Cryptogamie, Bryologie, 2003, 24 (3): 253-263

Thuidium delicatulum (Hedw.) Schimp. (Thuidiaceae) – another bipolar moss disjunct from Subantarctic Marion Island

Ryszard OCHYRA[a], Valdon R. SMITH[b] & Niek J. M. GREMMEN[c]*

[a] Laboratory of Bryology, Institute of Botany, Polish Academy of Sciences, ul. Lubicz 46, 31-512 Kraków, Poland

[b] Department of Botany, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa

[c] Data Analyse Ecologie, Hesselsstraat 11, NL-7981 CD Diever, The Netherlands

(Received 16 January 2003, accepted 18 March 2003)

Abstract – *Thuidium delicatulum* (Hedw.) Schimp. is recorded from Marion Island in the Prince Edward Islands Archipelago in the Subantarctic. This is the first report of the genus *Thuidium* Schimp. from the subpolar region of the Southern Hemisphere and establishes *Th. delicatulum* as a bipolar species with intermediate localities in the tropical zone, in Central America and the northern and central Andes in South America. The Marion Island plants are described and their ecology and distribution on the island discussed. The world distribution of *Th. delicatulum* is reviewed and some speculations presented regarding the origin of the Marion Island population.

Bryophyta / Musci / Thuidiaceae / *Thuidium* / Subantarctica / Prince Edward Islands / Marion Island / Kerguelen Province / distribution / bipolar species

INTRODUCTION

The Prince Edward Islands Archipelago is located, along with Îles Crozet, Îles Kerguelen and Heard and McDonald Islands, in the Kerguelen Province of the Subantarctic. It consists of two small islands near the centre of the West Indian Ocean Ridge in the vast Southern Ocean, just north of the Polar Frontal Zone. It lies 1800 km to the south-east of Africa and 2300 km to the north of Dronning Maud Land on the Antarctic continent. Marion Island (290 km^2 area, lat. 46º49'–59'S, long. 37º35'–54'E) is the larger, and Prince Edward Island (44 km^2 area, lat. 46º36'–40'S, long. 37º52'–38º00'05''E) the smaller, of the two islands which represent twin peaks of a coalescing shield volcano rising over 1200 m above sea level (Kable *et al.,* 1971; Verwoerd, 1971) which, although quiescent, produced small eruptions on the south-west coast of Marion Island in the early 1980s (Verwoerd *et al.,* 1981). Both islands are geologically very young. The oldest potassium-argon dates available for Marion Island lavas indicate an age of approximately 250 000 years (McDougall, 1971), but it has been suggested that the

* Correspondence and reprints: r.ochyra@ib-pan.krakow.pl

island is about 0.5 to 1 million years old (Verwoerd, 1971; Smith & Verwoerd, 1985).

Marion Island was extensively glaciated between about 100 000 and 15 000 years ago (Hall, 1978). During the glacial episodes the temperatures were probably 4–7ºC lower than they are at present (Hall, 1981; Zinderen Bakker, 1973; Hays *et al.,* 1976) and the island's extant vegetation would have been absent, except possibly for some mosses and lichens and the cushion plant *Azorella selago* Hook. f. (Apiaceae) (Schalke & Zinderen Bakker, 1971). At present, permanent snow and ice are restricted to above 1000 m altitude on Marion Island. Prince Edward Island shows no sign of having been glaciated and does not currently have permanent ice or snow.

The Prince Edward Islands have a cool, extremely oceanic climate characterized by a high precipitation (annual mean 2350 mm), high relative humidity (annual mean 83%), relatively low mean air temperature (annual mean 5.6ºC, warmest month mean 7.7ºC, coldest month mean 3.6ºC) and a high degree of cloudiness (on average, direct sunshine occurs on only 3.7 hours per day). These values are for Marion Island between 1949 and 2000; the precipitation, temperature and sunshine values are from the data set analysed by Smith (2002), and the relative humidity value is from Schulze (1971). Their locality in the 'Roaring Forties' makes the islands subject to strong, almost incessant, westerly winds. Gale force (>55 km h^{-1}) winds blowing for longer than 1 hour occur for 107 days per year, on average (Schulze, 1971).

Their volcanic origin, isolation from other land masses and the profound effect of the surrounding ocean on their climate and biota (Smith & Steenkamp, 2001) result in the Prince Edward Islands being biogeographically, biologically and ecologically truly oceanic. The islands' vegetation is a typical Subantarctic tundra made up of herbfield and swampy plant communities at lower, and fellfields at higher, elevations (Huntley, 1971; Gremmen, 1982). In the absence of trees, shrubs and other tall-growing plants the vegetation is dominated by graminoids, ferns and, especially, cryptogams. There is a great diversity of mosses, liverworts and lichens (Zanten, 1971; Grolle, 2002; Øvstedal & Gremmen, 2001). In contrast, the vascular flora is poor, only 22 indigenous species occur (Gremmen, 1982) although 18 alien vascular plant species have been recorded, a result of recent human introduction (Gremmen & Smith, 1999).

