 19 fossil diatom species were identified from the Konteh rock shelter, while 14 species had percent abundances of greater than 2% to be included in the diatom diagram (Fig. 2). Only one freshwater sample, *Fragilaria construens*, was encountered in fossil samples (that are abundant in the Konteh lake sample). Others are either aerial or sub-aerial. Pronounced dominant taxon is *Hantzschia amphioxys*, whose percentage varies from 25% to 45% throughout the sediment profile. *H. amphioxys* is described as eurytopic, tolerating a wide range of chemical content in terms of total dissolved solids, pH, alkalinity, and ionic compositions (Gasse, 1986). It is also eurythermal and survives subareal conditions. In the present study, *H. amphioxys* is equally abundant throughout the strata and shows dominance since 7,000 years BP. It does not show much difference from century to century, displaying its tolerance to wide range of environmental conditions. *Orthoseira roeseana* (previously described as *Melosira roeseana* (Gasse, 1986)) is another dominant taxon. Its relative abundance was highest (34%) at about 3,600 years BP, and then steadily decreased until the present time (Fig. 2). *Orthoseira roeseana* is typically found in subareal habitats, particularly, in bryophyte communities growing on alkaline substrata and is rarely found in lakes and high order streams (Stoermer and Julius, 2003). The other species is *Pinnularia obscura*, which started to rise since the last 2,000 years BP. This species is a typical moss dwelling, aerophylous diatom (Beyens, 1989).

Diatom spectra of the Fincha Habera deposit are much more diverse than that of the Konteh - 27 species were recorded (Habte Debella, 2012). The alkaliphilic species *Diadesmis contenta* is the most frequently represented species (up to 56%). *H. amphioxys* and *O. roeseana*, which are dominant in the Konteh deposit are also numerous (up to 24% and 34%, respectively). The acidophilous species *Pinnularia lata* and *Pinnularia microstauron* are abundant in the lowest layers. The uppermost layer also differs - other alkaliphilic species *Ulnaria ulna* (=*Synedra ulna*) (36%) and *O. roseana* (34%) are dominant, while percentage of *D. contenta* is only 7% (Fig. 3).

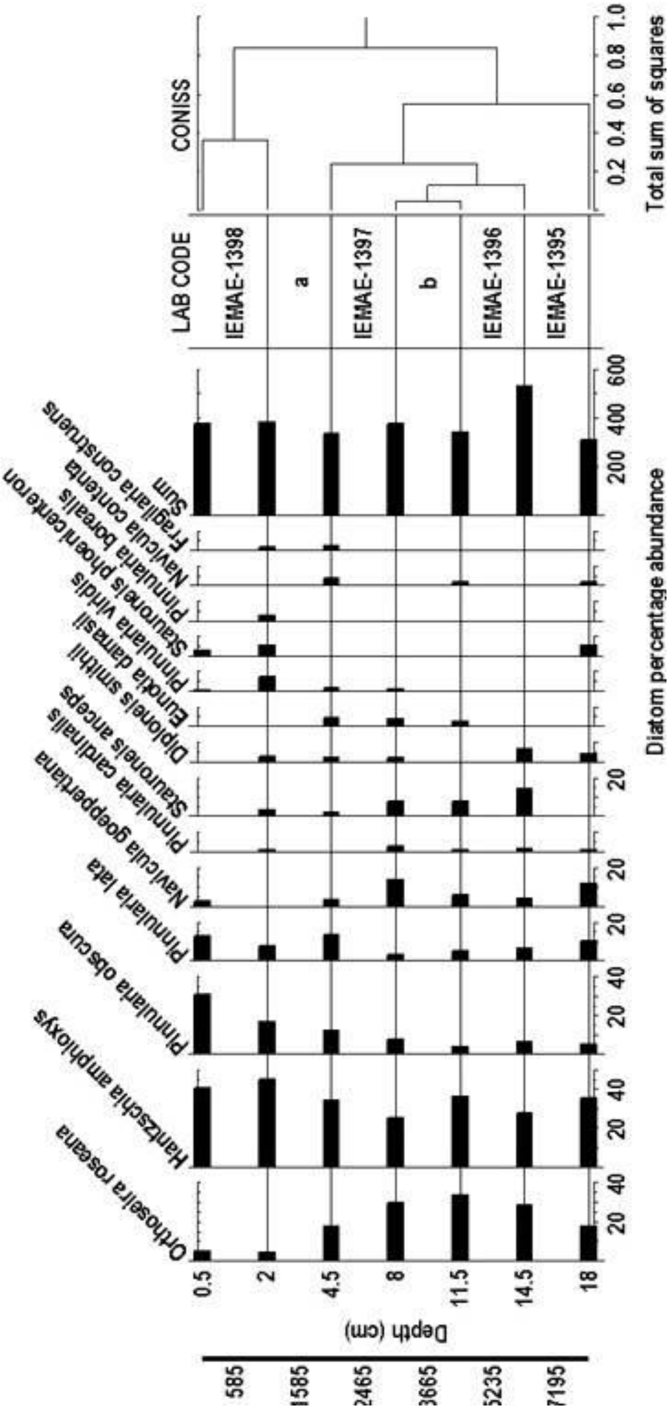

Fig. 2. Diatom diagram of the Konteh deposit.

