Mem. Natl Inst. Polar Res., Spec. Issue, 44, 247–253, 1986

SUBANTARCTIC ELEMENTS OF THE BRYOPHYTES IN EAST AFRICAN HIGHLANDS

Tarow SEKI

Miyajima Natural Botanical Garden, Faculty of Science, Hiroshima University, Murohama, Miyajima-cho, Saiki-gun, Hiroshima 739–05

Abstract: Disjunctive distribution of some bryophytes between East African Highlands and the subantarctic region are discussed. The subantarctic bryophytes in East African Highlands can be classified into three groups: Group 1 includes species growing on wet rocks in periglacial environment of the Afroalpine region such as *Andreaea subulata, Bryum ellipsifolium* and *Rhacocarpus purpurascens*; Group 2 includes those growing on trunks and rocks of forests in the Afromontane region such as *Clasmatocolea vermicularis, Catagonium nitens* and *Dicranoloma billardieri*; Group 3 is represented by *Aongstroemia julacea* on bare land of the Afroalpine region. The bryophytes of Groups 1 and 2 seem to be old elements which have been originated from the Gondwanaland. Group 1 seems to have been diffused from the region of Group 2 after the last glaciation. Group 2 has been restricted in the Afromontane forest since the Late Cretaceous. Group 3 is considered to have been newly distributed after the last glaciation because it is found in young volcanoes erupted in the Quaternary. The ice-age aridity in Africa affected the distribution of bryophytes severely. The Afromontane forests in the inselbergs of East Africa seem to have played an important role as refugia for Groups 1 and 2 during the glacial age.

1. Introduction

This article deals with the disjunctive distribution of some bryophytes between East African Highlands and the subantarctic region based on the author's actual field surveys in West Patagonia (1967), southeastern Australia and Tasmania (1981) and Kenya (1983–84). Here the subantarctic region is assigned to the area wider than that in usual sense, including southern South America, Subantarctic islands, South Africa, Tasmania, southeastern Australia, southern New Zealand, in some cases New Guinean Highlands, north Andes and Central American Highlands.

The definition of the following terms follows PIELOU (1979): disjunction, jump-dispersal, diffusion, secular migration and spread.

2. Historical Recognition of the Subantarctic Bryophytes in East African Highlands

HERZOG (1926) did not clearly mention any subantarctic bryophytes in the chapter, "Tropische-afrikanische Hochgebirge" in his book, "Geographie der Moose". At that time, bryological surveys in Africa and the subantarctic region were insufficient, and also taxonomical understanding of bryophyte species was incomplete. For example, ***Bryum***

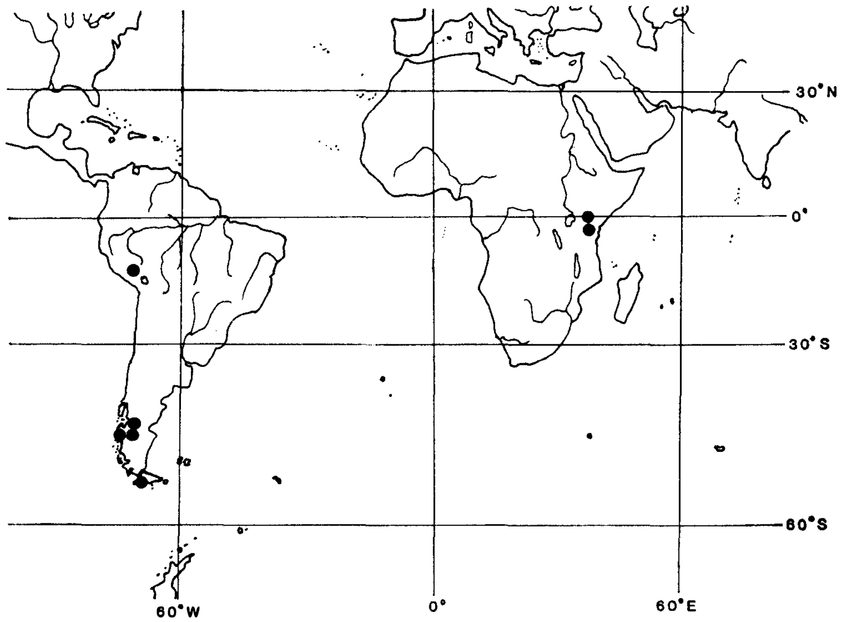

Fig. 1. Distribution of Bryum ellipsifolium *C. MUELL. Source: MÜLLER (1890), DUSÉN (1905), POTIER DE LA VARDE (1955), SEKI (1974), BIZOT et al. (1978) and HEGEWALD and HEGEWALD (1985).*