Up to 1971 the only information on the bryophyte flora of the Prince Edward Islands was the classic papers of Mitten (1876, 1884), based upon a collection made by H. N. Moseley in 1873 during the *Challenger* expedition. A much more comprehensive treatment of the mosses of the archipelago was published by Zanten (1971), based on a collection made by the South African Biological and Geological Expedition to the two islands in 1965–1966. Altogether 80 taxa of mosses were recorded by Zanten (1971), six of which could not be assigned to species due to scantiness of material. Subsequently, additional species were recorded for the archipelago; *Fissidens bryoides* Hedw. (Seppelt & Russell, 1986), *Anomobryum julaceum* (P. Gaertn., B. Mey. & Scherb.) Schimp. (Ochi, 1972) from Prince Edward Island, and eight species from Marion Island (Frahm, 1985; Lightowlers, 1986; Ochyra & Hertel, 1990). Considering these additions, and some taxonomic changes, in the late 1990s the Prince Edward Islands moss flora was known to comprise 83 species and a further five taxa which could not be assigned to species.

In 1999 the authors started an intensive bryological survey of the archipelago, with the purpose of producing a comprehensive moss flora of the Prince Edward Islands. So far, this survey has unearthed some interesting taxa, including

two species new to science – *Dicranella gremmenii* Ochyra (Ochyra, 1999a) and *Racomitrium valdon-smithii* Ochyra & Bednarek-Ochyra (Ochyra & Bednarek-Ochyra, 1999), and the new genus *Valdonia* Ochyra, comprised of a single species, *V. microcarpa* (Mitt.) Ochyra (Ochyra, 2003). Some of the new records are of considerable importance phytogeographically since they either complete a seemingly highly disjunct range of the species concerned or represent a considerable extension of their ranges, for example *Entosthodon productus* Mitt. (Ochyra & Smith, 2003), or are new generic records in the subpolar region of the Southern Hemisphere. An especially interesting species found on Marion Island is *Thuidium delicatulum* (Hedw.) Schimp., the first record of the genus *Thuidium* Schimp. in the Subantarctic. Here, we describe the morphology, ecology and local distribution of *Th. delicatulum* on Marion Island and review the species world distribution.

CHARACTERIZATION OF MARION PLANTS

Thuidium delicatulum collected from Marion Island (Fig. 1) corresponds perfectly in all taxonomically important characteristics with the populations known from other parts of the wide geographical range of the species. Marion Island **plants** are medium-sized to moderately large and robust, yellowish-green to yellowish-brown or reddish-brown in colour and grow in large patches or mats of loose wefts. The **fronds** are moderately elongate, flat and dense and they are rather regularly bipinnate. The **stems** are up to 10 cm long, rigid, straight or flexuose, prostrate to more or less arched-ascending and they almost lack rhizoids. In transverse section the stem consists of a small but distinct central duct and a 3–5-layered cortex of small, thick-walled and dark red cells which surrounds gradually larger, hyaline medullary cells with moderately thickened walls. The stems and primary branches are densely covered by **paraphyllia**. These are polymorphous, mostly uniseriate but branched or sometimes foliose with uniseriate filaments. The cells of the **paraphyllia** are mostly rectangular, papillose, with median papillae. The pseudoparaphyllia are foliose and the axillary hairs are filiform and consist of a short, quadrate and brown basal cell and two hyaline, elongate distal cells. The stem and branch **leaves** are strongly differentiated. The former are ovate-triangular, 1.1–1.3 mm long, 0.8–0.9 mm wide, abruptly and broadly acuminate, concave, distinctly plicate and mostly shortly decurrent. They are closely appressed when dry and erect-spreading on wetting. The margins are papillose-serrulate throughout, flat above and recurved in the proximal half. The costa is single and strong, usually ceases at a distance of 1/5 of the leaf length from the apex but it does not fill the acumen. The laminal cells are rounded to elongate-elliptical, mostly to 5 times as long as wide, unipapillose, with stout straight or curved papillae, centrally located over the lumina. The cell walls are thick, smooth or slightly porose. The cells across the leaf insertion and in the decurrencies are rectangular, smooth and have incrassate and porose walls. The branch leaves are erecto-patent, ovate to ovate-lanceolate, 0.3–0.5 mm long, concave, non-decurrent and smooth. They are unicostate, with a costa often forked at the apex and extending to 2/3–3/4 way up. The margins are papillose-serrulate, plane to erect. The laminal cells are oval and have single, stout, curved papillae on the dorsal surface. The apical cells are mostly truncate and crowned with 2–4 papillae. The Marion plants are **dioecious**. **Perichaetia** are occasionally present but sporophytes have not been found. The