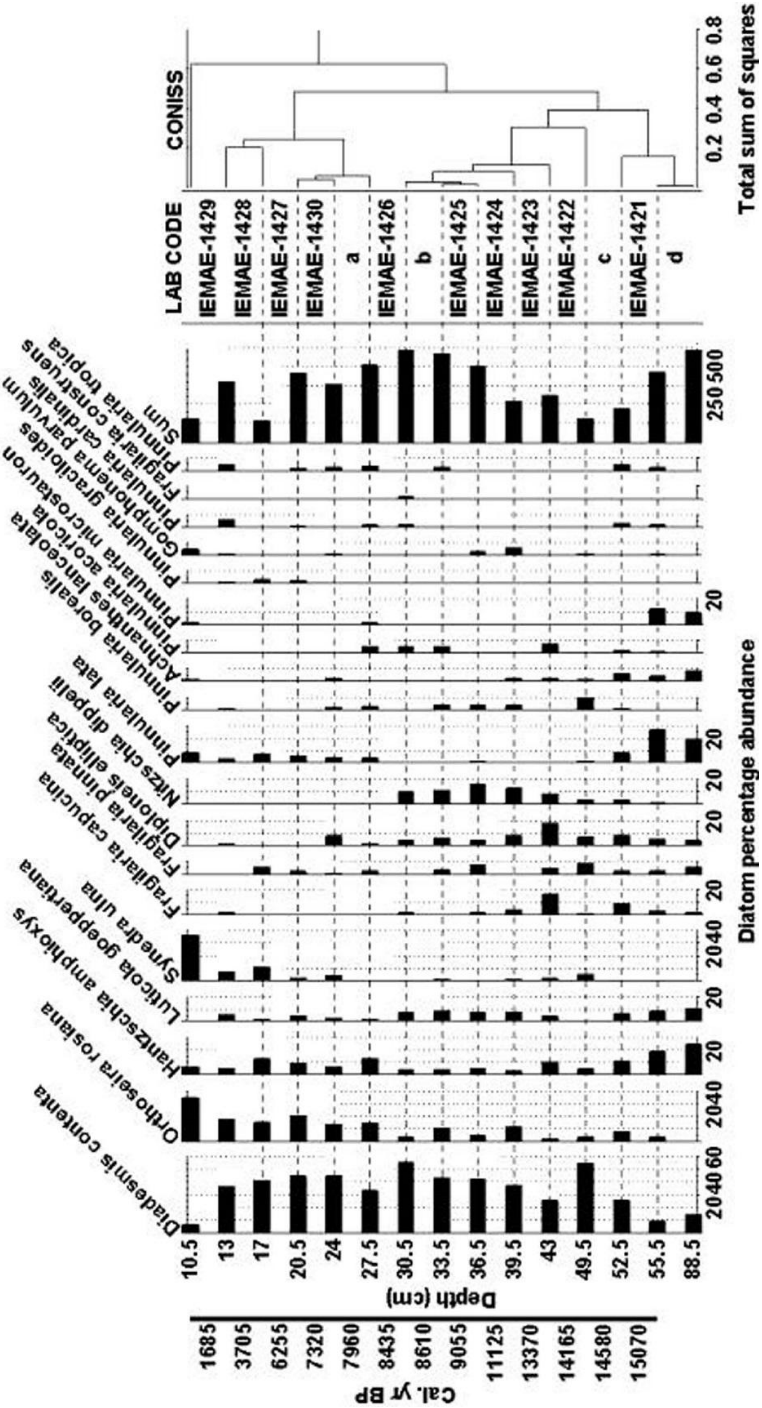

Fig. 3. Diatom diagram of the Fincha Habera deposit.

Pollen analysis

A total of 23 pollen and spore types were distinguished in samples from the Konteh deposit. There are five arboreal palynotypes (Ericaceae, *Hagenia abyssinica*, *Juniperus*, *Olea*, *Podocarpus*), 17 non-arboreal palynotypes and one fern spore (Polypodiaceae s.l.). Non-arboreal pollen prevails in the spectra (71–97%). Podocarp (*Podocarpus*) pollen is upmost among arboreal taxa, aster pollen (Asteroideae) (Asteraceae), prevails among non-arboreal taxa. Furthermore, Asteraceae is predominant in the pollen spectra of the Konteh deposit (20–70%). Total pollen concentration (TPC) varies from 10,000 to 2,941,000 pollen grains per gram. Two pollen zones (PZ) were defined in the deposit profile: PZ-1 (14–20 cm; 7,300–4,600 years BP) and PZ-2 (0–14 cm; 4,600 years BP - present).

Twenty two taxa were identified in spore-pollen spectra of the Fincha Habera deposit. Seven of them are trees and shrubs, 14 - herbaceous plants, and 1 - fern (Polypodiaceae s.l.). The pollen spectra are characterized by absolute predominance of non-arboreal pollen (for 88 to 99% of the defined pollen). The spectra are monodominant: pollen of grasses (Poaceae) amounts 50–92%. Asteroideae percentages range from 2 to 13%. The percentage of arboreal pollen ranges from 1 to 11%. *Podocarpus* prevails among tree pollen, its percentages varying from 0.2 to 3%. Pollen spectra of the lower stratum (86–96 cm) are poor and represented by three palynotypes (Asteroideae, Poaceae, and *Artemisia*). TPC in this stratum is 250,000–320,000 grains/cm^3. TPC in the upper stratum varied from 1,413,000 to 3,791,000 grains/cm^3. Five pollen zones (PZ) were distinguished in the upper profile: PZ-1 (48–57 cm; before 15,000 years BP), PZ-2 (35–48 cm; 15,000–10,000 years BP), PZ-3 (26–35 cm; 10,000–8,200 years BP), PZ-4 (15–26 cm; 8,200–5,000 years BP) and PZ-5 (15–10 cm; 5,000–1,500 years BP).

Spore-pollen spectra from the Katcha deposit are taxonomically richer in comparison to that of the Konteh and Fincha Habera. We identified 32 taxa, 10 of them are trees and shrubs palynotypes, 19 - herbaceous palynotypes, and three - spores of ferns and mosses. Likewise, the Katcha spore-pollen spectra are characterized by a predominance of non-arboreal palynotypes. Their percentage ranges from 44 to 80%. The percentage of arboreal pollen varies from 1 to 16%. The pollen spectra can also be described as monodominant - Poaceae pollen, accounted for 11–67% of all identified pollen. TPC varies from 92,200 to 497,000 grains/gram. Two pollen zones (PZ) were distinguished: PZ-1 (48–132 cm; 6,500–2,500 years BP) and PZ-

2 (0–45 cm; 2,500 years BP - present).

DISCUSSION

Diatom diversity and ecological state of the Bale Mountains during the Holocene based on diatom metrics

Ecology of the diatom species explains the character of encountered diatom groups. One of the most determinant factors of diatom distribution is moisture (availability of water). Based on their moisture requirement some diatoms are terrestrial (requiring relatively small amount of water) and some are aquatic living only in a water body. Some are yet capable of leading both life styles. Most species discovered in the Konteh and Fincha Habera deposit (such as *Diadesmis contenta*, *Orthoseira roseana*, *Hantzschia amphioxys*, and others), were found in caves and rock shelters (Poulíčková and Hašler, 2007). These are terrestrial diatom species that inhabit places with variable humidity, capable to withstand long periods of desiccation, so their dominance in the sediment spectra is not surprising. *Diadesmis* species are most often found in subareal habitats like mosses, as well as inhabit the extreme environments such as hot springs, rocks and caves. Predominance of *Diadesmis contenta* in the Fincha Habera diatom spectra is probably due to this evidence (Fig. 3). *Hantzschia amphioxys*, typical ubiquist, has a high tolerance to environmental conditions. Therefore, it is no wonder that this species is predominant in the Konteh deposit (Fig. 2).

