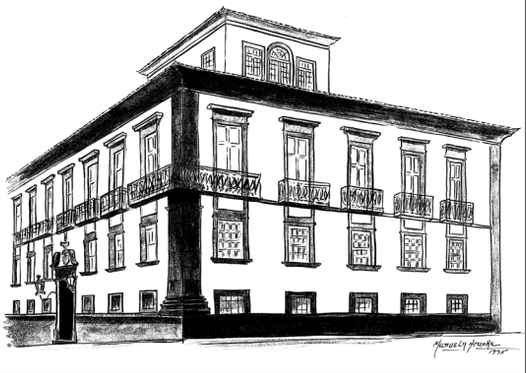

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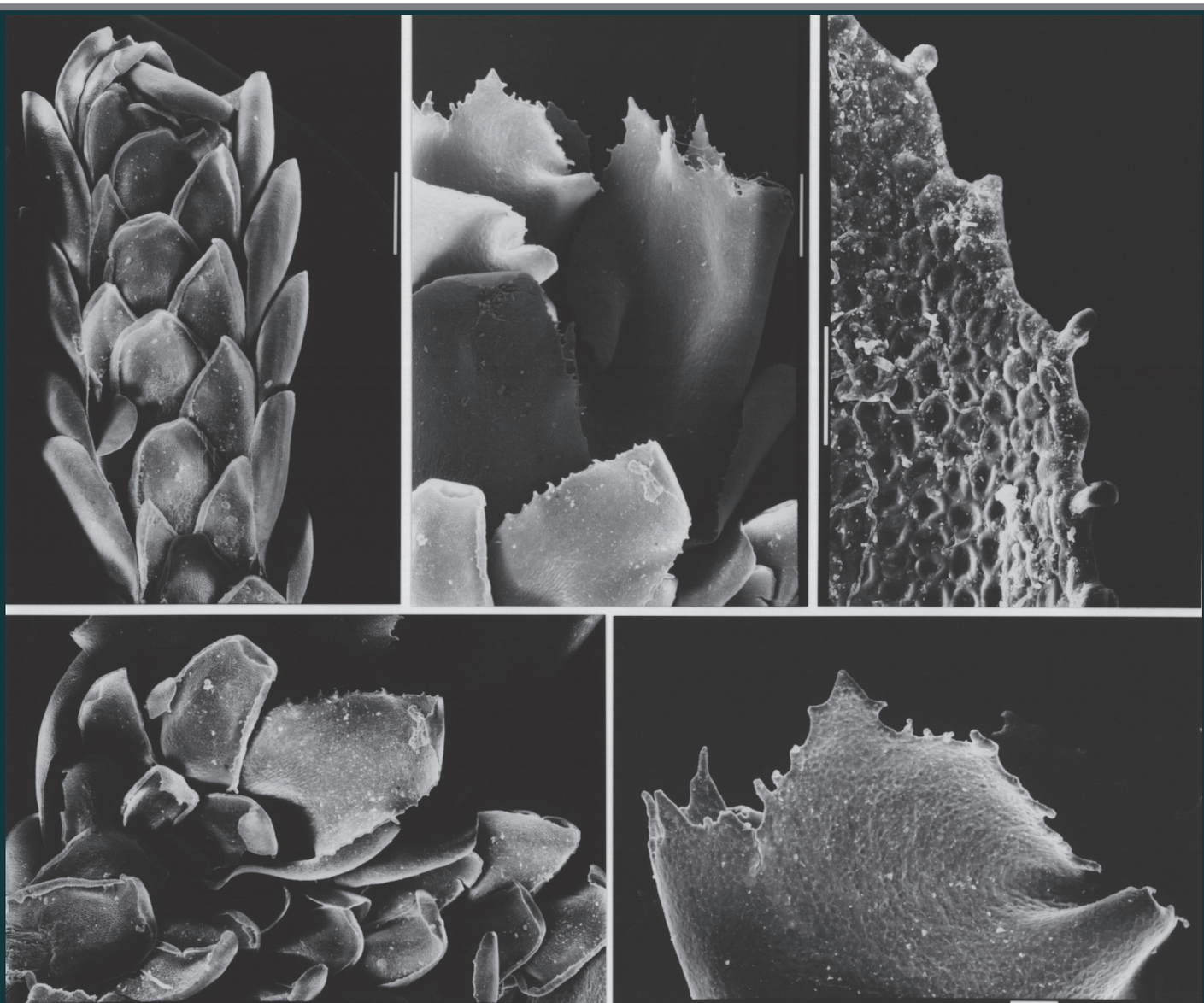

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Manuel José Biscoito
Departamento de Ciência e de Recursos Naturais da CMF
E-mail: manuel.biscoito@cm-funchal.pt

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**Secretariado e correspondência // Address:**
Museu de História Natural do Funchal
Rua da Mouraria, 31
9004-546 Funchal
Madeira – Portugal
Telefone // Phone: (+351) 291 229761
Fax: (+351) 291 225180
E-mail: mmf.pubs@cm-funchal.pt

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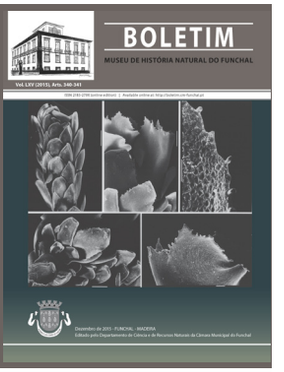

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# Prof. Dr. Lipke Bijdeley Holthuis and the Canary Islands carcinology: a tribute

By José A. González [1]

With 4 figures

*[1] EMAP – Ecología Marina Aplicada y Pesquerías, i-UNAT, Universidad de Las Palmas de Gran Canaria, Campus Universitario de Tafira, 35017 Las Palmas de Gran Canaria, Spain. E-mail: pepe.solea@ulpgc.es*

**ABSTRACT**: This paper is dedicated to the memory of the Dutch carcinologist, Lipke Bijdeley Holthuis (1921-2008) as a tribute to his legacy. His carcinological interests and his contribution to the carcinology of the Canary Islands are summarized. His discoveries in the Canaries within the framework of the CANCAP project, amongst other great scientific expeditions in the eastern Atlantic, are referenced. Also highlighted is the importance he attributed to taxonomy.

**Keywords**: L. B. Holthuis, tribute, carcinology, Canary Islands.

**RESUMO**: Este artigo é dedicado à memória do carcinologista holandês Lipke Bijdeley Holthuis (1921-2008), constituindo um tributo ao seu legado. O autor sumariza os interesses carcinológicos de L. B. Holthuis e as suas contribuições para a carcinologia das Ilhas Canárias. É também feita referência à sua contribuição no âmbito do projeto CANCAP, entre outras grandes expedições científicas no Atlântico oriental, e à importância que ele atribuía à taxonomia.

**Palavras-chave**: L. B. Holthuis, tributo, carcinologia, Ilhas Canárias.

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Professor Dr. Lipke Bijdeley Holthuis was a "living encyclopaedia" who dedicated his exceptional and interesting life to the taxonomy and systematics of Crustacea, zoological nomenclature and the history and bibliography of natural history. He was also regarded as "The institutional Memory" of the Leiden Museum where he worked for 67 years. Holthuis is considered one of the "undisputed greats" of carcinology and "the greatest carcinologist of our time" (Fransen & van Oijen, 2008; Pieters & Cadée, 2009; Fransen *et al*., 2010).

An extensive Holthuis' biography was published by Fransen *et al*. (2010), including his early years, education, work at the Rijksmuseum van Natuurlijke Historie (now Naturalis) in Leiden, collecting and collections, carcinological interests, *Crustaceana* and editorship, the history of natural history, nomenclature, teaching, awards, "Krabbelaria" (he collected everything related to Crustacea), and publication statistics.