ellipsifolium C. MUELL., which is now known as a typical subantarctic element in East African Highlands, was already described by MÜLLER (1890) from Kilimanjaro based on the collection by H. MEYER in 1889, but it was not known that *B. ellipsifolium* is conspecific with *B. myurella* DUSÉN, which was described from Tierra del Fuego by DUSÉN (1905), until the taxonomical revision of African Bryoideae by OCHI (1972) and the recent range extension to Peru by HEGEWALD and HEGEWALD (1985) (Fig. 1).

After the Second World War, information has been gradually accumulated for the bryophyte flora of Africa and the subantarctic region. POTIER DE LA VARDE (1955) reported *Andreaea subulata* as a new addition to the moss flora of Africa based on the collection by O. HEDBERG from Ruwenzori in 1948. Taxonomical study of this species was done in detail by SCHULTZE-MOTEL (1970) and its disjunctive distribution between East African Highlands and the subantarctic region became clear. GROLLE (1969) showed a map of *Clasmatocolea vermicularis*, but at that time the occurrence of this species in East Africa was unknown. By later discoveries of this species in Tanzania by BIZOT and PÓCS (1974) and BIZOT *et al.* (1978), *C. vermicularis* came to be a typical subantarctic hepatic found in East African Highlands.

SEKI (1973) proposed the *Podocarpus* type as a distributional pattern of the Patagonian mosses. The representative species are *Andreaea subulata, Dicranoloma billardieri* and *Rhacocarpus purpurascens*. Their distribution covers the Central American Highlands, Guiana Highlands, north Andes, southern Brazil, Patagonia, New Zealand, Tasmania, southeastern Australia, New Guinea, Celebes, Borneo, Sumatra, East African Highlands, Madagascar, South Africa and the subantarctic islands. This range almost coincides with that of the living *Podocarpus* species shown by FLORIN (1963).

BIZOT and PÓCS (1974) defined as the subantarctic elements as "distributed in temperate South America, Australia and sometimes New Guinea, New Zealand and the subantarctic isles, finally in South Africa and in the East African mountains: *Bazzania convexa*, *B. decrescens*, *Metzgeria violacea*, *Dicranoloma billardieri*, *Rhacocarpus purpurascens* and *Catagonium nitens*". Pócs (1976) discusses the subantarctic species in tropical Africa as follows: "one of the striking features is the high number of subantarctic elements. The greater part of them is restricted in Africa to the Cape, but many of them penetrate deeper northwards and reach the East African high mountains, as *Clasmatocolea vermicularis*, *Marchantia berteroana*, *Jamesoniella colorata*, *Catagonium nitens*, *Rhacocarpus purpurascens* and others".

3. Grouping of the Subantarctic Elements in East African Highlands

According to their habitats and distributional causes, the subantarctic bryophytes which are disjunctively distributed in East African Highlands can be classified into three groups as follows:

Group 1 is composed of *Andreaea subulata*, *Bryum ellipsifolium*, *Rhacocarpus purpurascens*, etc. found growing on wet rocks in the periglacial environment of the Afroalpine region, sometimes down to the Afromontane region.

Group 2 includes *Bazzania convexa*, *B. decrescens*, *Catagonium nitens*, *Clasmatocolea vermicularis*, *Dicranoloma billardieri*, *Metzgeria violacea*, *Zygodon intermedius*, etc. found growing on trunks, branches and rocks in forests of the Afromontane region, sometimes up to the subalpine region.

Group 3 is represented by *Aongstroemia julacea* found growing on bare land of the Afroalpine region.