However, diatom spectra recorded in the deposits are formed not only by species living in caves, but also by species that lived directly on the surface of the accumulating sediment (dung, pellets, hair, etc.). The spectra are also appended by planktonic species and fouling species that lead from hyrax and other animals dung. Herbivores might feed on plants, inhabiting by certain diatom species and, possibly, drink water from nearby water bodies. Hence, there is receipt of plankton and benthic species (*Nitzschia amphibia*, *Navicula gawaniensis*, *Stauroneis phoenicenteron* and others).

The Weyib valley diatom metrics show that the valley is characterized by alkaline pH; high saprobity; high trophic state and low oxygen content. Drought and wet periods alternated during some periods and currently the water quality of the region declined compared to earlier periods. The Weyib valley (as seen from diatom spectra of the Fincha Habera deposit) remained relatively arid from 15,000 to 8,610 years BP. A short humid period commenced at or about 8,435 years BP. This period lasted until 8000 years BP (Habte Debella, 2012). Some changes in the environment are evidenced by a decrease in diatom species diversity in the Fincha Habera deposit, which started about 8,000 years BP. The number of diatoms species gradually disappears from the spectra, and it attains minimum value in the top layer - only nine species (Fig. 3). We can assume that these changes were associated with the establishment of more severe environmental conditions. Perhaps the conditions deteriorated due to gradual climate aridization, when the water availability and prolonged desiccation became the main limiting factor (Johansen, 2004). Species that are less adapted to dry conditions have disappeared from the spectra. However, diatom moisture requirement shows that starting from ca. 2,500 years BP, the Weyib valley was experiencing a relatively humid period. In three cases of diatom metrics: saprobity, moisture and oxygen, there was a time when the most abundant species were disentangled from the Shannon's Diversity Index to be replaced by the new species that tended to adapt to a new change. Such saprobity change occurred between oligosaprobous state and α-meso/polysaprobous, which occurred between 3,700 and 1,600 years BP. During the same time span, moisture and oxygen requirements also changed. Oxygen requirements changed from high (about 100% saturation) to moderate (above 50% saturation). Moisture changed from drier to rather wet regime. These changes are direct indicators of changes on the Weyib valley between 3,700 and 1,600 years BP. Moisture requirements reversed from aerial species to more aquatic ones.

Samples from the Konteh zoogenic deposit was dominated by those species that mainly occur on wet and moist or temporarily dry places during the Holocene. In any case, these species do not withstand drought for a long time. Therefore, the Sanetti plateau was relatively wet during the past 7000 years with some fluctuations in moisture. Diatom species compositions are an assemblage of species from the surrounding landscapes and aquatic ecosystems by the animals, which lived there. Accordingly, the seven diatom metrics: pH, salinity, saprobity, trophic state, oxygen, moisture and nitrogen uptake metabolism unanimously became asynchronous at about 1,500 years BP. The plateau's diatom diversity and abundance remained stable until 1,600 years BP. The pH of the Sanetti plateau was between circumneutral and alkalobiontic from 7,000 to 2,500 years BP and showed a clear circumneutral pH from 2,500 years BP to the present time. The Sanetti plateau experienced more oxygenated systems after 2,500 years BP until now than before. This is because of the creation of new lakes such as the Lake Konteh and Micro-Lake, which were only swamps before this time as indicated by the diatom diagram (Habte Debella, 2012). This was confirmed by the appearance of the aquatic species (*Fragillaria construens*) in the samples dated as 2,500−1,500 years BP (Fig. 2). This climatic regime is a humid period of the Sanetti plateau. These lakes are shallow and wind-induced mixing allows more oxygen to enter into them than when they were swamps. Actually, there are a lot of palaeoecological studies that show the increase in humidity in the region occurred in this period (Messerli and Winiger, 1992; Mohammed and Bonnefille, 1998; Foerster *et al.*, 2012; etc.). Until about 1,500 years BP the Sanetti plateau shows β-mesosaprobous state. At about 600 years BP, however, the saprobic state shows the decrease (Habte Debella, 2012). That is, while some water bodies in the plateau are organically polluted, some are still unpolluted. The sources of organic pollution are obviously the increased human impact and natural organic pollution from the rodents and hyraxes' dung. Organic pollution can also be a result of flood driven soil and its organic components to the surrounding lakes and streams that continue decomposing in the aquatic ecosystem.

Interpretation features of pollen spectra from zoogenic deposits

The pollen spectra of investigated deposits are characterized by a pronounced monodominance. Predominant palynotype in the pollen spectra of the Fincha Habera and Katcha deposits is pollen of grasses (Poaceae). In the Konteh deposit pollen spectra prevails pollen of Asteraceae family (notably subfamily Asteroideae). Monodominant composition of pollen spectra is explained by dung origin of the deposits. The main component in all examined deposits is dung of herbivores. Predominance of a single palynotype is also down to the accessibility for herbivores of a particular vegetation type near by the rock shelters. Prevalence of Asteraceae in the Konteh pollen spectra is due to the vegetation structure of the Sanetti plateau. Cushion shrubs mainly belonging to *Helichrysum* (Asteraceae) are the most prominent constituents of Afroalpine plant communities of Sanetti plateau and represent the major part of rock hyrax's diet in the vicinities of Konteh niche especially in the dry season. The pollen spectra of the Fincha Habera and Katcha deposits are characterized by predominance of the Poaceae pollen. These rock niches are located below the Konteh niche (3500 m a.s.l. (Fincha Habera) and 2700 m a.s.l. (Katcha). Most likely, the availability of grasses (Poaceae) as a food item has always been sufficient, so herbivores do not have to look for any other food. Therefore, when we analyze the pollen spectra of zoogenic deposit we should propose the presence of a particular feed in specific plant communities, rather than the food preferences of animals whose faeces deposit is formed.