His scientific career started in 1941 with his first publications. His last publication was issued in 2009, many months after he passed away. In those 69 years (1941-2009), he produced 620 titles. He was the most prolific carcinologist of the 20th century. This stream of publications resulted in the description of 428 taxa new to science, including 338 new species (Fransen & van Oijen, 2008; Fransen *et al*., 2010). Except for a few plant taxa, these were all crustaceans, with a clear bias towards the decapods (90%) (Fransen *et al*., 2010). For a complete listing of all publications by L. B. Holthuis see: www.repository.naturalis.nl, or also see Fransen *et al*. (2010).

## L. B. Holthuis' carcinological interests and contributions to the Canary Islands carcinology

Holthuis studied various groups of Crustacea: stomatopods (*e.g*. Holthuis, 1941, 1984; Holthuis *et al*., 1980), isopods (*e.g*. Holthuis, 1949b), mysidaceans (*e.g*. Holthuis & Sivertsen, 1967), cirripeds (*e.g*. Holthuis & Sivertsen, 1967), and groups of decapods like shrimps, lobsters (Holthuis, 1983), and true crabs (*e.g*. den Hartog & Holthuis, 1984).

A new isopod species from the Canary Islands, *Zonophryxus dodecapus* (Isopoda, Dajidae), was described by Holthuis (1949b). Many years later, a colour photograph of this ectoparasite attached to the top of the cephalothorax of a narwal shrimp (*Plesionika narval*) from the type locality, was first published by me (González, 1995). Another isopod (same species?) was also observed by me on stripped soldier shrimps (*Plesionika edwardsii*) from both the Canary and the Cape Verde Islands.

In the late 1940's Holthuis started to devote more and more studies to caridean and stenopodidean shrimps (*e.g*. Dohrn & Holthuis, 1950; Holthuis & Maurin, 1952; Lewinsohn & Holthuis, 1978). The 1955 publication of keys to help identify recent genera of these groups of shrimps (Holthuis, 1955) was one of his early seminal works that resulted from these studies. His major research effort was directed towards these groups for the rest of his life, culminating in a much revised and extended version of the publication in the early 1990s (Holthuis, 1993).

A remarkable contribution to the carcinology of the Canary Islands was 'The Caridean Crustacea of the Canary Islands' (Holthuis, 1949a). This paper is based mainly on littoral material collected in the Canaries during 1947 by Dr. G. Thorson of the Universitets Zoologiske Museum at Copenhagen and, to a lesser extent, by Dr. C. O. van Regteren Altena of the former Rijksmuseum van Natuurlijke Historie at Leiden. At that time, the shrimp fauna of the Canary Islands was very poorly known (just seven species, mainly reported by Viera y Clavijo (1799-1810), Brullé (1837-1839), Heller (1863), Koelbel (1892), Rathbun (1900) and Balss (1925)). The material examined by Holthuis (1949a) consisted of 12 species, nine of which were not recorded previously from the Canary Islands, bringing the total number of known caridean species from that archipelago up to 16. As the very few data about the carcinological fauna of the region were scattered over several publications, Holthuis thought it useful to include in his paper, a compilation of all the information about the Canary Islands Caridea (deep-sea species excluded) known to him. Holthuis pointed out that one of the main reasons that the shrimps of the Canaries were so little known, was probably the inaccessibility of the larger part of the shores, which made collecting possible only at certain places and at certain times.

The work of Holthuis (1949a) is, therefore, the first annotated catalogue of the caridean shrimps from the Canary Islands, including the first record of *Gnathophyllum americanum* (Gnathophyllidae), *Periclimenes scriptus* (Palaemonidae), *Latreutes fucorum*, *Lysmata seticaudata* and *Trachycaris restricta* (Hippolytidae), *Aegaeon cataphractus* (as *Pontocaris cataphracta*) and *Philocheras trispinosus* (as *Pontocaris trispinosus*) (Crangonidae). The

presence of *Gnathophyllum elegans* (Gnathophyllidae), *Palaemon serratus*, *P. xiphias* (Palaemonidae) and *Athanas nitescens* (Alpheidae) in the Canary Islands was also confirmed by Holthuis (1949a).

As a result of the Danish scientific expedition to the coasts of Tropical West Africa in 1945-1946 on board the R/V "Atlantide", Holthuis (1951) made a remarkable contribution to the knowledge of the Caridea of this eastern Atlantic region, including the first record of *Hippolyte coerulescens* (Hippolytidae) from the Canary Islands.

Based on specimens from the North Atlantic deep-sea collected by the 1910 Norwegian expedition on board the vessel "Michael Sars", Sivertsen & Holthuis (1956) recorded many decapod crustaceans for the first time from the Canary Islands and adjacent waters: *Acanthephyra tenuipes* (as *A. gracilipes*), *A. stylorostratis*, *Heterogenys microphthalma* (as *Acanthephyra microphthalma*), *Hymenodora gracilis*, *Meningodora vesca* and *Notostomus distirus* (Acanthephyridae), *Systellaspis debilis* (Oplophoridae), *Nematocarcinus ensifer* (Nematocarcinidae), *Heterocarpus grimaldii* and *Plesionika heterocarpus* (Pandalidae). The presence of *Stylopandalus richardi* (Pandalidae) in the Canary Islands was also confirmed by Sivertsen & Holthuis (1956).

Holthuis also kept his interest in other groups, with numerous studies appearing on Dendrobranchiata and various lobsters groups. This is reflected in the extensive reference catalogues he accumulated for these taxa over the past six decades (Fransen *et al*., 2010).

As a result of the French expeditions on board the "Travailleur" (1882) off Morocco and the Canaries, and the "Talisman" (1883) between the Strait of Gibraltar and the Cape Vert in Senegal, Holthuis (1980a) reported on the identity of *Benthonectes filipes* (as *Hapalopoda investigator*) (Benthesicymidae) and other shrimps collected.

With the aid of these catalogues he prepared the annotated FAO species catalogues on shrimps and prawns (Holthuis, 1980b, 1987), lobsters (Holthuis, 1981a, 1987, 1991), and true crabs (Holthuis, 1981b), which are of interest to fisheries.

His studies on Brachyura gained momentum when his cooperation with Raymond B. Manning started in the 1970s (Fransen *et al*., 2010). The first major product of this cooperation was the impressive study of West African Brachyuran Crabs (Manning & Holthuis, 1981), followed by the revision of deep-sea red crab family Geryonidae (Manning & Holthuis, 1989), among other crab families.

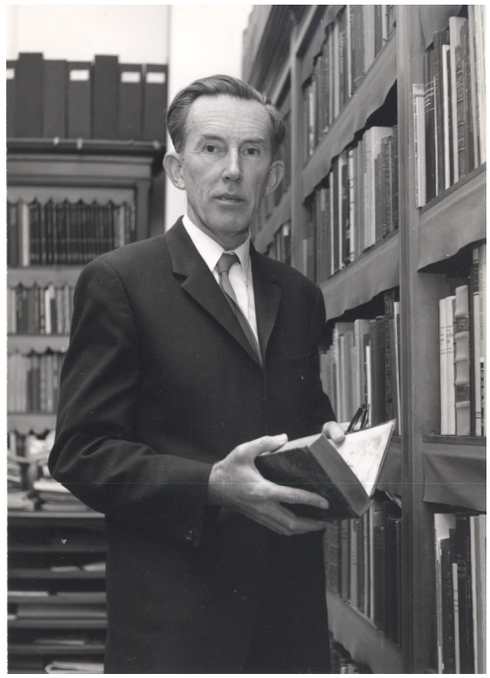

**Fig. 1** – Lipke Bijdeley Holthuis in 1973.

Holthuis *et al*. (1980) first recorded the brown spiny lobster *Panulirus echinatus* (Palinuridae) from the Canaries, and reported on its restricted distribution in a few localities of both the western (NE Brazil and off-shore islands) and eastern (Canary and Cape Verde Islands) Atlantic Ocean.