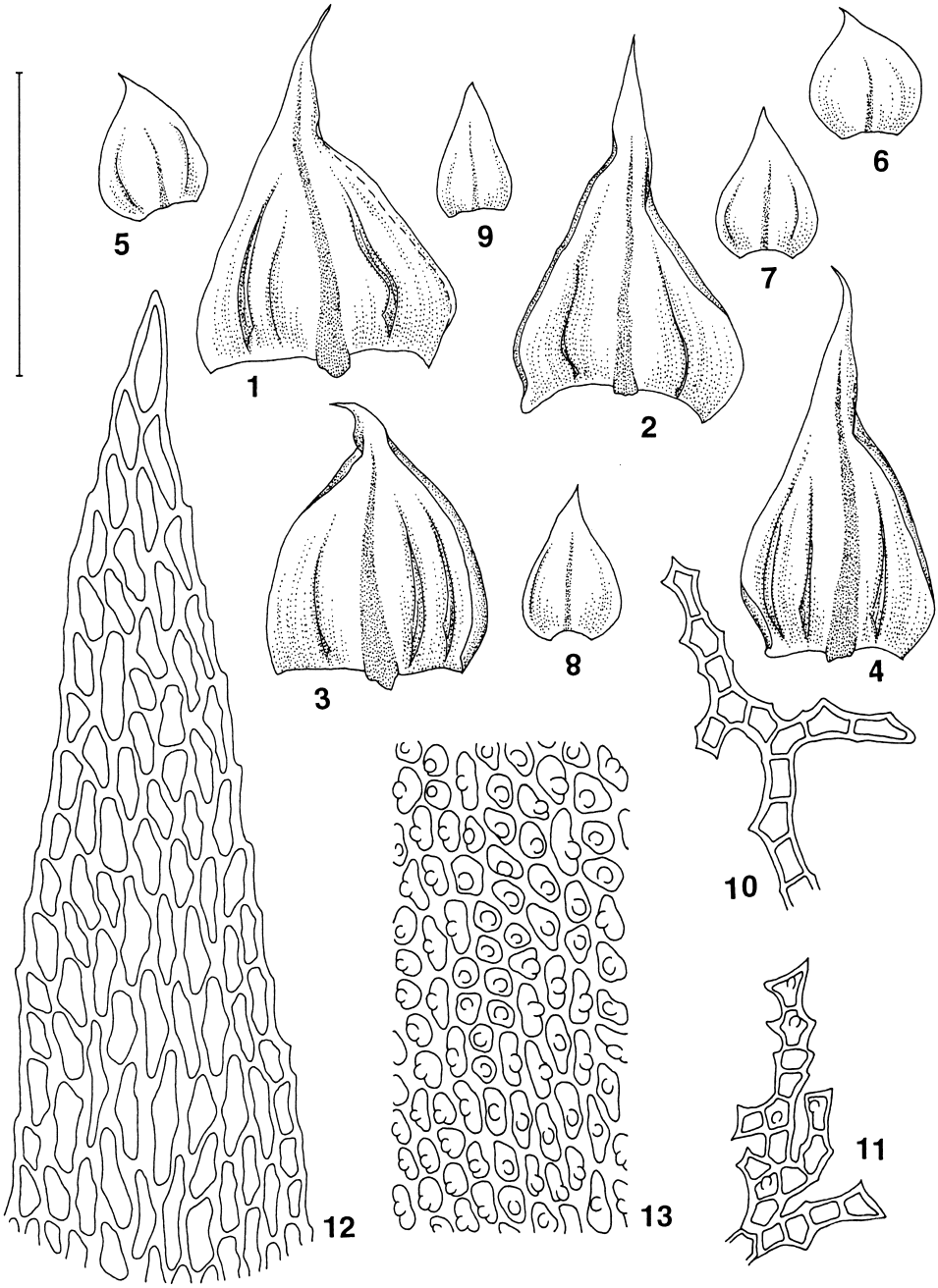

Fig. 1. *Thuidium delicatulum* (Hedw.) Schimp. — **1–4.** Stem leaves. **5–9.** Branch leaves. **10–11.** Paraphyllia. **12.** Apex of stem leaf. **13.** Laminal cells of branch leaf. [All from *Gremmen 96/1,* KRAM]. Scale bar: 1 mm (1–9) and 100 μm (10–13).

perichaetial leaves are erect, linear-lanceolate, to 5 mm long and taper to a long-lorate apex. They are distinctly plicate and have margins serrulate above and sparsely ciliate at about two thirds. The cilia are uniseriate throughout or biseriate at their bases. The costa is single and ends in the acumen but it does not fill it. The laminal cells are long-rectangular to linear, smooth or indistinctly unipapillose and have strongly incrassate walls.

Thuidium delicatulum is a distinctive species which is diagnosed by (1) variously branched paraphyllia composed of mostly rectangular cells with almost all cells papillose over the middle of the lumina; (2) ovate-triangular stem leaves which are gradually or rapidly narrowed to a broad but never capillary-pointed acumen; (3) truncate and pluripapillose apical cells of the branch leaves. In the Marion Island flora the species is unmistakable because it is the only representative of the family Thuidiaceae and of the genus *Thuidium,* whose members exhibit a strikingly regular and attractive architecture. Apart from the common *Orthotheciella varia* (Hedw.) Ochyra, it is the only moss species in the Prince Edward Islands with paraphyllia. These are sparse, filiform and unbranched in *O. varia,* whereas in *Th. delicatulum* the paraphyllia are very abundant, branched and densely cover the stems and primary branches.