Another way of pollen sedimentation, so-called "pollen rain", should also be taken into account in the analysis of zoogenic deposits. Pollen rain mostly reflects regional vegetation unlike pollen from faeces in zoogenic deposits which characterizes generally local vegetation. Thus, it can be difficult to trace the dynamics of the palynotypes reflecting the regional vegetation as there is often complete dominance of one palynotype (in our case, Asteraceae and Poacaeae) in pollen diagrams showing percentage abundances of the plant taxa. Therefore, pollen percentages may not be reliable for reconstruction of regional vegetation and climate. Study of pollen spectra from Azykh Cave (south-eastern foothills of the Karabakh Range, Caucasus) demonstrates that not only taxa which pollen is dominant in the spectra are informative in the context of the palaeoclimatic reconstructions but also taxa which pollen is marked by individual pollen grains (Zelikson and Gubonina, 1985). Therefore, it is necessary to use method of pollen concentration counting. In our research we increasingly use pollen concentration diagrams for the environmental reconstructions but percentage diagrams are also useful for data specification.

Vegetation and climate history of the Bale Mountains

The age of bottom layers of the Fincha Habera deposit could not be determined. It is obvious that the age of these layers predates 15,000 years BP. The composition of pollen spectra of the lowest layers suggests the existence of high-mountainous desert-like grassland which was dominated by grasses (Poaceae), asters (Asteraceae), pigweeds and/or amaranths (Chenopodiaceae/Amaranthaceae) species at altitudes of about 3000 m a.s.l. Such spectra indicate the cold and dry climate in the highlands, which was typical for the Last Glacial Maximum (LGM). The same palynological data recorded in other deposits of the studied region (Hamilton, 1982; Umer *et al.*, 2007). Numerous palaeoecological researches conducted in different parts of African continent show that the end of Pleistocene epoch was characterized by cold and arid climate. Mountain peaks reached 4000 m a.s.l., and more, were covered by ice caps (Messerli *et al.*, 1977; Messerli and Winiger, 1992; Umer *et al.*, 2004; Osmaston *et al.*, 2005). The glaciation in the Bale Mountains was the most extensive among all mountain ranges of Ethiopia (at least 600 km^2 with the snowline at about 3700 m a.s.l.). Also relatively high concentration of juniper pollen (*Juniperus*) points to dry and cold conditions indicating the widespread dry conifer forests in the lower mountain belt. *Juniperus* occupies drier habitats than *Podocarpus* (Hamilton, 1982), so juniper forests are the driest type of mountain forests in these areas (Uhlig, 1988). The absence or low concentration of other arboreal palynotypes indicates that the mountain forest vegetation occupied a much smaller area than the present, and was located at the lower altitudes.

Noticeable changes in the vegetation structure of the Bale Mountains occurred at about 15,000 years BP. *Juniperus* has dropped from the pollen spectra hence its presence in mountain forest structure has declined. Juniper forests were replaced by forests with *Podocarpus* indicating more humid forest type. At the same time there are new herbaceous palynotypes in the spectra (Apiaceae, Caryophyllaceae, and Fabaceae) (Fig. 4A). These changes suggest a noticeable warming and humidification in the region in response to which vegetation was enriched with new taxa and vegetation cover has become more closed. Numerous studies carried out in North and East Africa have also shown that the period of significant humidification and warming began ~15,000−14,500 years BP (deMenocal *et al*., 2000; Ivory *et al*., 2012; Otto-Bliesner *et al*., 2014; etc.). The pluvial period which began at this time is known as "African Humid Period" (AHP). It was the most outstanding episode in the palaeoenvironmental history of Africa. The onset and termination of the AHP marks the most dramatic changes in the climate of the past 20,000 years.

The AHP has been attributed to a strengthening of the African monsoon and northward shift of the Intertropical Convergence Zone (ITCZ) due to gradual orbital increases in summer season insolation (deMenocal *et al*., 2000; Timm *et al*., 2010). It caused noticeable increase in African lake levels (Gasse, 2000; Prentice *et al*., 2000; Barker *et al*., 2004; Foerster *et al*., 2012; Gebru *et al*., 2013; Junginger *et al*., 2014) and the "greening" of Sahara and Sahel (Kuper and Kröpelin, 2006; Kröpelin *et al*., 2008; deMenocal and Tierney, 2012).

The AHP was interrupted by dry and cold event as reflected in the significant accumulation rate decline of the Fincha Habera deposit at about 13,000−12,500 years BP (Kuzmicheva *et al*., 2013). Cooling and drying were abrupt and severe, and it was noted throughout the African continent north of 10°S (deMenocal *et al*., 2000; Tierney *et al*., 2011; Foerster *et al*., 2012; Ivory *et al*., 2012). This event coincided with the final stage of the last glaciation in the Northern Hemisphere, and it is known as the Younger Dryas (Huntley and Webb III, 1988). At the same time there is an increase in *Artemisia* concentration and simultaneous decrease in *Podocarpus* concentration in the pollen spectra of the Fincha Habera deposit (Fig. 4A). These changes point out lowering of the timber-line and spread of xeromorphic cold-tolerant plant communities of grasses, sagebrush (*Artemisia*) and Asteraceae (especially *Helichrysum* species) in the highlands. Pollen analyses of cores taken from Garba Guracha Lake also located in the Bale Mountains and from Badda peatbog in the Arsi Mountains close to the Bale show the similar changes in the pollen spectra indicating the unfavorable conditions of the Younger Dryas (Hamilton, 1982; Umer *et al*., 2007). The Younger Dryas has been reflected in numerous palaeoecological records across East Africa. Significant regression of the Rift Valley lakes has been registered at 12,500–10,000 years BP, for example, Ziway-Shala basin (Gillespie *et al*., 1983), Lake Tanganyika (Gasse *et al*., 1989), Lake Victoria (Stager and Johnson, 2000). Pollen data from Lake Malawi suggest the opening of the lowland vegetation and replacement of drought-intolerant tropical seasonal forest by grassland and woodland at 12,300 years BP (Ivory *et al*., 2012). Rapid shift towards arid conditions is indicated by increased K (potassium) values around 12,800 years BP which has been registered in the Chew Bahir basin (Foerster *et al*., 2012).