Manning & Holthuis (1981) surveyed the West African marine brachyuran crab fauna, comprising 218 named species in 120 genera and 26 families. Sixteen new genera and 24 new species were recognized. Several of these brachyuran species were reported from the Canary Islands, including the first record of *Detocarcinus balssi* (as *Neotroglocarcinus balssi*) (Cryptochiridae).

Quoting Fransen *et al*. (2010), "Holthuis insisted that taxonomy was a core biological discipline…This was even during times when taxonomy was dismissed as irrelevant and people flocked to new disciplines, such as molecular science… Whilst modern day systematic scientists are often forced by the vagaries of funding and the bureaucratic pressure to devote the majority of their research time to the pursuit of phylogenetic publications, invariably in higher profile journals, we would do well to remember his firm stance to focus on collection expansion and that most fundamental of biological sciences, taxonomy.".

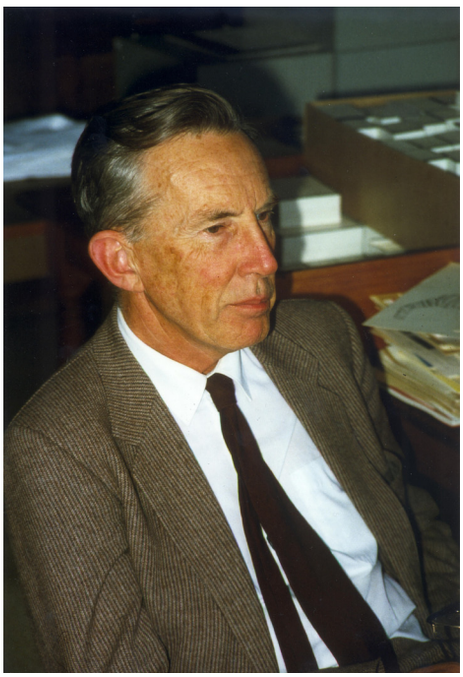

**Fig. 2** – Lipke Bijdeley Holthuis in 1982.

### CANCAP Expeditions and its encouragement to the carcinology of the Canary Islands

In the framework of the CANCAP (Dutch 'Project for marine biological research in the CANarian-CAPeverdean Region') (1976-1986), seven expeditions were made on board the R/V "Tydeman" to the North Atlantic, between Morocco and Senegal, as well to the Macaronesian archipelagos. These expeditions included a series of shore collecting in Canary Islands' waters (den Hartog, 1984). As a result, an enormous amount of carcinological material was examined and many papers were published. For instance, a note about an interesting association between Zoantharia species and the crab *Platypodiella picta* (Xanthidae), recorded at this time for the first time from the Canaries, was published by den Hartog & Holthuis (1984).

I had the opportunity to lead the fishing survey campaign "Canarias 85" on board the R/V "Taliarte" in which, during June and July of 1985, we collected a lot of fishes and decapod crustaceans with longlines and pots in all the islands of the Canary archipelago between 100 and 1000 meters of depth. We received help from Lipke Holthuis and Charles Fransen for the identification of several crustaceans in subsequent years. The faunistic and fishing results were published by González *et al*. (1988).

In the late 1980's and early 1990's, Fransen visited me two or three times at my laboratory in the 'Instituto Canario de Ciencias Marinas' (at that time 'Centro de Tecnología Pesquera de Gran Canaria'), in order to establish a cooperation between his collecting activities and our identification works. Holthuis became curator of the Division of Crustacea of the former Rijksmuseum van Natuurlijke Historie at Leiden, in 1950 and remained in this position until his retirement in 1986. At that time, Fransen was a researcher at this Museum and working in the Holthuis' group. Within that cooperative atmosphere, Fransen talked to me about Prof. Dr. Holthuis, handed me his last publications (Fransen, 1990, 1991a, 1991b, among others) and encouraged me to enlarge my research from fishes to decapod crustaceans.

On the occasion of the *5th Symposium Fauna and Flora of the Cape Verde Islands*, held at Leiden in October of 1989, Charles Fransen kindly invited me to stay for a week at the Museum and introduced me to Holthuis. My colleague and friend Manuel Biscoito, a marine zoologist working as curator at the Funchal Natural History Museum, accompanied us during that unforgettable visit to Holthuis' impressive office, who greeted us kindly, offering us a cup of tea that he prepared at the time and maintaining an interesting conversation with us. Another series of events took place those days. Manuel contributed to this Symposium with probably his seminal work on deep-sea decapod crustaceans (latter appeared as Biscoito, 1993), and kindly helped me with the English of my presentation on the biology of the Macaronesian parrotfish. Therefore, it is absolutely true that during that stage of my career, I received important professional influences from Lipke B. Holthuis, Charles Fransen and Manuel Biscoito.

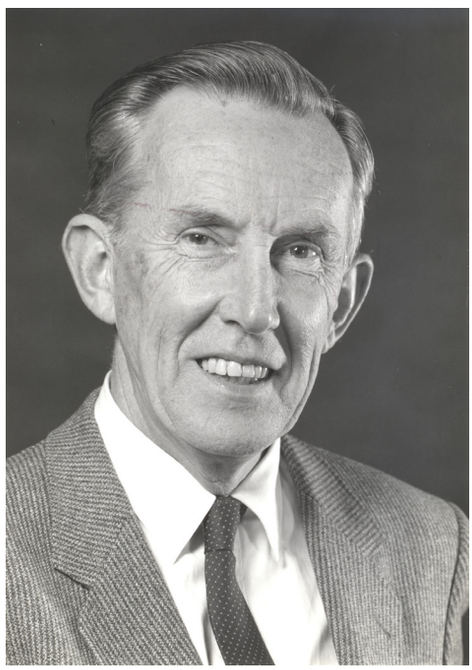

**Fig. 3** – Lipke Bijdeley Holthuis in 1995.

My studies on crustaceans gained momentum when this cooperation with these colleagues commenced and also due to the fact we had to deal with many specimens belonging to new or poorly known species from the Canary Islands waters. Since 1988 (González *et al*., 1988), to date, fishes apart, I have authored or co-authored 53 titles on taxonomy, biology, conservation or fisheries of mysidaceans, cirripeds and mainly decapods (94%) (Triay-Portella *et al*., 2014; Biscoito *et al*., 2015). Fourteen of these articles (26%) appeared before December of 1995 (mainly in national or Macaronesian journals) and 39 publications (74%) after this date (mainly articles in peer-reviewed journals and books).

In early 1995, I sent a letter (there was no email) to Fransen, asking for his critical review of a draft manuscript on the decapod crustaceans from the Canary Islands. In that letter I also asked for a prologue, as well as photographs of the great European carcinologists whose work has contributed to the knowledge of decapods of the Canaries to illustrate my work. Then something amazing happened. I was informed by Holthuis that Fransen was currently participating in expeditions in Asia and would not return before the scheduled date of the publication of the manuscript. Holthuis therefore kindly accepted to address all my requests in Fransen's absence. As the manuscript was in Spanish and Holthuis' knowledge of this language was very limited, mistakes on records and/or distribution of species from the Canaries are attributable only to me. Holthuis gave me excellent photographs to illustrate the history chapter on carcinology of the Canary Islands (see González, 1995), and also prepared a magnificent prologue to accompany his portrait. Until the last day of my life I shall be indebted to Holthuis and Fransen; their advice, literature, support and assistance made the publication of my annotated and illustrated "Catálogo de los crustáceos decápodos de las islas Canarias" possible, including 266 decapod species regularly occurring in the Canary Islands waters, with more than 200 original colour photographs of more than 100 species.