Seki (1974) supposed that mosses of the *Podocarpus* type might be of very ancient origin before the separation of the Gondwanaland according to Schuster (1972). The genus *Andreaea*, in particular, is a phylogenetically old moss and it represents great diversity in the Southern Hemisphere (Schultze-Motel, 1970). As mentioned by Seki (1974), all moss species of the *Podocarpus* type do not actually grow in the *Podocarpus* forest. Some of them grow in the periglacial environment which is situated in the upper zone of the *Podocarpus* forest, and the others actually grow in the forest associated with *Podocarpus* spp. Mosses of the *Podocarpus* type thus include species of both Group 1 and 2.

The disjunction of the members of Group 1 took place during the geomorphological changes caused by the continental drift in the Cretaceous Period. Until the present time, they continue to diffuse from the refugia. The refugia seem to have been the forest zone of the Afromontane region. According to Bizot and Pócs (1974), *Rhacocarpus purpurascens* is occasionally found growing in the Afromontane regions of Tanzania and Malawi such as Nguru Mountains (1850 m alt.), Uluguru Mountains (1800–1900 m alt.) of Tanzania and Mulanje Mountain (900–1600 m alt.) of Malawi.

The members of Group 2 are essentially found growing in the mountain rainforest which is situated between the periglacial zone and the lower arid vegetation zones. Generally speaking, glaciers, periglacial environments (patterned ground, bog, lake, heath, etc.), mountain rainforests, and arid vegetations (savanna, steppe, etc.) form a geographical set in the tropics as a result of climatological and geomorphological effects (Flenley, 1979; Hedberg, 1951, 1964; Lind and Morrison, 1974). In Africa, the

Afromontane zone can be assigned to the mountain rainforest which is situated between the periglacial zone and the arid vegetation zone. It has played an important role as refugia for various plant species (AXELROD and RAVEN, 1978; WHITE, 1978).

With respect to the bryophytes common to Madagascar, Mascarenes and East Africa, BIZOT and PÓCS (1974) stress an important role of the old crystalline inselbergs as follows: "these old crystaline massifs, where they coincide with favorable climate conditions at the eastern edge of the great Central African Plateau form a chain of forest covered inselbergs from South Kenya through Tanzania to Malawi."

A geomorphological term inselberg (German–island mountain) describes any isolated hill or hills which stand prominently above a level surface (PRITCHARD, 1979). The representative inselbergs in East Africa are Taita, Sagala, Kasigau, Shimba Hills in southeastern Kenya, and Pare, Usambara, Kanga, Nguru, Ukaguru, Uluguru, Usagara and Uzungu Mountains in Tanzania (Fig. 2). Most of them are composed of the Pre-Cambrian crystalline rocks. On the other hand, the volcanic mountains in East Africa such as Mt. Kilimanjaro and Mt. Meru in Tanzania, and Mt. Kenya, Mt. Elgon and