Numerous researches point out the Younger Dryas lasted for 1000–2000 years (Carlson, 2013). The dates of the Younger Dryas termination and the AHP resumption vary in the different studies on African climate history. The palaeoclimatic data from the Chew Bahir basin indicate the return to the wet conditions around 11,800–11,600 years BP (Foerster *et al*., 2012). Kilimanjaro ice cores investigation has shown that the Younger Dryas ended at 11,700–11,600 years BP that was reflected in the intensification of ice accumulation (Thompson *et al*., 2002). Other studies show that the AHP continuation had taken place between 10,000 and 9,000 years BP in the Sahel region and during the 9,000–6,000 years BP for Western Saharan region (Hély *et al*., 2009). Low resolution of the Fincha Habera deposit does not permit the timing of this event to be defined more precisely.

According to available data from the Fincha Habera deposit, the end of the Younger Dryas and the AHP continuation is registered at about 10,000 years BP. There is increase in *Podocarpus*, Poaceae, Apiaceae and Ericaceae concentration and disappearance of *Artemisia* pollen (Fig. 4A). Such changes in pollen spectra suggest about upward shift of the tree line and widespread ericaceous vegetation to the maximum altitude (above 4000 m a.s.l.). Herbaceous vegetation of the highlands has become more mesophytic. The same trend is observed in the pollen spectra of Garba Guracha Lake. There is also increase in the tree pollen at the time (about 10,000 years BP), which also shows a wider distribution of forest communities (Umer *et al*., 2007).

The increased precipitation during the first half of the Holocene was reflected both in the composition of pollen spectra (see above), and in the raised accumulation rate of the Fincha Habera deposit (see Kuzmicheva *et al*., 2013). This phenomenon could be caused by an increase in the number of animals inhabiting in the area and visiting the cave, in response to the development of the dense vegetation, increase the availability of food resources in the highlands. The beginning of the Holocene was very humid and warm according to many palaeoenvironmental records throughout the Africa and the Northern Hemisphere on the whole. Thus, study of palaeoshorelines of the Lake Turkana shows the prolonged period of high stand lasted from 11,500 to 8,500 years BP (Garcin *et al*., 2012). This study suggests that there was water, presumably river, connection between Turkana Lake and the Nile Basin during the early Holocene. Studies in the environmental history of the Sahara also indicate the wet conditions at the time. For example, pollen evidences suggest that the areas currently occupied by the Sahara Desert, in the early Holocene have turned into open grassy savannah with scattered groups of trees and shrubs, similar to those that exist today in the area located a few hundred kilometers south of the Sahara (Nicholson and Flohn, 1980; Jolly *et al*., 1998;. Kuper and Kröpelin, 2006; Kröpelin *et al*., 2008; deMenocal and Tierney, 2012).

While the early and middle Holocene was characterized by humid conditions of the AHP, it was interrupted by several arid episodes. The most notable dry event took place around 8,200 years BP. *Juniperus* pollen reappeared in the Fincha Habera deposit at the time, indicating the re-development of the juniper dry mountain forests on the northern macroslope of the Bale Mountains. Decrease in *Podocarpus* pollen suggests about replacement of *Podocarpus* with *Juniperus* in mountain forest structure. However, these changes were probably of short duration, as evidenced by the subsequent disappearance of juniper pollen. These data are consistent with pollen records from other areas of East Africa and Sahara (Thompson *et al*., 2002; Adkins *et al*., 2006; Garcin *et al*., 2012). Pollen data from the Takarkori rock shelter (Central Sahara, Libya) indicate a decrease in the water availability at about 8,200 years BP (Cremaschi *et al*., 2014). Sedimentation rate of the Fincha Habera deposit slightly decreased at 8,200 years BP, but was still relatively high (Kuzmicheva *et al*., 2013).

In the period 8,200–5,000 years BP there are changes in the pollen spectra of the Fincha Habera indicating the shift to more xerophilous vegetation. Gradual substitution of *Podocarpus* to *Juniperus* occurred in composition of tree vegetation, and *Artemisia* appeared again simultaneously with decrease of less drought-resistant species (Apiaceae, Fabaceae) in composition of herbaceous vegetation around 6,200 years BP. Decreasing total pollen concentration could be suggestive of more sparse vegetation cover (Fig. 4A). However, a variety of other palaeoecological studies testifies quite humid climate in Africa during this period. The climatic optimum occurred between 8,200–5,000 years BP (Messerli and Winiger, 1992; Miehe and Miehe, 1994; Umer *et al*., 2007). The Sahara areas have reduced to insignificant scale in comparison with the current state (Nicholson and Flohn, 1980). The sedimentation rate of deposit in the Takarkori rock shelter (Libya) between 8,180 and 5,610 years BP increased in response to the acceleration of livestock visits to the cave due to availability of water resources around the rock niche and, as a consequence, the development of plant communities, suitable for active grazing (steppe and/or savannah) (Cremaschi *et al*., 2014). Studies conducted in the Bale Mountains likewise suggest that the climate at the mid-Holocene was quite moist. This is evidenced by the vast extension of mountain forest registered by the increase in arboreal pollen in the pollen spectra from the Garba Guracha Lake (Umer *et al*., 2007). However, the first signs of climate aridity in the Garba Guracha was recorded about 6,000 years BP. The percentage of xerophilous arboreal taxa - *Podocarpus* and, mostly, *Juniperus* - increased in response to rainfall reduction (Umer *et al*., 2007). Gradual drop in hygrophilous palynotypes with simultaneous increase in dry forest pollen (*Podocarpus*, *Juniperus*, and *Olea*) is also observed in the Badda swamp (Hamilton, 1982).

Pollen data from the Konteh zoogenic deposit, located directly on the Sanetti Plateau (4110 m a.s.l.) indicate a sufficiently humid climate at the mid-Holocene. Poaceae pollen dominates at the bottom of the sediment formed between 7,300−4,600 years BP (Fig. 4B). Perhaps, grasses composed large portion in vegetation of the Sanetti Plateau and/or their growing period was longer. Therefore, an availability of grasses for hyraxes, from whose dung the Konteh deposit consists, was slightly higher than at present as a food object. The predominance of Poaceae during the mid-Holocene indicates warm and humid conditions prevailing during the AHP. However, low pollen and spores concentration in the samples from the bottom of the Konteh deposit as well as the percentage prevalence of uncertain pollen does not permit to reconstruct complete palaeoecological history of the Sanetti Plateau. Probably over-humidity during the AHP did not supply the preservation of pollen and spores properly, resulting in the destruction of most of the pollen and spores and the "smudge" of the pollen spectra.