In his preface (Holthuis, 1995) of my catalogue (González, 1995), Holthuis (Fig. 3) kindly wrote that, "like the book of Zariquiey (1968) on the Iberian decapods is being used throughout the Mediterranean and western Europe by all professionals and amateur carcinologists, this publication of Dr. González will transcend far beyond the area of the Canary Islands and shall also be consulted by specialists and enthusiasts in the broadest sense.".

I am convinced that the teachings and encouragement of my three mentors were instrumental in my career as a marine taxonomist, part-time between carcinology and ichthyology due to many research projects in the Canary Islands region and Macaronesia *sensu lato* (Cape Verde Islands and southern Morocco and Western Sahara included) in which I have participated. My great fortune and opportunity was that my three mentors came my way, encouraging me to feel passion for taxonomy, nomenclature and the etymology of marine fishes and crustaceans.

**Fig. 4** – Lipke Bijdeley Holthuis in 2007.

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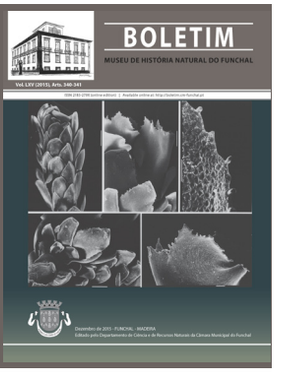


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# Morphologic boundaries of *Porella canariensis* (Web.) Underw. (Porellaceae, Marchantiophyta) in Madeira (Portugal)

By Susana Fontinha [1, 2 *], Manuela Sim-Sim [2, 3], Cecília Sérgio [2, 3] & César Garcia [2]

With 4 figures,1 table and 1 appendix

[1] *ISOPlexis Universidade da Madeira, Campus da Penteada, 9000-390 Funchal, Madeira, Portugal.*

[*] *Corresponding author: susanafontinha@gov-madeira.pt*

[2] *Museu Nacional de História Natural e da Ciência, cE3c – Centre for Ecology, Evolution and Environmental Changes, Rua da Escola Politécnica, 58, 1250-102 Lisboa, Portugal.*

[3] *Faculdade de Ciências da Universidade de Lisboa, cE3c – Centre for Ecology, Evolution and Environmental Changes, Lisboa, Portugal.*

**ABSTRACT**: In Madeira a total of 55 populations of *Porella* were analyzed. Among the 44 populations of *P. canariensis*, 73% tasted acrid, 41% presented mature perianths and 23% presented mature spores with 40 (50-60) 80 µm diameter 21% of them being longer than usual for the genus; female individuals were relatively frequent (52%) whereas males were scarce (7%); female and male shoots were found intermixed in 27% populations and 14% were sterile. Among the 11 populations of *P. obtusata* none tasted acrid, 18% presented mature perianths, 9% presented mature spores of 50 µm diameter, no males were identified and female stems were present in 73% populations, and 27% were sterile. Sixty morphological characters were scrutinized, including 15 quantitative traits, 16 ratios and 29 qualitative traits.

Despite partial overlap between species in form, there are morphological characters that can be used to distinguish them without difficulty, such as: median cells size; lobe, lobule and underleaf width; lobule and underleaf surface; decurrent part of the lobe and the underleaf; margin of the female and male bracts and perianths.

**Keywords**: Liverwort, Jungermanniopsida, *Porella*, phenotypic plasticity, Macaronesia.

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**RESUMO**: Foram analisadas um total de 55 populações de indivíduos do género *Porella* na Madeira. Em 44 populações de *P. canaiensis*, 73% apresentam sabor picante, 41% têm periantos maturos e 23% compreendem esporos maturos com 40 (50-60) µm de diâmetro, dos quais 21% são maiores do que o referido para o género. Os indivíduos femininos são relativamente frequentes (52%), os masculinos são raros (7%), foram encontrados ramos femininos e masculinos misturados em 27% das populações e 14% apresentam ramos estéreis.

Em 11 populações de *P. obtusata* nenhuma apresenta sabor picante, 18% contemplam periantos maturos, 9% compreendem esporos maturos com 50 µm de diâmetro, não foram identificados indivíduos masculinos e os femininos estão presentes em 73% das populações, 27% apresentam ramos estéreis.

Foram examinados sessenta carateres morfológicos, dos quais 15 são quantitativos, 16 correspondem a cálculos entre estes e 29 são qualitativos.

Embora em relação à morfologia estas espécies se sobreponham parcialmente, existem carateres morfolóicos que podem ser usados para as distinguir, como: o tamanho das células medianas; a largura do lobo, lobulo e anfigastro; a superfície do lobulo e anfigastro; a parte decorrente do lobulo e anfigastro; a margem da bráctea feminina, da masculina e do perianto.

**Palavras-chave**: Hepática, Jungermanniopsida, *Porella*, plasticidade fenotípica, Macaronésia.

## INTRODUCTION

Species of *Porella* L. (Porellaceae) are dioecious foliose liverworts, characterized by deeply conduplicate-bilobed, incubous leaves with a large dorsal lobe and small ventral lobule with very short keel, large unlobed underleaves and gametangia developing on short lateral branches; the sporophytes are ephemeral thus rarely seen, spores are small (35-50 µm diameter) and leaf or shoot fragments function as asexual propagules (Bischler *et al*., 2006). *Porella* presents high phenotypic plasticity with species showing significant morphological intergradations (Bischler *et al*., 2006).

*Porella canariensis* (Web.) Underw. has often been considered to be conspecific with *P. arboris-vitae* (With.) Grolle or *P. obtusata* (Taylor) Trevis, or a transition between them: Casares-Gil (1919) refers *P. canariensis* (sub *Madotheca canariensis* Nees) as doubtful species, considering it a variety of *P. arboris-vitae* [sub *Madotheca laevigata* (Schrad.) Dumort. var. *subintegra* Kaal]; Machado (1925) states that *Madotheca laevigata* (Schrad.) Dumort. var. *subintegra* Kaal can match *Madotheca canariensis* Nees, which is very polymorphous and may be a transition to *P. obtusata* [sub *Madotheca thuja* (Dicks.) Dum.]; Trabut (1941) notes *P. canariensis* (sub *Madotheca canariensis* Nees) and states that can be a transitional form between *P. arboris-vitae* (sub *M. laevigata*) and *P. obtusata* (sub *M. thuja*); also Grolle (1975) questioned whether *P. canariensis* is an independent species.

The first reference to the occurrence of *Porella* in Madeira is in the 19th century (Nees & Montagne, 1836; Barker-Webb & Berthelot, 1840; Cosson, 1868). Overall, until the mid-20th century, eight species were reported from Madeira. Recent studies have reduced the number of species to four that correspond to 50% of the *Porella taxa* reported from Europe (Frey *et al*., 2006): *P. canariensis*, *P. cordaeana* (Hüb.) Moore, the endemic *P. inaequalis* (Gottsche ex Steph.) Perss. and *P. obtusata* (Schumacker & Váňa, 2000; Söderström *et al*., 2002; Fontinha, 2004; Bischler, 2004; Bischler *et al*., 2006; Ros *et al*., 2007; Sérgio *et al*., 2008; Fontinha *et al*., 2010).

