Pireella cymbifolia (Pterobryaceae) new to the flora, with comments on sea level and other factors influencing the phytogeography of Bermuda

The isolated North Atlantic island of Bermuda, lying 1000 km ESE of Cape Hatteras, North Carolina, USA, has received scant attention from bryologists since the last compilations of nearly a century ago (EG Britton, 1918; Evans, 1918), plus a few additions (Andrews, 1923; Dixon, 1936). Of the mosses listed by EG Britton (1918), those that are not widespread in both Europe and North America are of New World distribution, with a number having connections with the southern United States and particularly the West Indies. In the course of palaeontological investigations, I made collections of bryophytes in various localities in Bermuda, particularly at the entrances of caves. Among the specimens yet identified is one species not previously recorded from the island.

Pireella cymbifolia (Sull.) Cardot, new to Bermuda

BERMUDA. Hamilton Parish, NW end of isthmus between Harrington Sound and Castle Harbour, *ca* 200 m NE of 32 20′ 50.9″N, 64 42′46.0″W, Fern Sink Cave (Olson *et al.*, 2005: 229; Grand Canyon Cave of Hearty *et al.*, 2004), 11 February 2004, vertical limestone in deep crevice at edge of dark zone at entrance of cave, S. L. Olson and F. V. Grady, *Olson BDA-04-2* (in US). Det. H. Robinson.

Pireella cymbifolia occurs in peninsular Florida (Breen, 1963), practically throughout the West Indies, and from Mexico to Brazil on the mainland where it may occur either on treetrunks or limestone (Buck, 1998). The Bermuda record is of more than local interest as it constitutes the northernmost occurrence of the genus *Pireella* and the northernmost outpost of the Pterobryaceae in the Western Hemisphere, although the family occurs as far north as Honshu, Japan, in the western Pacific (Noguchi, 1989).

The persistence of such an essentially tropical species in temperate Bermuda can probably be explained by the unique nature of the collecting locality, which is a great vertical fault cleft in the limestone of the Bermuda platform, unusual in an area that is now tectonically inactive. This cleft, over 2 m wide, with sheer walls, descends at a steep incline until it intersects one of Bermuda's many karstic cave systems. The *Pireella* was collected deep in this cleft but where light from above still penetrated, although at this point the floor of the cleft was some 4 to 5 m below ground surface. This environment would provide complete protection from wind and perhaps salt spray carried by storms, whereas emanations of cave air would ameliorate the possible effects of heat, cold, or desiccation at the surface. Direct sunlight could reach the walls of the crevice where the moss was growing for only a few minutes each day, but overgrowing vegetation, now consisting only of introduced trees and brush, essentially prevents even this.

Four of the main forces that have effected the composition of the flora of Bermuda have long been recognized (Lefroy, 1884; Verrill, 1901–1902; NL Britton, 1918, Sterrer *et al.*, 2004)---human agency, birds, currents, and wind. Of perhaps even greater importance, have been isostatic changes in sea level.

Bermuda has been a British colony since it was settled in 1609 and in the ensuing centuries hundreds of species of plants were deliberately introduced to the island for agricultural, ornamental, or other purposes (Verrill, 1901–1902; Sterrer *et al.*, 2004). Bermuda was also a logical stopping point for commercial vessels returning from British possessions in the West Indies such as the Bahamas, Barbados, and Jamaica. Bryophytes might easily have been introduced to Bermuda as adventives in potted plants brought from the West Indies and elsewhere so that an anthropogenic origin is conceivable for almost any species of bryophyte occurring on the island, particularly terricolous ones.

Some 60 species of birds use Bermuda as a stopover on a major transoceanic flyway from North America to the Neotropics and another 150 species are regular vagrants (Amos, 1991), so that transportation of plant propagules in the digestive tract or clinging to feathers is another potential source of plant colonists, although unlikely to be of much importance for any bryophytes except perhaps a few aquatic species. As Bermuda lies in the northward flowing Gulf Stream current that originates in the West Indies, waterborne transportation of Antillean fauna and flora to Bermuda's shores is another possible factor in introducing plants (Verrill, 1901–1902), but again not very likely for salt-intolerant bryophytes.

Famous as the setting for Shakespeare's play *The Tempest*, Bermuda is regularly struck by forceful hurricanes, many of which first pass over parts of the West Indies (Tucker, 1982). The small anemochores (wind-borne fragments) of bryophytes, both sporophytic and gametophytic, are quite likely to be transported to Bermuda in this fashion. In the southern hemisphere, floristic similarities in bryophyte communities were found to have a stronger correlation with 'wind connectivity than with geographic proximities' (Muñoz *et al.* 2004: 1144). Wind would seem to be the more likely source of *Pireella cymbifolia* in Bermuda, given the recondite locality in which the plants were found and the fact that this species does not normally grow on soil, so as to make it less likely to have arrived by human aid.

By far the predominant factor affecting the survival, as opposed to colonization, of the flora of Bermuda, however, is isostatic change in sea level. During glacial lowstand events, which typically last much longer than interglacial highstands that reduce land area through flooding, sea levels fall below the rim of the Bermuda platform exposing a land area of about 1000 km^2 (Olson *et al.*, 2005). In the present interglacial (Marine Isotope Stage [MIS] 1), sea levels have risen so as to flood the platform, reducing land area by some twentyfold to 56 km^2. In the past million years, sea levels have risen to even greater heights in at least three interglacials---MIS 5, 9, and 11 (Olson, Hearty & Pregill, 2006). Each of these, including the present interglacial, are known to have caused extinctions among terrestrial vertebrates and breeding seabirds, presumably through reduction in land area and dramatic change in ecological conditions (Olson & Hearty, 2003; Olson *et al.*, 2005; Olson *et al.*, 2006). The most extreme of these was MIS 11, when, 400 000 years ago, sea levels rose to more than 20 m above present (Hearty *et al.*, 1999; Olson & Hearty, 2003), reducing Bermuda to a few islets, many probably subject to storm overwash (Olson & Hearty, 2003). Any endemic plant of Bermuda, of which Sterrer (1998) lists 17, including two mosses (down from 61 endemics listed by NL Britton, 1918), that could not survive in these conditions either differentiated in less than 400 Kyr or must be suspected as not being a true endemic. Actually, the span of time available for differentiation may be even less, as in the last interglacial (MIS 5), sea level rose 6 to 9 m above present 120 000 yr ago (Hearty & Neumann, 2001; Hearty, 2002), reducing land area to considerably less than the existing 56 km^2 (Hearty *et al.*, 2004), so that the environment would have been even more maritime than today, with higher levels of salt stress. In the historic period, the fiercer storms have repeatedly caused major dieoffs of vegetation from salt spray (Tucker, 1982).This would mean that colonization of plants carried by wind would have been much more likely during glacial periods than during interglacials and that on Bermuda the present manifestation of *Pireella cymbifolia,* for example, is probably no older than the last glacial period.

The period of time available for the differentiation of most endemic plants of Bermuda may well be less than 120 Kyr and certainly no more than 400 Kyr. These time constraints must be taken into consideration in any systematic analysis of the flora of Bermuda or the degree of genetic differentiation of any of its elements.

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