At the same time, vegetation recorded on the southern macroslope of the Bale Mountains at 2700 m a.s.l., where the Katcha rock shelter is located, also indicates wet climate conditions. The sedimentation in the Katcha niche began around 6,500 years BP. Non-arboreal pollen is dominated in the pollen spectra between 6,500 and 5,000 years BP, especially Poaceae, Rosaceae and Cyperaceae (Fig. 4C). It may indicate the absolute dominance of the bamboo thickets at the altitude (2700 m) in this time that may testify intense humidification of the southern slopes of the Bale Mountains at the mid-Holocene. However, there is no difference between the bamboo pollen and other Poaceae, as well as the inability to trace the dynamics of bamboo flowering in the pollen spectra of the deposit does not make sure in this assumption. Nevertheless, high concentration of Cyperaceae pollen is also evidence of high moisture availability during this period. All of this points to the presence of the AHP wet conditions in the Bale Mountains southern slopes.

According to the palaeocological data, the AHP ended about 5000 years BP (Adkins *et al.*, 2006; Berke *et al.*, 2012; Foerster *et al.*, 2012; Gebru *et al.*, 2013). But certain dating of the AHP end still remains a subject of research dispute. Ongoing studies, even in the same region, often produce inconsistent results. Many investigations point out that the end of the AHP was extended in time and/or did not happen at the same time in different regions of Africa (Kröpelin *et al.*, 2008; Junginger, 2011; Cremaschi *et al.*, 2014). Climate change could variously affect the objects currently used for the vegetation and climate reconstructions because of the orographic matter, taphonomic features, etc.

Vegetation changes of the Sanetti Plateau that appeared in the pollen spectra of the Konteh zoogenic deposit specify the AHP termination time. According to our data, the end of the humid phase and the beginning of aridity took place 4,600 years BP. The predominance of Asteraceae and appearance of Chenopodiaceae/Amaranthaceae indicates change in the vegetation of the Sanetti Plateau to more drought-resistance plant communities with prevalence pulvinate Asteraceae shrubs. There is also a trend of gradually increasing pollen concentration of juniper, which indicates the beginning of the expansion of dry mountain juniper forests on the northern slopes of the Bale Mountains (Fig. 4B). The same tendency of increase in the percentage of juniper pollen about 4,500 years BP is observed in the pollen spectra in the Garba Guracha Lake sediment (Umer *et al*., 2007). Some palaeoenvironmental research in East Africa gives evidence of this AHP termination data, for example, there is a precipitous drop in Lake Turkana (Kenya) level by 4,600 years BP (Forman *et al*., 2014).

Vegetation changes on the southern slopes at 2700 m a.s.l. (Katcha deposit) showing a decrease in moisture availability are also observed at 4,600 years BP. In response to the beginning of climate aridity Cyperaceae fall out from pollen spectra of the Katcha deposit, concentration of Poaceae and Polypodiaceae sharply decreases. Arboreal part of the spectra also undergoes some changes: for example, *Celtis*-type appears in significant concentration (Fig. 4C). Similar pattern (peak of *Celtis*-type pollen at about 4,500-3,000 years BP) is observed in the pollen spectra from the lacustrine deposit of Makoma Lake (Uganda), located at 2960 m a.s.l. (Livingstone, 1967; Hamilton, 1982). Currently, *Celtis* species inhabit Harenna forest communities at significantly lower altitudes of 1600−1900 m a.s.l., where they form a dense evergreen forest with *Podocarpus*. Probably around 4,600 years BP bamboo thickets became more sparse, and *Celtis*, which is considered a tree species, with the fastest colonizing open areas in the forest (gaps, clearing, felling) (Gunton *et al*., 2010), invaded all suitable habitats in these altitudes (about 2700 m a.s.l.). Perhaps the transition from the humid conditions of the AHP to the arid climate was smoother on the southern slopes, and Harenna vegetation communities responded to this gradually due to the location of the Bale Mountains southern macroslope, and more continuous rainfall throughout the year. Similar conditions registered in some other regions of the African continent. For example, the same gradual trend of aridization was shown in the study of lacustrine sediments of Lake Yoa (Chad) during the 5,000-3,000 years BP (Kröpelin *et al*., 2008).

Particular attention should be given to the age-depth models of the deposits (Kuzmicheva *et al*., 2013; Kuzmicheva, 2015). The Konteh deposit accumulated evenly and very slowly. There are no changes in the sediment accumulation rate probably due to the fact that this deposit has very small thickness (20 cm), and the accumulation time is more than 7,000 years (Kuzmicheva *et al*., 2014). As the result of low resolution, it is not possible to trace the sedimentation dynamics of the Konteh deposit. In contrast, decrease in sedimentation rate of the Fincha Habera deposit was observed around 5,000 years BP. The age-depth model of the Katcha zoogenic deposit shows a rather abrupt decrease in the growth rate 4,600 years BP, indicating that the changes occurred in the environment conditions. As in the case with the Fincha Habera, the deceleration of the growth rate of the deposits indicates the aridity in the region. Changes in the sedimentation rates of examined deposits together with pollen data from these deposits enable more accurate estimation of the time of AHP end and the beginning of the aridity in the Bale Mountains.

Significant changes in the vegetation near the Katcha rock shelter are registered in the pollen spectra about 2,500 years BP. There is severe increase in olive, podocarp and *Hagenia* pollen, as well as disappearance of *Celtis*-type (Fig. 4C). Such alterations testify to the vast extension of dry forests and falling out of some other arboreal species (eg, *Celtis*) from the vegetation. Sharp increase of Ericaceae pollen takes place simultaneously. It may indicate stepped-up pace of climate aridity. Maximum concentration of Chenopodiaceae/Amaranthaceae pollen and increase in concentration of *Artemisia* also testify strong aridity. The same changes are observed in the pollen spectra from peat and lake sediments found on Mount Elgon (Kenya) (Hamilton, 1982). At this time *Podocarpus* pollen concentration also increased, and pollen concentration of some arboreal species (*Rapanea*, *Macaranga*) begins to drop out (Hamilton, 1982). All these changes indicate a strengthening aridization trend during the last 2,500 years. Some lake records from Eastern Africa suggest that the region experienced an episode of pronounced aridity around 2,000 years BP, possibly the driest period of the middle-late Holocene (Verschuren and Charman, 2008; Nash *et al.*, 2016).