Morphologic and genetic research considering nine species of *Porella* from Europe and Macaronesia showed that continental populations of *P. arboris-vitae*, *P. canariensis* and *P. obtusata* were clearly distinct whereas the Madeiran samples of *P. canariensis* and *P. obtusata* overlapped partially (Bischler *et al*., 2006).

High levels of isozyme or RAPDs variation have been reported for *P. canariensis*, *P. obtusata*, *P. arboris-vitae* and *P. platyphylla* (Therrien *et al*., 1998; Freitas & Brehm, 2001; Wyatt *et al*., 2005; Bischler *et al*., 2006).

More recently, Lopes *et al*. (2014) clearly distinguish *P. canariensis* and *P. obtusata* and support the existence of two molecular lineages within *P. canariensis*, in contrast to Hentschel *et al*. (2007) and Heinrichs *et al*. (2011). This supports earlier indications of a higher genetic diversity in Madeira than in other parts of Macaronesia (Freitas & Brehm, 2001; Fontinha, 2004; Bischler *et al*., 2006).

*Porella canariensis* is a close relative of *P. obtusata* and both species share overall morphology and ecology, being the variation of *P. canariensis* and *P. obtusata* higher on Madeira than on Europe or other Macaronesian Archipelagos (Bischler *et al*., 2006).

Considering the above, the present study aims to i) clarify the morphologic boundaries of *P. canariensis*, ii) compare the morphologic boundaries of *P. canariensis* with those of *P. obtusata*.

## MATERIALS AND METHODS

### Sampling

Forty four *P. canariensis* populations were sampled, being 39 from Madeira Island, four from Porto Santo Island and one from Deserta Grande Island; additionally 11 populations of *P. obtusata* from Madeira Island were surveyed. The populations are defined as continuous carpets ranging from 10 $cm^2$ to 20 $cm^2$ in cover, each comprising several tens of stems (Bischler *et al*., 2006). From each population 10 shoots were selected and for each, five measurements were performed on the gametophyte and one on the gynoecia. Each shoot was considered an individual. Voucher specimens (Appendix 1) are housed in the herbarium MADJ.

Other herbarium vouchers of *P. canariensis*, *P. obtusata* and *P. arboris-vitae* were examined from Portuguese herbaria: COI, LISU, MADJ, MADS and from other herbaria such as BM, BONN, JE, MO, PC, STAATL, STR and TFC as well as private collections such as from Bischler, Düll, Hübschmann and Mues. Herbaria abbreviations follow Vitt *et al*. (1985) and *Index Herbariorum*. Type-specimens were observed.

*Porella* species are dioecious, thus stems with reproductive structures analysed were female or male. Some populations were sterile.

The plant material used in the scanning electron microscope was fixed, dehydrated and prepared in accordance to Sim-Sim (1999). Scanning electron microscopy (SEM) observations of dry plant material were made with a JEOL (JSM 5200 T220).

### Morphological characters

A total of 60 morphological characters were selected, following previous studies (Bischler *et al*., 2006; Fontinha, 2004; Fontinha *et al*., 2010). Fifteen quantitative morphological characters were considered: lobe length (Lc), lobe width (Ll), diameter of lobe cells (Lcm), lobule length (llc), lobule length without deccurence (lcsd), lobule width (ll), diameter of lobule cells (lcm), underleaf length, decurrent part included (ac), underleaf length without deccurent part (acsd), underleaf width (al), diameter of underleaf cells (acm), stem width (Rl), perianth length (Pc), perianth width (Pl), spore diameter (Et). Sixteen ratios were also into account: Lobe surface (Rls), lobule surface (Rls), underleaf surface (Ras), lobule decurrent part (Rld), underleaf decurrent part (Ra), lobule width / stem width (Rb), underleaf width / stem width (Rc), underleaf width / lobule width (Rd), lobe width / lobule width (Re), lobule length / decurrent part of the lobule length (Rf), underleaf length / decurrent part of the underleaf length (Rg), lobule length (without decurrent part) / lobule width (Rh), lobule length / lobule width (Ri), lobe surface / lobule surface (Rj), lobe surface / underleaf surface (Rk) and lobule surface / underleaf surface (Rl).

In addition, twenty nine qualitative morphological characters were considered: lobe apex (La), lobe dorsal margin (Lms), lobe ventral margin aspect (Lmmi), lobe ventral margin type (Lmi), lobe position (Lp), trigones of lobe cells (Ltc), lobule apex (Lla), lobule margin (Lmm), lobule margin aspect (lM), lobule base (Lb), underleaf margin (Amm), underleaf margin aspect (aM), underleaf base (Ab), underleaf bilobed (Ax), hemiphyll bilobed (Hx), rhizoids (Riz), asexual reproduction (Prv), male bracts and bracteole (Bm), male bracts apex (Bma), male bracts margin (Bmm), female bracts size (Bft), lobe apex of female bracts (bfLa), lobule apex of female bracts (Bflla), lobe margin of female bracts (bfLm), lobule margin of female bracts (Bfllm), apex of female bracteole (Btfa), margin of female bracteoles (Btfm), perianth margin (Pm) and spore shape (Ef). Analyses of these characters are presented in the description of both species.

## RESULTS

In order document morphologic traits, scanning electron micrographs of the gametophyte and sporophyte are presented in Figs. 1 & 2. The description of both Porella species was based on the study of Madeira's plant material.

### Morphology and sexual conditions

A total of 55 populations, containing 550 individuals were analyzed. In 44 populations of *P. canariensis*, 73% tasted acrid, 18 populations (40.9%) presented mature perianths and only 10 (22.7%) comprised mature spores. A total of 120 perianths and 145 spores were studied. Within the spores, 110 (from MADJ 2796, 2797, 2799, 2811, 2880, 2807, 2813) measured 50 µm diameter (76%), 20 (from MADJ 2796, 2797, 2808) measured 60 µm diameter (14%), 10 (from MADJ 2798, 2884) measured 40 µm diameter (7%), and 5

spores (from MADJ 2885) measured 80 µm diameter (3%). Only female individuals were frequently observed in 52.3% populations, whereas males were scanty (6.8%). Female and male stems have been found intermixed in 27.3% populations and 13.6% were composed by sterile stems. In 11 populations of *P. obtusata*, none (0%) tasted acrid, two populations (18.2%) presented mature perianths and one (9.1%) comprised mature spores. A total of 15 perianths and 5 mature spores were studied. All spores measured 50 µm long (100%). No males were observed and female stems were present in 72.7% populations, being 27.3% composed by sterile stems. Averages of the values (minimum, medium and maximum) of all the quantitative characters were determined and in addition ratios were performed, being presented in Table 1. The graphical representation of quantitative traits and calculations between characters are respectively presented in Figs. 3 & 4.


**Fig.1** – Scanning electron micrographs of *P. canariensis*. A: ventral view of apical gametophyte segment; B: ventral view of ramification and gametophyte segment; C: ventral view of antheridia branch; D: spores and elaters; E-H: perianth; F: ventral view of male branch bracts and bracteoles with vegetative propagation; G: female bracts and bracteole; I: gametophyte growing on lobe surface. A, B, C (MADJ 2192); D (MADJ 2880); E (MADJ 2885); F (MADJ 2849); I (MADJ 2879); G, H (LISU 161857). Scale bars: A = 100 µm; B, C, E, F, H, I = 500 µm; D = 10 µm; G = 100 µm.