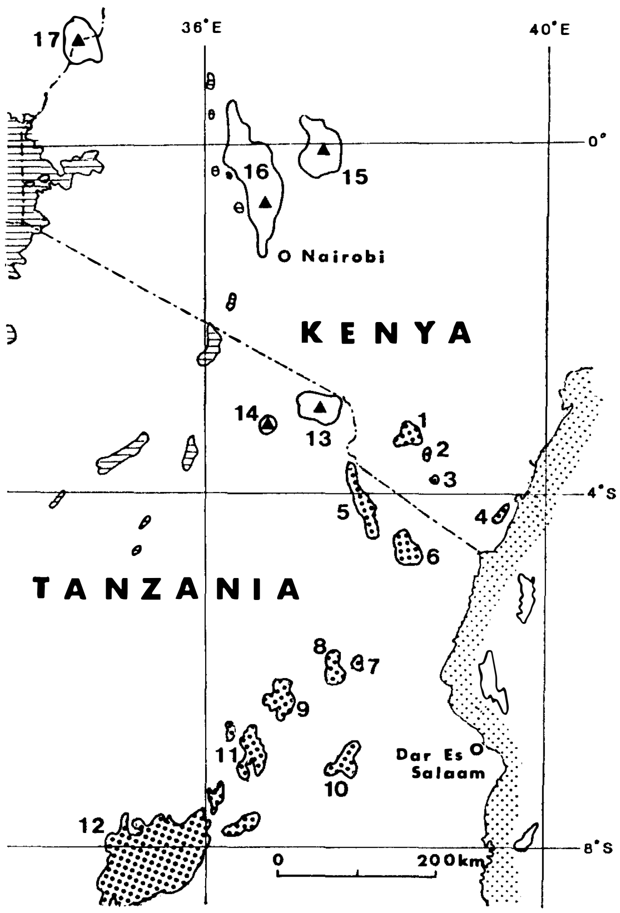

Fig. 2. Inselbergs and volcanic mountains in East Africa. 1. Taita, 2. Sagala, 3. Kasigau, 4. Shimba, 5. Pare, 6. Usambara, 7. Kanga, 8. Nguru, 9. Ukaguru, 10. Uluguru, 11. Usagara, 12. Uzungu, 13. Mt. Kilimanjaro, 14. Mt. Meru, 15. Mt. Kenya, 16. Aberdare Mountains and 17. Mt. Elgon. Dotted areas show the inselbergs.

Aberdare Mountains in Kenya are geomorphologically separated from the inselbergs. These volcanic mountains were formed from the Oligocene to the Holocene Period (NYAMWERU, 1980). However, the members of Groups 1 and 2 are, at the present time, growing in the Afromontane and Afroalpine regions of these volcanoes. According to AXELROD and RAVEN (1978), the lowland and mountain rainforests have extended widely in Africa since the Late Cretaceous, and by the warping of the African continent during the Tertiary Period they were divided into several blocks. This possible fact is supported by the present situation of the vegetation and animal distribution in Africa (LIND and MORRISON, 1974) although there are several disputable problems about long jump-dispersal possibilities. Taking these into consideration, the bryophytes of Group 2 seem to have survived in the Afromontane forest of such inselbergs, since the Late Cretaceous and have diffused into new territories of the Tertiary volcanic mountains.

Group 3 is assigned to the species with the typical natural jump-dispersal as defined by PIELOU (1979). According to BIZOT *et al.* (1978), *Aongstroemia julacea* is distributed in Himalaya (Mt. Everest, 6170 m alt.), Mongolia, Japan (Mt. Fuji, the summit, 3776 m alt.), Ecuador (Chimborazo and Quito), Venezuela, Tierra del Fuego, Kerguelen Island, New Zealand, Auckland Island, Campbell Island, Madagascar, Reunion, S. Africa (Natal) and E. Africa (Mt. Kilimanjaro). In the case of Mt. Fuji, TAKAKI (1951) reported this species (as *Anomobryum fuji-alpinum*) from near the crater of the summit. Mt. Fuji was formed from the Late Pleistocene to the Holocene at the same time as Mt. Kilimanjaro. For Group 3, the long jump-dispersal by the jet stream or other air current seems to be highly suggested. Furthermore, a volcanic eruption might have helped the long jump-dispersal of bryophytes by dispersing the spores or gametophytes into the atmosphere of high altitudes.

4. Effect of the Aridity during the Quaternary Glaciation in Africa on the Bryophyte Distribution

AXELROD and RAVEN (1978) mention that the African rainforest was progressively impoverished as aridity spread during the Miocene, and notably in the Pliocene as the ice cap developed on Antarctica (after 5 million years), bringing the driest part of the Tertiary to low-middle latitudes. This was followed by several episodes of "ice-age aridity" that must have had a disastrous effect on the moisture-sensitive rainforest taxa, eliminating many from Africa. For example, the Palmae in Africa have 16 genera and 116 species. This contrasts with 29 genera and 132 species in the nearby but much smaller Indian Ocean islands (Mascarenes, Comoro Islands and Madagascar). The poverty of the palm plants in Africa (the whole continent has fewer palms than Singapore Island) is believed to have resulted from dessication during the Pleistocene which greatly reduced the extent of moist habitat (WHITEMORE, 1978). On the other hand, SCHUSTER (1972) suggested that the scantiness of primitive angiosperms in the present Africa seems to be caused by early separation of the African block from the Gondwanaland.