Climate aridity intensifying over the last 4,600 years BP was interrupted by short relatively humid period 2,000−1,000 years BP, as evidenced by changes registered in the pollen spectra from the Bale Mountains. There is increase in pollen of moisture-loving species (Apiaceae, Brassicaceae, Liliaceae s.l.) in the Konteh pollen spectra (Fig. 4B). Such changes may indicate an increase in vegetation diversity of the Sanetti plateau and more density of sward in that period, and therefore the availability of various food items for herbivores become significantly higher than ever before. These alterations give evidence of more humid climatic condition during this period. The upper layer of the Fincha Habera deposit is 1,500 years old as evidenced by its radiocarbon calibrated dates (Table 2). Probably sedimentation in the Fincha Habera rock niche terminated at this time, and the surface of the deposit was not buried under new layers. However, most likely, the erosion of the upper part of the deposit took place in the niche, whereby the upper layers could completely disappear. Despite the absence of the top deposit, pollen data from the remaining upper layers can provide some further information about climatic trend during the last two thousand years. Thus, disappearance of *Juniperus* pollen was observed in the two upper layers of the Fincha Habera deposit (Fig. 4A). That may indicate a dropping out of juniper from the forest cover of the northern macroslope of the Bale Mountains in response to climate humidification during this period.

Noticeable humidification in the region, interrupting the main trend of aridity, was also registered in the palaeoecological records from the Rift Valley lakes, and from other regions. However, they did not take place simultaneously. Thus, the period of high standing water for the Ziway-Shala lake basin (Ethiopia) dated 2510±100 years BP (Gillespie *et al*., 1983). Pollen data from Lake Abiyata (also Ziway-Shala basin) as well as pollen and isotope data from Lake Turkana (Kenya) indicate the relatively wet period 1,700−1,600 years BP (Bonnefille *et al*., 1986; Mohammed *et al*., 1996). Palaeoshorelines data from Lake Bosumtvi (Ghana) suggest the wet period lasted from 2200±100 to 1700±200 years BP (Shanahan *et al*., 2006). The authors point out that although the level of the shorelines suggests the relative humidification of climate in this period, it is much lower than the levels at the early- and mid-Holocene.

A similar pattern is observed on the southern macroslope of the Bale Mountains. There is increase in Apiaceae and Fabaceae pollen about 1,500 years BP indicating certain climate humidification. *Syzygium* pollen concentration increases around 1,500−1,000 years BP (Fig. 4C). *Syzygium* species currently inhabits in the Harenna forest significantly lower - at altitudes from 1700 m to 2200 m a.s.l. During the climate humidification period which lasted from about 1,500 to 1,000 years BP it could climb up the slopes and gain a foothold in a locally more moisture habitats. According to published data and our results, this period ended about 1,000 years BP (Messerli and Winiger, 1992; Mohammed and Bonnefille, 1998; Foerster *et al*., 2012; Kuzmicheva *et al*., 2014; Kuzmicheva, 2015), as evidenced by a decrease in moisture-loving taxa in the pollen spectra of the Konteh and Katcha zoogenic deposits.

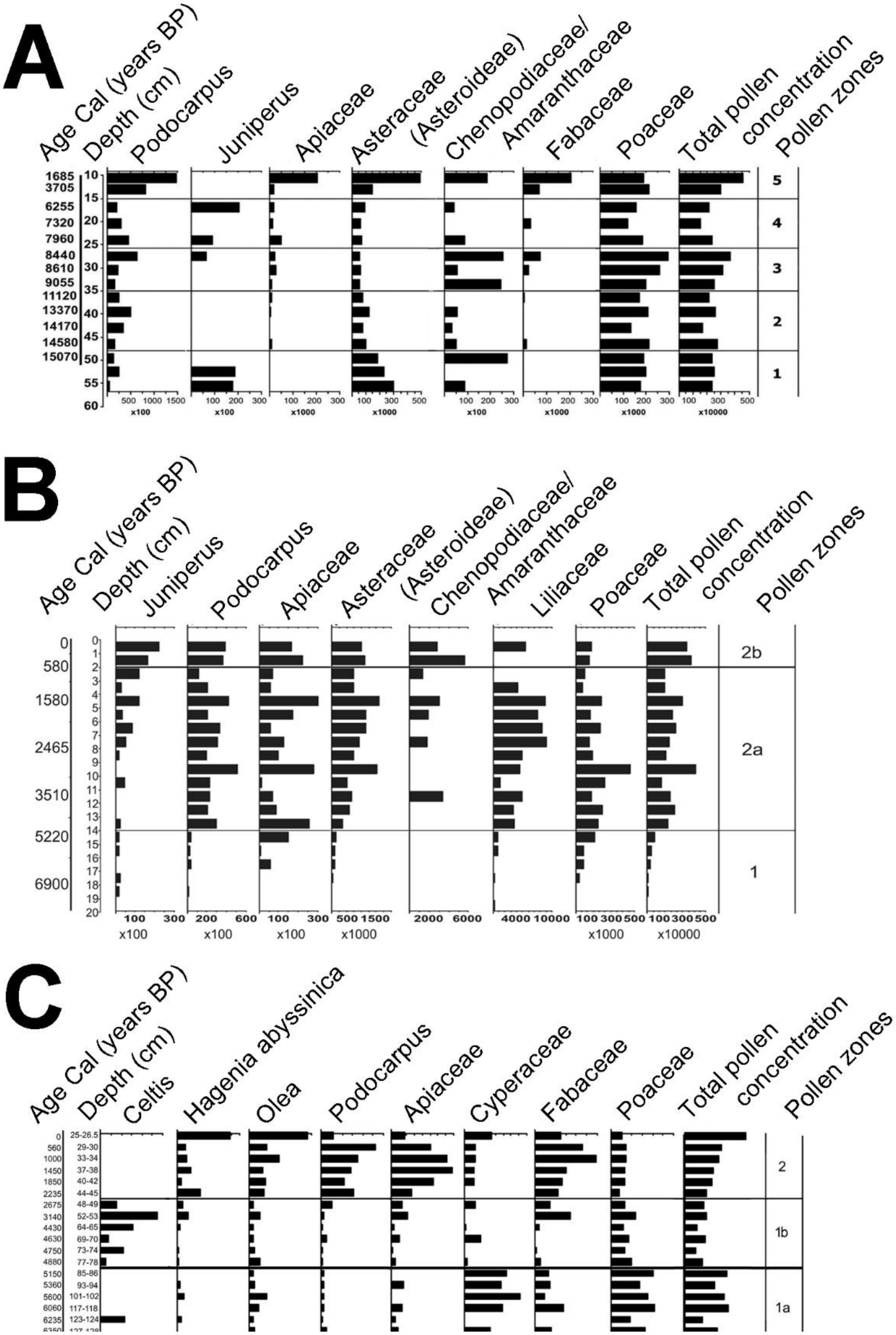

Fig. 4. Pollen concentration diagram of the most significant palynotypes (A - Fincha Habera deposit; B - Konteh deposit; C - Katcha deposit).