LOCAL DISTRIBUTION AND ECOLOGY

Thuidium delicatulum is exceedingly rare on Marion Island; an intense survey of about two thirds of the island's surface yielded only three populations, in close proximity to each other in a small area 50–150 m above sea level between the meteorological station and Junior's Kop on the island's north-eastern coastal plain.

SUBANTARCTICA. Prince Edward Islands. Marion Island: (1) in a gully below Penis Rock by path leading to the meteorological station, 300 m north-east of Junior's Kop, lat. 46º52'40''S, long. 37º50'15''E, alt. *ca* 100 m, on soil in fernbrake, shaded by dense growth of *Blechnum penna-marina,* associated with *Sanionia uncinata* and *Brachythecium rutabulum;* 13 Apr 1999, *Ochyra & V. R. Smith 787/99* (KRAM); (2) at the northern foot of Junior's Kop, lat. 46º52'45''S, long. 37º49'55''E, alt. 150 m, on level, rocky and relatively dry ground dominated by the *Lycopodio magellanici–Jamesonielletum coloratae* association, with a small admixture of *Sanionia uncinata* and *Brachythecium austrosalebrosum;* 14 Apr 1999, *Ochyra & V. R. Smith 935/99* (KRAM); (3) Nellie Humps south of meteorological station, lat. *ca* 46º53'S, long. *ca* 37º51'30''E, alt. *ca* 50 m, in fernbrake, 1996, *Gremmen 96/1* (KRAM).

On Marion Island *Thuidium delicatulum* grows exclusively in two plant communities which develop in relatively dry and ecologically similar type of habitats. It occurs in about equal abundance and vitality in both. One community is *Isopterygio pulchelli-Blechnetum penna-marinae* association, subassociation *brachythecietosum rutabuli,* a fernbrake community that occurs in depressions and shallow drainage lines on well-drained slopes in the lowlands of the Prince Edward Islands (Gremmen, 1982). There, it forms almost pure stands on soil under a dense canopy of the fern *Blechnum penna-marina* (Poir.) Kuhn., in which the grass *Agrostis magellanica* Lam. and the cushion plant *Azorella selago,* may also occur. Other bryophytes usually present are *Orthotheciella varia, Sanionia uncinata* (Hedw.) Loeske and *Brachythecium rutabulum* (Hedw.) Schimp. The other plant community in which *Th. delicatulum* is found is the *Lycopodio magellanici-Jamesonielletum coloratae* association, subassociation *catagonietosum politi,* which is the driest of all the mire communities on the island (Gremmen, 1982) and which

also supports a substantial cover of *B. penna-marina. Th. delicatulum* occurs on soil under the fern cover and the most frequent bryophyte associates in this community are *Racomitrium lanuginosum* (Hedw.) Brid., *Jamesoniella colorata* (Lehm.) Schiffn., *Leptoscyphus expansus* (Lehm.) Grolle and *Gymnocoleopsis cylindriformis* (Mitt.) R. M. Schust.

A REVIEW OF GLOBAL DISTRIBUTION

Hitherto, *Thuidium delicatulum* has been considered as a Northern Hemisphere species that penetrates into the tropical zone at altimontane elevations in Central and South America. It is widely distributed, though highly disjunct, in the Holarctic and shows clear oceanic tendencies. Its maximum occurrence is in Europe where it occurs throughout the continent, extending from the British Isles (Wigginton, 1994) to the Southern Ural in the east (Ignatov & Afonina, 1992) and southern Fennoscandia in the north (Söderström, 1998). In addition, it has been found at two stations in southern Iceland (Jóhannsson, 1996). In Asia, *Th. delicatulum* is scattered and occasional in Siberia (Bardunov, 1974; Ignatov & Afonina, 1992), the Russian Far East (Bardunov & Cherdantseva, 1982), in Japan (Watanabe, 1972) and China (Wu *et al.,* 2002). In North America its distribution is not fully known since the species has often been misunderstood and not distinguished from the closely-related *Th. philibertii* Limpr. (which is sometimes treated as a variety of *Th. delicatulum*). It appears to occur only in eastern parts of North America, from Newfoundland to western Ontario, Minnesota, Nebraska, Kansas and eastern Texas, south to Louisiana and Florida, with isolated occurrences in southern Arizona (Crum & Anderson, 1981). In western North America the species has been reported from British Columbia, Alaska and Yukon, but these data are probably erroneous and refer to *Th. philibertii*.

Thuidium delicatulum has been recorded from many localities on the Central American isthmus, from Mexico to Costa Rica (Delgadillo *et al.,* 1995), the West Indies (Buck, 1998) and the northern and central Andes, from Venezuela to Bolivia, where it occurs at high elevations, from 900 to 3700 m (Churchill *et al.,* 2000). Various sources have reported *Th. delicatulum* from Oceania (Miller *et al.,* 1978), but these data have never been confirmed and the species is excluded from the bryoflora of the Pacific region (Touw, 2001).

So far, no records of *Thuidium delicatulum* are known from southern South America (Gier, 1980; Greene, 1986), Africa (Touw, 1976) and Australasia (Touw & Falter-van den Haak, 1989). The discovery of *Th. delicatulum* on Marion Island is thus the first record of the species in the subpolar region of the Southern Hemisphere, representing a major extension to its range and establishing it as another bipolar moss species.