According to the recent investigations by Japanese geographers in Cameroon and Kenya, the aridity during the Quaternary ice-age was very strong and the areas of the lowland rainforest seems to have been remarkably restricted (HORI, 1982). FLENLEY (1979) gives a conclusion as follows: "the evidence for dessication is from many areas especially the East African Plateau, Australia and South America, and consists mainly of records of vegetation characteristics of drier climates than occur at the sites today." He also stresses that the old "pluvial" theory must therefore be replaced with a new one in which the glacial periods of temperate areas are reflexed in equatorial regions as periods much cooler and more arid than the present.

For the bryophytes, an aridity, even if it is for a short time, brings a disastrous effect. For example, in 1982–83, the Galapagos Islands suffered the strongest and most prolonged "El Niño" effect, which was disastrous for many lichens and mosses (WEBER and GRADSTEIN, 1984). SEKI and YAMAGUCHI (1985) report that the increase in the saturation deficit in the summer season seems to be one of the limiting climatic factors for the developing of the bryophyte community in the Yaeyama Islands, Ryukyu Archipelago, southern Japan. Such climatic conditions are caused by the geographical situation of these islands.

The savanna and semi-arid vegetations in East Africa could be assigned to an "ocean" for the distribution of forest bryophytes, and the inselbergs are just "islands" in the "ocean" (Fig. 3). In the present situation, at least after the last glaciation, the forest bryophytes could not spread their range by diffusion or secular migration over these "oceans". Some possibilities of "short" jump-dispersal among these "islands" might be suggested for some species.

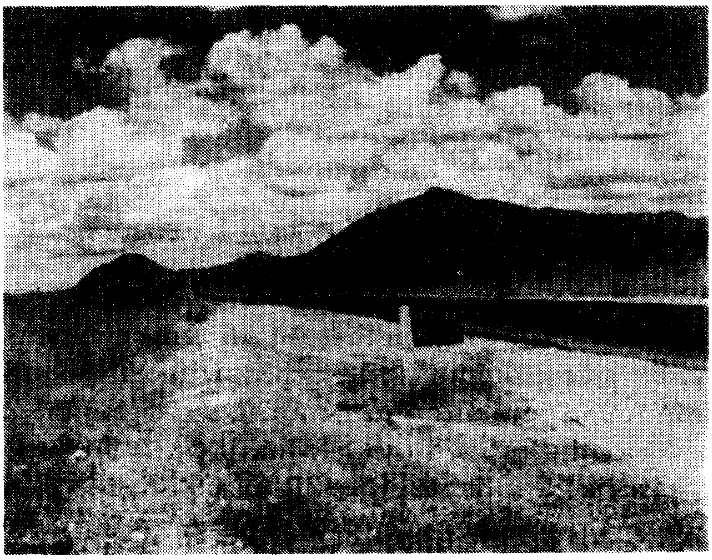

Fig. 3. Taita Hills (Mbololo Hill), Kenya. A view from Mombasa Road. Photo by T. SEKI, April 1984.

Acknowledgments

The author is deeply indebted to Dr. N. HORI, Faculty of Integrated Arts and Science, Hiroshima University for his valuable suggestions on African geography, and to Miss C.H.S. KABUYE, East Africa Herbarium, National Museums of Kenya, for her kind help in studying the East African mosses, and to Mr. H. MURAGE, Lecturer of Faculty of Agriculture, Jomo Kenyatta College of Agriculture and Technology, Kenya, who read the manuscript and gave valuable comments.

References

AXELROD, D. I. and RAVEN, P. H. (1978): Late Cretaceous and Tertiary vegetation history of Africa. Biogeography and Ecology of Southern Africa, ed. by L. WERGER. The Hague, Junk, 77–130.

BIZOT, M. and PÓCS, T. (1974): East African bryophytes I. Acta Acad. Paedagog. Agriensis-Nova Ser., **12**, 383–449.

BIZOT, M., FRIES, I., LEWINSKY, J. and PÓCS, T. (1978): East African bryophytes IV. Danish collections. Lindbergia, **4**, 259–284.

DUSÉN, P. (1905): Musci nonnulli novi e Fuegia et Patagonia reportati. Bot. Not., **1905**, 299–310.