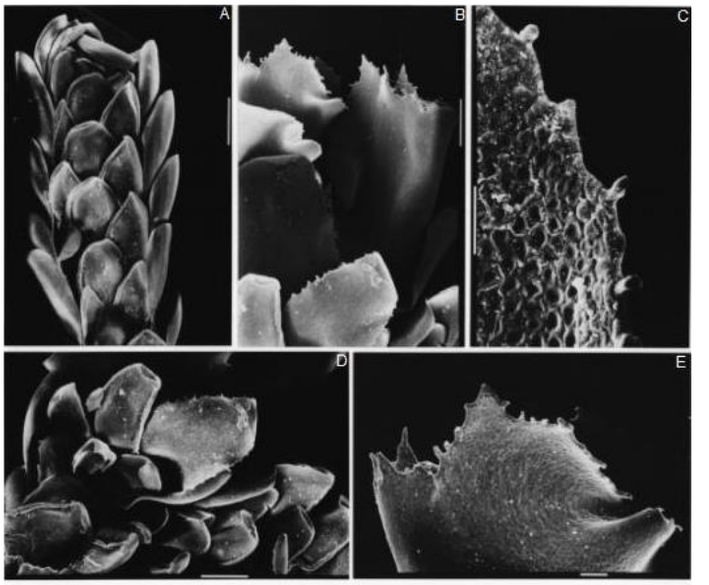


**Fig. 2** – Scanning electron micrographs of *P. obtusata*. A: ventral view of apical gametophyte segment; B: female bracts and perianth; C: female bract margin; D: ventral view of lateral female ramification with bracts and bracteoles; D: perianth mouth margin. A, B, D (LISU 161874); C (MADJ 2788). Scale bars: A, B, D = 500 µm; C = 50 µm; E = 100 µm.

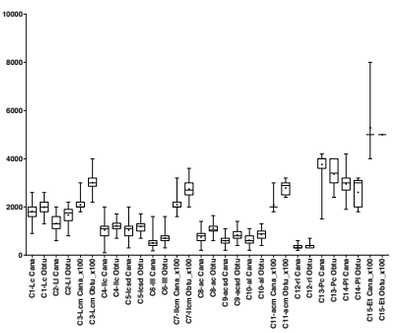


**Fig. 3** – The variation of 15 morphological characters scrutinized. The abbreviations and the number of examined specimens are according to the parameters defined in the methodology. The edges of the longer segment represent the minimum and the maximum values of each character. Values are in µm.

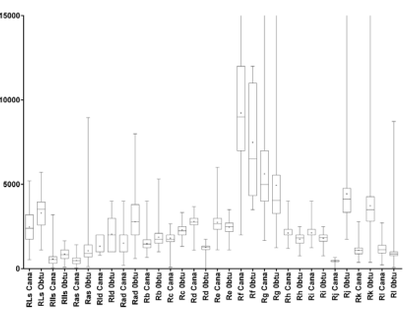


**Fig. 4** – The variation of 16 ratios of morphological characters scrutinized. The abbreviations and the number of examined specimens are according to the parameters defined in the methodology. The edges of the longer segment represent the minimum and the maximum values of each character.

**Table 1** – Averages of 32 morphological characters scrutinized. Abbreviations of characters and ratios are in accordance with the methodology. N corresponds to the total number of individuals analysed (440 *P. canariensis* plus 110 *P. obtusata*). Values of 15 quantitative morphological characters are in µm (on the left side is the minimum, in parenthesis the medium and on the right side the maximum). In addition 17 ratios were calculated.

| Characters | N | *P. canariensis* | *P. obtusata* |
|---|---|---|---|
| Lc - lobe length | 550 | 900 (1800) 2600 | 1300 (2000) 2600 |
| Ll - lobe width | 550 | 600 (1300) 2000 | 800 (1750) 2200 |
| Lcm - diameter of lobe cells | 550 | 18 (20) 30 | 22 (30) 40 |
| llc - lobule length | 550 | 300 (1100) 2000 | 700 (1200) 1710 |
| lcsd - lobule length without deccurence | 550 | 300 (1100) 2000 | 700 (1200) 1710 |
| ll - lobule width | 550 | 180 (500) 1600 | 300 (700) 1600 |
| lcm - diameter of lobule cells | 550 | 16 (20) 32 | 20 (27) 36 |
| ac - underleaf length, decurrent part included | 550 | 200 (800) 1400 | 600 (1040) 1640 |
| acsd - underleaf length without decurrent part | 550 | 200 (600) 1100 | 400 (800) 1400 |
| al - underleaf width | 550 | 200 (600) 1100 | 400 (880) 1300 |
| acm - diameter of underleaf cells | 550 | 18 (20) 30 | 24 (28) 32 |
| Rl - stem width | 550 | 200 (300) 600 | 300 (400) 700 |
| Pc - perianth length | 135* | 1500 (4000) 4200 | 2400 (3400) 4000 |
| Pl - perianth width | 135* | 1900 (3000) 4200 | 1800 (3000) 3200 |
| Et - spore diameter | 150* | 40 (50-60) 80 | 50 |
| RLS - ($10^6$) Lobe surface | 550 | 2,5 | 3,2 |
| Rls - ($10^5$) lobule surface | 550 | 5,8 | 8,7 |
| Ras - ($10^5$) underleaf surface | 550 | 4,9 | 10,6 |
| Rld - lobule decurrent part | 550 | 8 | 35 |
| Ra - underleaf decurrent part | 550 | 147 | 279 |
| Rb - lobule width/stem width | 550 | 1 | 2 |
| Rc - underleaf width/stem width | 550 | 2 | 2 |
| Rd - underleaf width/lobule width | 550 | 1 | 1 |
| Re - lobe width/lobule width | 550 | 3 | 2 |
| Rf - lobule length/decurrent part of the lobule length | 550 | 9 | 7 |
| Rg - underleaf length/decurrent part of underleaf length | 550 | 6 | 5 |
| Rh - lobule length without decurrent p. /lobule width | 550 | 2 | 2 |
| Ri - lobule length/lobule width | 550 | 2 | 2 |
| Rj - lobe surface/lobule surface | 550 | 5 | 4 |
| Rk - lobe surface/underleaf surface | 550 | 6 | 4 |
| Rl - lobule surface/underleaf surface | 550 | 1 | 1 |

* 120 perianths and 145 spores from *P. canariensis* plus 15 perianths and 5 spores from *P. obtusata*.

*Porella canariensis* (F. Webber) Underw. 1897

Trelease W., Bot. Observ. Azores (in 8th annual Report Missouri Bot. Gard.): 186. [synonym of *Porella canariensis* (F. Webber) Bryhn, Kongel. Norske Vidensk. Selsk. Skrift. (Trondheim. (1908) (8): 10. 1908.] B.: *Jungermannia platyphylla* δ. *canariensis* F. Webber Hist. Musc. Hep. Prodromus: 16. Kiel. 1815. T: Teneriffa, leg. BORY; Holo: S (!), Iso: STR (SCHIFFN. Hedwigia 41:276. 1902). K. Müller 1956: *Madotheca canariensis* (F. Webber) Nees.