POSSIBLE EXPLANATION OF THE DISJUNCT RANGE OF *THUIDIUM DELICATULUM*

The distribution of *Thuidium delicatulum* is strange and difficult to explain. There are several examples of bipolar bryophyte species (Schofield & Crum, 1972; Schofield, 1974; Ochyra, 1992) but almost all are distributed along one

or more trans-tropical pathways, including (1) the Cordilleran track across tropical America; (2) the East African mountain track across tropical Africa; and (3) the Indomalayan-Melanesian track across the chain of high Malesian islands. Accordingly, these taxa have as their Southern Hemisphere polar/subpolar occurrences, respectively, (1) southern South America and the Antarctic, (2) southern Africa and some Subantarctic islands and (3) Australia and New Zealand.

We offer three possible explanations to the presence of *Thuidium delicatulum* on Subantarctic Marion Island. The first is that it is a result of migration of the species via the East African track and subsequent long-distance oceanic dispersal from Southern Africa to the island. *Amphidium lapponicum* (Hedw.) Schimp., is an analogous example; it occurs in some localities in Southern Africa (Rooy, 1992) and was recently discovered on Subantarctic Îles Kerguelen (Ochyra & Poulsen, in press). Against this explanation is a total lack of intermediate localities of the species in East and South African mountains (Touw, 1976), although future bryological exploration of subsaharan Africa might well show such localities.

Thuidium delicatulum is quite widespread in the Neotropical mountains but is absent from southern South America (Greene, 1986). However, there are examples of bryophyte species with a strange Andean-Subantarctic distribution pattern; for example *Holodontium strictum* (Hook. f. & Wilson) Ochyra (Ochyra, 1993), *Schistidium falcatum* (Hook. f. & Wilson) B. Bremer (Ochyra, 1998) and *Brachythecium austrosalebrosum* (Müll. Hal.) Kindb. (Ochyra, 1999b). Possibly the Marion Island occurrence of *Th. delicatulum* is the result of long-distance dispersal from Andean stations using the prevailing westerlies.

A third possible explanation of the occurrence of *Thuidium delicatulum* on Marion Island is that the species was introduced relatively recently by man. Since the first documented landing there in 1804 (Hänel & Chown, 1998), Marion Island was the centre of the intensive sealing activities for over a century and for the past 53 years has been occupied permanently by teams of meteorologists and biologists. Strong evidence of the effect of human activity on the island's biota are the numerous introductions of vascular plant species. The *Challenger* expedition in 1873 recorded only two alien vascular plant species on the island (Moseley, 1874; Oliver, 1874) whereas 125 years later the number of introduced vascular species had increased to 18 (Gremmen & Smith, 1999). The greatest concentration of adventive species is in the vicinity of the meteorological station and all records of *Th. delicatulum* are from this area.

Thuidium delicatulum is not the only moss species on the island that shows a disjunct distribution pattern, where there is no obvious connection between the northern part of its range and its occurrence on Marion Island, and for which there is a possibility that it was introduced to the island by humans. For instance, *Leptodontium gemmascens* (Mitt.) Braithw. was reported from Marion Island by Zanten (1971) as *L. proliferum Herzog,* a rare Andean species (Zander, 1972). However, the Subantarctic specimens correctly belong to *L. gemmascens* which is a European endemic known from south-eastern England (Blockeel, 1992) and on the continent is scattered from the Pyrenees to Denmark (Rogeon & Schumacker, 1984). No intermediate stations of this species between Europe and Marion Island are known. *L. gemmascens* is consistently sterile but produces obovoid to fusiform gemmae in great profusion. These appear to be a very effective mean of dissemination over short distances but are not good candidates for long-distance dispersal due to their large size (50–100 μm long). Hence, the occurrence of *L. gemmascens* on Marion Island may be due to human introduction. The species is very common and widespread on the island, occurring in coastal areas

in tussock grasslands strongly affected by seals and penguins. This example suggests that accidental, human-mediated introduction of bryophytes to remote oceanic islands may well occur and we feel that *Th. delicatulum* possibly reached Marion Island in this manner. The lack of comprehensive distribution data for bryophytes in large areas of the Southern Hemisphere, however, means that the above explanations are merely speculative.

There are examples of moss species being introduced to oceanic islands by man. Possibly the best known is *Pseudoscleropodium purum* (Hedw.) M. Fleisch. which has established itself as an adventive, weedy element of the moss floras of several oceanic islands, such as St. Helena and Tristan da Cunha (Dickson, 1967), Réunion and the Hawaiian Islands (Allen & Crosby, 1987) and also on larger land masses such as New Zealand (Lewinsky & Bartlett, 1982) and Sri Lanka (Allen & Crosby, 1987).

Acknowledgements — Thanks are due to the South African Department for Environmental Affairs and Tourism for providing logistical support for the field work on the Prince Edward Islands. This study was supported financially by the Polish State Committee for Scientific Research through grant No. 6 P04C 002 18. Halina Bednarek-Ochyra designed the plate and her assistance is gratefully acknowledged.