FLENLEY, J. R. (1979): The Equatorial Rain Forest; A Geological History. London, Butterworths, 162 p.

FLORIN, R. (1963): The distribution of conifer and taxad genera in time and space. Acta Horti Bergiani, **20**, 121–312.

GROLLE, R. (1969): Grossdisjunktionen in artarealen lateinamerikanischer Lebermoose. Biogeography and Ecology in South America, ed. by E. J. FITTKAU *et al.* The Hague, Junk, 562–582.

HEDBERG, O. (1951): Vegetation belts of the East African Mountains. Svensk Bot. Tidskr., **45**, 140–202.

HEDBERG, O. (1964): Features of Afroalpine plant ecology. Acta Phytogeogr. Suec., **49**, 1–144.

HEGEWALD, E. and HEGEWALD, P. (1985): Eine Moossammulung aus Peru III. Nova Hedwigia, **41**, 219–271.

HERZOG, T. (1926): Geographie der Moose. Jena, Gustav Fischer, 439 p. 8 taf.

HORI, N. (1982): Zoku • kamerûn de kangaeta koto (3) (Thinking in Cameroon, 2nd report (3)). Chiri (Geography), **27**, 79–88.

LIND, E. M. and MORRISON, M. E. S. L. (1974): East African Vegetation. London, Longman, 257 p.

MÜLLER, C. (1890): Die Moose von vier Kilimandscharo-Expeditionen. Flora, **73**, 465–499.

NYAMWERU, C. (1980): Rifts and Volcanoes. A Study of the East African Rift System. Nairobi, Thomas Nelson, 128 p.

OCHI, H. (1972): A revision of African Bryoideae, Musci (First Part). J. Educ. Tottori Univ., **23**, 1–126.

PIELOU, E. C. (1979): Biogeography. New York, J. Wiley, 351 p.

PÓCS, T. (1976): Correlation between the tropical African and Asian bryofloras, I. J. Hattori Bot. Lab., **41**, 95–106.

POTIER DE LA VARDE, R. (1955): Mousses récoltées par M. le Dr. Olov Hedberg en Afrique orientale, au cours de la mission suédoisé de 1948. Ark. Bot., **3**, 125–204.

PRITCHARD, J. M. (1979): Landforms and Landscape in Africa. London, Edward Arnold, 136 p.

SCHULTZE-MOTEL, W. (1970): Monographie der Laubmoosgattung *Andreaea*. 1. Die costaten Arten. Willdenowia, **6**, 25–110.

SCHUSTER, R. M. (1972): Continental movements, "Wallace's Line" and Indomalayan-Australalasian dispersal of land plants; Some eclectic concepts. Bot. Rev., **38**, 3–86.

SEKI, T. (1973): Distributional patterns of the Patagonian mosses. Proc. Jpn. Soc. Plant Taxon., **3**, 13–15.

SEKI, T. (1974): A moss flora of Provincia de Aisén, Chile. Results of the Second Scientific Expedition to Patagonia by Hokkaido and Hiroshima Universities, 1967. J. Sci. Hiroshima Univ., Ser. B, Div. 2, **15**, 9–101, pl. I-IV.

SEKI, T. and YAMAGUCHI, T. (1985): The effect of climatic factors on the floristic diversity of bryophytes in the Yaeyama Islands, the Ryukyu Archipelago, Southern Japan. Origin and Evolution of Diversity in Plants, ed. by H. HARA. Tokyo, Academia Scientific Book, 60–76.

TAKAKI, N. (1951): Fuji sanchô no Sentairui (Muscinées des hauts sommets de la mte. Fuji, Japon). J. Hattori Bot. Lab., **6**, 1–5.

WEBER, W. A. and GRADSTEIN, S. R. (1984): Death on the Galapagos. Bryol. Times, **26**, 1.

WHITE, F. (1978): The Afromontane region. Biogeography and Ecology of Southern Africa. ed. by M. J. A. WERGER. The Hague, Junk, 463–513.

WHITEMORE, T. C. (1978): Palmae. Flowering Plants of the World, ed. by V. H. HEYWOOD. Oxford, Oxford Univ. Press, 301–304.

(Received June 30, 1986; Revised manuscript received September 20, 1986)