Plants medium-sized to large, sometimes small and attenuated, glossy or not, usually with acrid taste, leaf lamina translucent to opaque, forming extensive or small, dense or loose, green to brownish-green mats. *Frullania*-type branched 1 (2-3) irregularly pinnate, stems (1.3-) 5.6 (-11.5) cm in length and (200-) 300 (-600) cm in width. Cortex cells narrower than those from the medulla. Dorsal lobes contiguous, 1/3 imbricate, rarely separate, crossing partially the stem, apex obtuse-rounded or slightly truncate and acute, margin entire to undulate, occasionally paucispinose, oval to oblong, longer (900-) 1800 (-2600) µm than wide (600-) 1300 (-2000) µm and entire at base. Median cells oval to polygonal (18-) 20 (-30) µm diameter. Ventral lobes slightly or not decurrent, with the same width as the stem, longer (300-) 1100 (-2000) µm than wide (180-) 500 (-1600) µm, apex usually truncate, occasionally apiculate, rounded to oblong, margin paucispinose to entire. Median cells oval to polygonal (16-) 20 (-32) µm diameter. Underleaves slightly to not decurrent, wider than the stems, margin paucispinose to entire, sometimes reflexed, longer (200-) 800 (-1400) µm than wide (200-) 600 (-1100) µm. Median cells oval to polygonal (18-) 20 (-30) µm diameter. Rhizoids, when present, pale brownish, usually in tufts from the middle basal cells of the underleaves. Gynoecia terminal or on lateral abbreviate branches. Archegonia branches 4 (8-12) per stem, with 2 pairs of bracts. Margin of bracts and bracteoles irregularly dentate or ciliate to paucispinose. Antheridial branches 10 (16-32) per stem, with 8 pairs of bracts, bilobed, and closely imbricate, bracts more or less closed to bracteoles with entire margin. Antheridia spherical with short pedicels. After the release of gametes, apical part of male stems may continuously grow. Number of perianths per stem 4 (6-8). Perianth longer (1500-) 4000 (-4200) µm than wide (1900-) 3000 (-4200) µm, margin lobed or not, irregularly dentate to paucispinose. Capsule spherical to slightly ovoid, opening by four valves. Spores warty, (40-) 50 (-80) µm diameter. Elaters free, yellow, thin, elongate and 2 (-3) spiralled. Asexual reproduction by cell release.

It presents the widest distribution in the archipelago, existing in Madeira Island, Porto Santo Island and Deserta Grande Island, where colonizes different habitats from the lowest till the highest altitudes (Fontinha *et al*., 2010). It is one of the most dominant bryophytes in laurel and heather forest formations (Sim-Sim *et al*., 2014). Atlantic distribution, not found north of the Iberian Peninsula. Its distribution is restricted to continental Europe (Portugal and Spain, including Baleares Islands), Morocco, Macaronesia (Azores, Madeira and Canary archipelagos) and Cape Verde (Söderström *et al*., 2002; Fontinha, 2004; Sérgio *et al*., 2013). The species needs equilibrated climates with cool summers and mild winters and substrata with low pH (Fontinha *et al*., 2010).

*Porella obtusata* (Taylor) Trevis

Memorie Reale Instit. Lombard. Sci. Mat. Nat. Ser. 3. 4: 407. 1877. B: *Madotheca obtusata* Taylor. London Journ. Bot. 5: 380. 1846. T: Kanaren, leg. Lemann (in errore "Lemain" in sched.); Holo: FH masc. (Grolle, Lindbergia 3: 53. 1975)!, Iso: JE masc.!, MANCH masc.!, S masc.!, W masc., LINDENB. Hep. No. 5713! K. Müller 1956: *Madotheca thuja* auct., non (Dicks.) Dum. Nom. illeg.; vgl. Grolle, 1969, 1975b.

Plants medium-sized to large, glossy or not, not tasting acrid, leaf lamina opaque, forming extensive, dense

green to brownish-green mats. Frullania-type branched 1 (2-3) irregularly pinnate, stems (1,6-) 4,5 (-9,5) cm in length and (300-) 400 (-700) cm in width. Cortex cells narrower than those from the medulla. Dorsal lobes contiguous, 1/3 imbricate, crossing partially the stem, apex rounded to oval, margin entire to undulate, longer (1300-) 2000 (-2600) µm than wide (800-) 1750 (-2200) µm and entire at base. Median cells oval to polygonal (22-) 30 (-40) µm diameter, trigones bulging and confluent. Ventral lobes not decurrent, wider than the stem, longer (700-) 1200 (-1710) µm than wide (300-) 700 (-1600) µm, apex usually rounded to oblong, margin entire. Median cells oval to polygonal (20-) 27 (-36) µm diameter. Underleaves slightly decurrent, wider than the stems, margin entire and reflexed, longer (600-) 1040 (-1640) µm than wide (400-) 880 (-1300) µm. Median cells oval to polygonal (24-) 29 (-32) µm diameter. Rhizoids, when present, pale brownish, usually in tufts from the middle basal cells of the underleaves. Gynoecia terminal or on lateral abbreviate branches. Ciliate margin of the archegonia bracts, with cilia similar to papillae. Androecia not observed on material from Madeira. Perianth longer (2400-) 3400 (-4000) µm than wide (1800) 3000 (-3200) µm, margin not lobed, irregularly dentate, with cilia similar to papillae. Capsule spherical opening by four valves. Spores warty, 50 µm diameter. Elaters free, yellow, thin, elongate and 2 (-3) spiralled. Vegetative propagation may occur.

It is recorded only to Madeira Island, mainly at the peaks, 900-1850 m *a.s.l*, being more abundant in the heather forest, but also occurring in the humid laurel forest (Fontinha *et al*., 2010). It withstands high summer temperature and grows in the lowlands (Bischler *et al*., 2006; Fontinha *et al*., 2010). Continental distribution (north and west Europe, central Asia, north America) and Atlantic distribution including Macaronesia, existing in Madeira Island, Azores and Canary Islands, being this last archipelago the meridional limit of the species distribution.

## DISCUSSION

The Madeiran samples of *P. canariensis* and *P. obtusata* overlap partially, however there are morphological characters that can be used to distinguish them easily, as the following ones.

In general the diameter of the median cells of lobe, lobule and underleaf of *P. canariensis* are 20 µm, and the cells present uniformly thickened walls; in contrast *P. obtusata* presents median cells 30 µm size, with large bulging trigones.

The width of the lobe, lobule and underleaf are smaller in *P. canariensis* than in *P. obtusata* as well as the lobule and underleaf surfaces; in contrast the lobe surface is smaller in *P. canariensis* than in *P. obtusata*. The decurrent part of the lobe and the underleaf is smaller in *P. canariensis* than in *P. obtusata*.

The female bracts of *P. canariensis* presents dentate or ciliate to paucispinose margins, male bracts entire to paucispinose margins, and perianths with lobed or unlobed, irregularly dentate to paucispinose margins without papilla-like teeth; in contrast *P. obtusata* shows female bracts with ciliate margins, male bracts with entire margins, and perianths with unlobed, irregularly dentate margins with papilla-like teeth.

The acrid taste is usually present in *P. canariensis*; in contrast the plants of *P. obtusata* do not taste acrid.

In *P. canariensis* male individuals were less numerous than female, as observed in many others liverworts (Bischler *et al*., 2006); in contrast no males were observed within *P. obtusata* populations. A high number of females with perianths characterize *P. canariensis*, being in accordance to Bischler *et al*., 2006; in contrast only 18% of *P. obtusata* populations showed perianths.

Within *P. canariensis* 23% populations carried mature spores, and 17% of them (14% and 3% respectively 60 µm and 80 µm diameter) were larger than 35-50 µm diameter mentioned for the genus (Bischler *et al*., 2006). No mixed spore's size was found within populations. More research concerning the spores should be done.

Further studies should be done regarding the size of the spores within *P. canariensis* populations.

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## Appendix 1

### Voucher specimens

UTM squares (1 x 1 km$^2$) are referred.