REFERENCES

ALLEN B.H. & CROSBY M.R., 1987 — *Pseudoscleropodium purum* re-established in South America. *Journal of Bryology* 14: 523-525.

BARDUNOV L.V., 1974 — *Listostebel'nye mkhi Altaya y Sayan* [The mosses of the Altai and Sayan Mts.]. Novosibirsk, Izdatel'stvo Nauka, Sibirskoye Otdelenye: 168 p.

BARDUNOV L.V. & CHERDANTSEVA V.YA.,1982 — *Listostebel'nye mkhi Yuzhnogo Primorya* [The mosses of the Southern Primorye]. Novosibirsk, Izdatel'stvo Nauka, Sibirskoye Otdelenye: 207 p.

BLOCKEEL T.L., 1992 — *Leptodontium gemmascens* (Mitt. ex Hunt) Braithw. *In:* Hill M.O., Preston C.D. & Smith A.J.E. (eds), *Atlas of the bryophytes of Britain and Ireland*. 2. Mosses (except Diplolepideae). Colchester, Harley Books: p. 330.

BUCK W.R., 1998 — Pleurocarpous mosses of the West Indies. *Memoirs of the New York Botanical Garden* 82: 1-400.

CHURCHILL S.P., GRIFFIN D.III & MUÑOZ J., 2000 — A checklist of the mosses of the tropical Andean countries. *Ruizia* 17: 1-203.

CRUM H.A. & ANDERSON L.E., 1981 — *Mosses of eastern North America.* 2. New York, Columbia University Press: pp. 665–1328.

DELGADILLO M.C., BELLO B. & CÁRDENAS S.A., 1995 — LATMOSS. A catalogue of neotropical mosses. *Monographs in Systematic Botany from the Missouri Botanical Garden* 56: 1-191.

DICKSON J.H., 1967 — *Pseudoscleropodium purum* (Limpr.) Fleisch. on St. Helena and its arrival on Tristan da Cunha. *The Bryologist* 70: 267-268.

FRAHM J.-P., 1985 — Afrikanische *Campylopus*-Arten (Dicranaceae, Musci). *Bryophytorum Bibliotheca* 31: 1-216.

GIER L.J., 1980 — A preliminary study of the Thuidiaceae (Musci) of Latin America. *Journal of Bryology* 11: 253-309.

GREENE D.M., 1986 — *A conspectus of the mosses of Antarctica, South Georgia, the Falkland Islands and southern South America*. Cambridge, British Antarctic Survey, Natural Environment Research Council: 314 p.

GREMMEN N.J.M., 1982 — *The vegetation of the Subantarctic islands Marion and Prince Edward*. The Hague, Junk Publishers: 149 p.

GREMMEN N.J.M. & SMITH V.R., 1999 — New records of alien vascular plants from Marion and Prince Edward Islands, sub-Antarctic. *Polar Biology* 21: 401-409.

GROLLE R., 2002 — The Hepaticae and Anthocerotae of the subantarctic and temperate islands in the eastern Southern Hemisphere (90°E to 0°): an annotated catalogue. *Journal of Bryology* 24: 57-80.

HALL K., 1978 — Evidence for Quaternary glaciation of Marion Island (sub-Antarctic) and some implications. *In:* Zinderen Bakker E.M. van sr.(ed.), *Antarctic glacial history and world palaeoenvironments*. Rotterdam, Balkema: pp. 137-147.

HALL K., 1981 — Geology as an aid to climatic-ecological reconstructions: an example from Marion Island. *Lamda* 3: 18-22.

HÄNEL CH. & CHOWN S., 1998 — *An introductory guide to Marion and Prince Edward Island special nature reserves. 50 years after annexation*. Pretoria, Department for Environmental Affairs and Tourism: vi + 80 p.

HAYS J.D., LOZANO J.A., SHACKLETON N.J. & IRVING G., 1976 — Reconstruction of the Atlantic and Western Indian Ocean sectors of the 18 000 B.P. Antarctic Ocean. *Geological Society of America Memoirs* 145: 337-372.

HUNTLEY B.J., 1971 — Vegetation. *In:* Zinderen Bakker E.M. van sr., Winterbottom J.M. & Dyer R.A. (eds), *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965–1966*. Cape Town, A. A. Balkema: pp. 98-160.

IGNATOV M.S. & AFONINA O.M. (eds), 1992 — Check-list of mosses of the former USSR. *Arctoa* 1: 1-85.

JÓHANNSSON B., 1996 — Icelandic bryophytes. Thamnobryaceae, Fontinalaceae, Thuidiaceae, Leskeaceae, Pterigynandraceae and Rhytidiaceae. *Fjörlit Náttúrufræ-∂istofnunar* 30: 1-55.

KABLE E.J.D., ERLANK A.J. & CHERRY R.D., 1971 — Geochemical features of lavas. *In:* Zinderen Bakker E.M. van sr., Winterbottom J.M. & Dyer R.A. (eds): *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965–1966*. Cape Town, A. A. Balkema: pp. 78-88.