Human impact on ecosystems of the Bale Mountains

Pollen evidences

The influence of humans on ecosystems of the Bale Mountains is worthy of special consideration. Initial appearance of humans in the Bale Mountains highlands was registered at about 7,000 years BP, when charcoals were found in investigated zoogenic deposits. The trace of significant human activities such as deforestation was registered about 2,000 years BP (Hamilton, 1982; Umer *et al*., 2007). There is sharp decrease in *Podocarpus* and Ericaceae pollen in the surface sample of the Katcha zoogenic deposit along with simultaneous increase in *Hagenia* pollen (Kuzmicheva, 2015). Clearance in the evergreen montane forests causes widespread replacement felled tree species specific to the forest belt (*Podocarpus*), to the pioneer species that form secondary forests and are most often anemophilous (*Hagenia*) (Bonnefille *et al*., 1993). The upper layers of the Tamsaa peat (1300 BP - present), located on the northern macroslope of the Bale Mountains, are also characterized by decrease in *Podocarpus* pollen, while pollen *Juniperus*, *Hagenia abyssinica* and *Dodonaea viscosa* reaches its maximum (Mohammed and Bonnefille, 1998). Decrease in *Podocarpus* pollen reflects the decline in the share of its participation in the vegetation as a result of selective cutting by humans.

Plantain pollen (*Plantago* sp.), which appeared in the Tamsaa peat about 2,000 years BP (Mohammed and Bonnefille, 1998), also suggests pronounced anthropogenic load on the vegetation at altitudes from 3000 to 3500 m a.s.l., since plantain pollen is one of the main indicators of human activity, such as pasturing (Behre, 1981; Miehe and Miehe, 1994). This is also evidenced by the appearance of Urticaceae pollen in the two upper layers of the Fincha Habera deposit (Kuzmicheva *et al*., 2013). Anthropogenic pressure directly on the Afroalpine vegetation (~4000 m a.s.l. (Sanetti Plateau)) increased about 600 years BP, as evidenced by changes in the pollen spectra of the Konteh deposit. There is increase in nettle pollen as well as uprise of plantain pollen. Urticaceae pollen grains were found throughout the sediment profile (Kuzmicheva *et al*., 2014). Nettle species is pronounced nitrophilous, so its permanent presence in the pollen spectra of the zoogenic deposit is not surprising. Specimens of *Urtica simensis* were observed near the entrance to almost each cave and rock niche in the Bale Mountains. However, the sharp increase of nettle pollen in the spectra of the top layers of Konteh deposit testifies to the active development of cattle breeding in this period. The appearance of plantain pollen indicates the presence of open pasture stumbled ground (Behre, 1981), and increase of Urticaceae pollen could occur as a result of origin of new suitable habitats for nettle due to the creation of a quantity of forages. Thus, agricultural activity, in particular, grazing and use of Afroalpine vegetation as pastures began at about 600 years BP.

Time of showing of anthropogenic indicators in high concentration coincides with a few historical data about these areas. Bale Mountains at this particular time (during XIV-XVI centuries) were at the center of the resettlement of the Eastern African Oromo tribes who were pastoralists (Bartnitsky and Mantel-Nechko, 1976).

The same trend is noted in the pollen spectra of Katcha zoogenic deposit. For instance, nettle pollen grains are observed over the entire sediment profile, and significant increase in its concentration is about 1,000 years BP. During one thousand years the concentration of nettle is equally high, and it is increased by several times in the surface layer indicating the most active agricultural use of Harenna forest area as pastoral lands at the present time. This is also evidenced by abrupt increase of *Plantago* pollen in the uppermost sample of the Katcha deposit. Features of the agricultural activity on the southern slopes with more favorable environmental conditions appeared a little earlier than on the northern slopes - about 1,000 years BP, but it is observed most heavily at the recent years.

It should be noted that nettle pollen grains were not recorded in the pollen spectra of lake deposits and peatbogs, studied in the Bale Mountains, and in other East African areas (Bonnefille and Mohammed, 1994; Mohammed and Bonnefille, 1998; Umer *et al.*, 2007). The simultaneous increase of Urticaceae and *Plantago* pollen testifying agricultural practices, particularly livestock grazing, is marked only in zoogenic deposits which we have examined. It demonstrates that the zoogenic deposits are largely unique and essential for the reconstruction of the centuries-old dynamics of climate and vegetation, and anthropogenic impact, especially in such areas.

Diatom evidences

The Sanetti plateau favored a continuous circumneutral pH throughout the Holocene as can be seen from samples from Konteh zoogenic deposit (Habte Debella, 2012). Changes came at about ca. 1,600−1,500 years BP. Alkalophilous species disappeared at 1,500 years BP, while during the same time an acidophilus species started emerging and flourishing. It is evident that the Sanetti plateau’s aquatic ecosystem is decreasing in pH even though the change is conservative due to the buffering capacity of dissolved volcanic ashes in the form of carbonates. Such changes in aquatic pH are associated with changes in terrestrial environments. Deforestation and overgrazing cause decrease in pH and increase in acidity in temperate regions (Feller, 2009). However, in tropical alpine environments such studies are scarce. Deforestation and overgrazing have all the effect of reducing pH and hence are signs of anthropogenic impact.

Gomphonema parvulum is one of the most pollution-tolerant diatom species (Lobo and Kobayasi, 1990). Its occurrence in the upper layers of the Fincha Habera deposit indicates rise in saprobity, trophic state and deterioration of water quality in the valley, which was also confirmed by diatom metrics (Habte Debella, 2012). Other factors being constant during this time, it is apparent that anthropogenic impact has come into picture. It seems that humans inhabited the Weyib valley much before the Sanetti plateau. Clear anthropogenic impact at the Sanetti plateau has not come into picture until about 1,600−1,500 years BP, while diatom proxies push the appearance of anthropogenic signatures to as far back as 2,500−2,000 years BP.

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