LEWINSKY J. & BARTLETT J., 1982 — *Pseudoscleropodium purum* (Hedw.) Fleisch. in New Zealand. *Lindbergia* 8: 177-180.

LIGHTOWLERS P.J., 1986 — Taxonomy and distribution of the subantarctic species of *Tortula. Journal of Bryology* 14: 281-295.

MCDOUGALL I., 1971 — Geochronology. *In:* Zinderen Bakker E.M. van sr., Winterbottom J.M. & Dyer R.A. (eds), *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition* 1965–1966. Cape Town, A. A. Balkema: pp. 72-77.

MILLER H.A., WHITTIER H.O & WHITTIER B.A., 1978 — Prodromus florae muscorum Polynesiae. *Bryophytorum Bibliotheca* 16: 1-334.

MITTEN W., 1876 — List of the Musci and Hepaticae collected by H. N. Moseley, naturalist to H.M.S. "Challenger". *Journal of the Linnean Society Botany* 15: 59-73.

MITTEN W., 1884 — Musci. *In:* Hemsley W.B. (ed.): *Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–76 under the command of Captain George S. Nares, R.N., F.R.S. and the late Captain Frank Tourle Thomson, R.N. Prince Edward Group. Marion Island*. 1 (Botany). London, Longmans & Co., etc.: pp. 197-201 + pl. iii.

MOSELEY H.N., 1874 — On the botany of Marion Island, Kerguelen's Land and Young Island of the Heard group. *Journal of the Linnean Society Botany* 14: 387-388

OCHI H., 1972 — A revision of African Bryoideae, Musci (First part). *The Journal of the Faculty of Education Tottori University Natural Sciences* 23: 1-126.

OCHYRA R. & HERTEL H., 1990 [1991] — Contribution to the moss flora of the subantarctic island Marion. *Polish Botanical Studies* 1: 19-34.

OCHYRA R., 1992 – *Amblyodon dealbatus* (Musci, Meesiaceae) — a bipolar disjunct. *Fragmenta Floristica et Geobotanica* 37: 7-12.

OCHYRA R., 1993 — Antipodal mosses: I. A taxonomic revision of *Holodontium* (Musci, Seligeriaceae). *Fragmenta Floristica et Geobotanica* 38: 75-98.

OCHYRA R., 1998 — *The moss flora of King George Island, Antarctica.* Cracow, Polish Academy of Sciences, W. Szafer Institute of Botany: xxiv + 278 p.
OCHYRA R., 1999a — *Dicranella gremmenii* (Musci, Dicranaceae) sp. nov. from Subantarctic Marion Island. *Fragmenta Floristica et Geobotanica* 44: 219-225.
OCHYRA R., 1999b — *Brachythecium austrosalebrosum* (Musci, Brachytheciaceae) new to Bolivia. *Fragmenta Floristica et Geobotanica* 44: 517–519.
OCHYRA R. & BEDNAREK-OCHYRA H., 1999 — *Racomitrium valdon-smithii* (Musci, Grimmiaceae) sp. nov. from Subantarctic Marion Island. *Fragmenta Floristica et Geobotanica* 44: 209-217.
OCHYRA R., 2003 — Antipodal mosses: VIII. *Valdonia* gen. nov. (Seligeriaceae) from the Kerguelen Province in the Subantarctic. *Cryptogamie, Bryologie* 24: 87-100.
OCHYRA R. & POULSEN R.S., 2003 — Four new moss records from Îles Kerguelen. *Journal of Bryology* 25.
OCHYRA R. & SMITH V.R., 2003 — *Entosthodon productus* Mitt. (Funariaceae) on Marion Island – the first record in the Subantarctic. *Cryptogamie, Bryologie* 24.
OLIVER D., 1874 — List of plants collected by H. N. Moseley, M.A. on Kerguelen's Land, Marion Island and Young Island. *Journal of the Linnean Society Botany* 14: 389-390.
ØVSTEDAL D.O. & GREMMEN N.J.M., 2001 — The lichen flora of Marion and Prince Edward Islands. *South African Journal of Botany* 67: 552-572.
ROGEON M.A. & SCHUMACKER R., 1984 — *Leptodontium flexifolium* (With.) Hampe et *L. gemmascens* (Mitt. ex Hunt) Braithw. sur les toits de chaume de la haute Adour (Hautes-Pyrénées, France). *Bulletin de la Société Botanique du Centre-Ouest Nouvelle Série* 15: 81-102.
SCHALKE H.J.W.G. & ZINDEREN BAKKER E.M. VAN sr., 1971 — History of the vegetation. *In:* Zinderen Bakker E.M. van sr., Winterbottom J.M. & Dyer R.A. (eds), *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965–1966.* Cape Town, A. A. Balkema: pp. 89-97.
SCHOFIELD W.B., 1974 — Bipolar disjunctive mosses in the Southern Hemisphere, with particular reference to New Zealand. *Journal of the Hattori Botanical Laboratory* 38: 13-32.
SCHOFIELD W.B. & CRUM H.A., 1972 — Disjunctions in bryophytes. *Annals of the Missouri Botanical Garden* 59: 174-202.
SCHULZE B.R., 1971 — The climate of Marion Island. *In:* Zinderen Bakker E.M. van sr., Winterbottom J.M. & Dyer R.A. (eds), *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965–1966*. Cape Town, A. A. Balkema: pp. 16-31.
SEPPELT R.D. & RUSSELL S., 1986 — *Fissidens bryoides* Hedw., new to the moss flora of subantarctic Prince Edward Island. *Lindbergia* 12: 57-59.
SMITH V.R. & VERWOERD W.J., 1985 — Geology. In: Pienaar R.N. (Ed): *A Guide to the Geology, Limnology, Fauna and Flora of Marion and Prince Edward Islands*. Pretoria, CSIR: pp. 1-3.
SMITH V.R. & STEENKAMP M., 2001 — Classification of the terrestrial habitats on Marion Island based on vegetation and soil chemistry. *Journal of Vegetation Science* 12: 181-198.
SMITH V.R., 2002 — Climate change in the sub-Antarctic: an illustration from Marion Island. *Climatic Change* 52: 345-357.
SÖDERSTRÖM L. (ed.), 1998 — *Preliminary distribution maps of bryophytes in north-western Europe*. 3. Musci (J–Z). Trondheim: Mossornas Vänner: 1–69.
TOUW A., 1976 — A taxonomic revision of *Thuidium, Pelekium,* and *Rauiella* (Musci: Thuidiaceae) in Africa south of the Sahara. *Lindbergia* 3: 135-195.
TOUW A. & FALTER-VAN DEN HAAK L., 1989 — A revision of Australasian Thuidiaceae (Musci), with notes on species from adjacent regions. *Journal of the Hattori Botanical Laboratory* 67: 1-57.
TOUW A., 2001 — A taxonomic revision of the Thuidiaceae (Musci) of tropical Asia, the western Pacific, and Hawaii. *Journal of the Hattori Botanical Laboratory* 91: 1-136.
VAN ROOY J., 1992 — The genus *Amphidium* in southern Africa. *Lindbergia* 17: 59-63.

VAN ZANTEN B. O., 1971 — Musci. *In:* Zinderen Bakker E.M. van sr., Winterbottom J.M. & Dyer R.A. (eds), *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965–1966*. Cape Town, A. A. Balkema: pp. 173-227.

VERWOERD W.J., 1971 — Geology. *In:* Zinderen Bakker E.M. van sr., Winterbottom J.M. & Dyer R.A. (eds), *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965–1966*. Cape Town, A. A. Balkema: pp. 40-62.

VERWOERD W.J., RUSSELL S. & BERRUTI A., 1981 — 1981 volcanic eruption reported on Marion Island. *Earth Planetary Science Letters* 54: 153-156

WATANABE R., 1972 — A revision of the family Thuidiaceae in Japan and adjacent areas. *Journal of the Hattori Botanical Laboratory* 36: 171-320.

WIGGINTON M.J., 1994 — *Thuidium delicatulum* (Hedw.) Mitt. *In:* Hill M.O., Preston C.D. & Smith A.J.E. (eds), *Atlas of the bryophytes of Britain and Ireland*. 3. Mosses (Diplolepideae). Colchester, Harley Books: p. 253.

WU P.-CH., WAI M.-Z. & ZHONG B.-G., 2002 — Thuidiaceae. *In:* Wu P.-Ch., Crosby M.R. & He S. (eds), *Moss flora of China. English Version.* 6. Hookeriaceae–Thuidiaceae. Beijing – New York, Science Press and St. Louis, Missouri Botanical Garden: pp. 150–207.

ZANDER, R.H. 1972 — Revision of the genus *Leptodontium* (Musci) in the New World. *The Bryologist* 75: 213-280.

ZINDEREN BAKKER E.M. VAN Sr. 1973 — The glaciation(s) of Marion Island (sub-Antarctic). *In:* Zinderen Bakker E.M. van sr. (ed.): *Palaeoecology of Africa, the surrounding islands and Antarctica*. 8. Cape Town, A.A. Balkema: pp 163-178.

Note added in proof:

When bryologizing on Marion Island in April 2003 we made some new observations on populations of *Thuidium delicatulum*. We found that the species grows well on the island and seems to expand. At station No. 1, besides some scattered groups under a canopy of *Blechnum penna-marina*, a large patch of about 1 m^2 consisting exclusively of *Th. delicatulum* (*Ochyra 1999/03*, KRAM) was discovered, forming a yellowish-brown carpet covering the fern. In addition, a new population was observed in the same general area. The latter is the largest stand of the species hitherto found on the island. The locality data for this fourth locality are as follows:

Marion Island: NE of Junior's Kop, lat. 46°52'54.0''S, long. 37°50'09.1''E, alt. 163 m, in *Acaena magellanica–Blechnum penna-marina* slope community on very damp soil; *Thuidium* patch occupies approximately 4 m^2, covering *ca* 80% of the area, surrounded by *Sanionia uncinata* as dominant in the moss layer; 24 Apr. 2003, *Gremmen G03-682B* (KRAM).