*Porella canariensis*
Deserta Grande Island: Risco, 350 m, CA5899, 15.05.1995, *Silva 2682*.
Madeira Island: Achada do Marques, 410 m, CB2130, 16.05.1993, *Fontinha 2794*; Achada do Teixeira, 1520 m, CB2026, 9.07.1993, *Fontinha 2809*; Achadas da Cruz, 400 m, BB9336, 5.11.1994, *Fontinha 2816*; Achadas da Cruz, 550 m, BB9235, 5.11.1994, *Fontinha 2818*; Achadas da Cruz, 750 m, BB9535, 8.04.1994, *Fontinha & Bischler 2805*; Achadas da Cruz, 240 m, BB9337, 5.11.1994, *Fontinha 2817*; Bica da Cana, 1250 m, CB0925, 17.01.1995, *Fontinha & Sérgio* 2846; Bica da Cana, 1300 m, CB0724, 27.01.1994, *Fontinha 2802*; Cabo Girão, 550 m, CB1214, 25.10.1994, *Fontinha 2810*; Camacha, 800 m, CB2616, 22.01.1994, *Fontinha 2812*; Camacha, 800 m, CB2718, 22.01.1994, *Fontinha 2800*; Camacha, 800 m, CB2820, 22.01.1994, *Fontinha 2813*; Camacha, 800 m, CB2718, 22.01.1994, *Fontinha 2801*; Camacha, 800 m, CB2719, 22.01.1994, *Fontinha 2799*; Caminho dos Pretos, 700 m, CB2317, 3.11.1994, *Fontinha 2811*; Fajã da Nogueira, 700 m, CB2025, 3.12.1993, *Fontinha 2797*; Fajã da Nogueira, 850 m, CB2025, 3.12.1993, *Fontinha 2879*; Fajã da Nogueira, 900 m, CB2025, 3.12.1993, *Fontinha 2885*; Fajã da Nogueira, 900 m, CB2025, 3.12.1993, *Fontinha 2796*; Fajã da Nogueira, 900 m, CB2025, 3.12.1993, *Fontinha 2864*; Fanal, 1100 m, BB9832, 13.05.1993, *Fontinha 2880*; Fanal, 1100 m, BB9932, 13.05.1993, *Fontinha 2792*; Fanal, 1100 m, BB9833, 13.05.1993, *Fontinha 2793*; Machico, 320 m, CB3521, 29.12.1994, *Fontinha 2819*; Monte, 550 m, CB2216, 3.11.1994, *Fontinha 2815*; Prazeres, 600 m, BB9425, 2.02.1995, *Fontinha 2849*; Ribeira Brava, 550 m, CB0817, 10.07.1993, *Fontinha 2795*; Ribeira da Janela, 500 m, BB9636, 3.02.1994, *Fontinha 2851*; Ribeira da Janela, 500 m, BB9635, 3.02.1994, *Fontinha 2804*; Ribeiro Frio, 900 m, CB2223, 19.10.1993, *Fontinha 2808*; Ribeiro Frio, 800 m, CB2323, 6.01.1994, *Fontinha 2814*; Ribeiro Frio, 800 m, CB2323, 6.01.1994, *Fontinha 2798*; Ribeiro Frio, 900 m, CB2223, 19.10.1993, *Fontinha 2807*; Santana, 900 m, CB2028, 29.05.1993, *Fontinha 2884*; Santana, 900 m, CB2028, 29.05.1993, *Fontinha 2883*; São Jorge, 600 m, CB1930, 2.06.1993, *Fontinha 2881*; São Jorge, 600 m, CB1930, 14.10.1993, *Fontinha 2882*; Seixal, 650 m, CB0230, 8.04.1994, *Fontinha & Bischler 2806*; Terreiro da Luta, 940 m, CB2217, 3.11.1994, *Fontinha 2852*.
Porto Santo Island: Pico Branco, 500 m, CB7862, 25.02.1995, *Fontinha 2848*; Pico Castelo, 600 m, CB7560, 23.01.1995, *Fontinha & Silva 2850*; Pico Castelo, 600 m, CB7560, 23.01.1995, *Fontinha & Silva 2845*; Pico do Facho, 500 m, CB7661, 27.02.1995, *Fontinha 2847*.

*Porella obtusata*
Madeira Island: Bica da Cana, 1300 m, CB0825, 27.01.1994, *Fontinha 2952*; Fajã da Nogueira, 900 m, CB2025, 03.12.1993, *Fontinha 2790*; Fanal, 1100 m, BB9932, 13.05.1993, *Fontinha 2783*; Fanal, 1110 m, BB9931, 13.05.1993, *Fontinha 2859*; Pico do Areeiro, 1750 m, CB1824, 24.06.1993, *Fontinha 2860*; Pico Ruivo de Santana, 1850 m, CB1825, 24.06.1993, *Fontinha 2784*; Pico Ruivo de Santana, 1850 m, CB1825, 24.06.1993, *Fontinha 2863*; Poiso, Achada Grande, 1540 m, CB2021, 19.10.1993, *Fontinha 2786*; Poiso, Achada Grande, 1540 m, CB2021, 19.10.1993, *Fontinha 2789*; Ribeiro Frio, 900 m, CB2323, 19.10.1993, *Fontinha 2788*; Santana, Caldeirão Verde, 900 m, CB2028, 29.05.1993, *Fontinha 2785*.

### Other specimens observed

*Porella arboris-vitae*
Germany: Gerolstein, Eifel, Sauer, 14.08.1985, (MADJ 2691 ex Herb. Mues 1166); Regensburg, Dolomitfelsen bei Etterzhaussen, Familler, 05.1906, (MO 2329860); Baiern, Isartall bei Hellriegelsgreuth an Nagelfluh und Bäumen, Neumann, 10.1903, (MO 2237103).
Bulgary: M. Strandza, *ad rupes silic*., *in fageto*, l. d. Goljam Draganovski dol, prope vic. Slivarovo, 200 m, Petrov, 29.05.1956, (MO 4436704).
Scotland: Ross, near Loch Maree, in wood, Carrington, 09.1889, (MO 2559687).
Spain: Astúrias, Oviedo, 300 m, Mues, 02.09.1980, (MADJ 2690 ex Herb. Mues 1163); Barcelona, Sant Llorenç del Munt,

canal de les Teixoneres, sobre *Buxus sempervirens*, 750 m, Casas, 16.04.1989, (MO 4412136); Barcelona, Montserrat, sobre pedras calcárias, xerófila, 950 m, Allorge, 18.04.1927, (MO 2567489).
France: Herault, 10 m, Boisselier, Bischler & Pujos, 14.10.1992, (MADJ 2772 ex Herb. Bischler 501); Le collet de Dèze-Lozère, 300 m, Cheminat, 08.1988, (MADJ 2699 ex Herb. Mues) (Qf); Tarn, saxícola, 350 m, Boisselier, Bischler & Pujos, 13.10.1992, (MADJ 2773 ex Herb. Bischler 480).
Hungary: Ungärn, Kokanu, 400 m, Mues, 14.08.1985, (MADJ 2692 ex Herb. Mues 1167) (Qf).
England: Bolton Abbey Woods, Yorkshire, Hodgetts, 23.06.1999, (MADJ 2976) (Qf); Tyn-y-groes, Merioneth, Pearson, 05.1877, (MO 2560460); Seatoller, Borrowdale, base of trees, Carrington & Pearson, 06.1890, (MO 2559688).
Romany: Carpatica, Transsilvania, Alpes Fogarasi, Havakok, 1200 m, Pocs, 28.07.1968, (MO 4447865).
Sweden: Skåne, "Skäralid", Lindberg, 14.07.1875, (MO 4432043).
Swizerland: Vaud, Montreux, Gorges du Chaudron, saxícola, 350 m, Bischler, 24.09.1992, (MADJ 2782 ex Herb. Bischler 461).
Turky: Esche, 1350 m, Sauer, 13.03.1985, (MADJ 2689 ex Herb. Mues).

*P. canariensis*
Azores: Faial, Cabeço dos Trinta, Fontinha, Gomes & Neves, 16.07.1997, (MADJ 2734); Faial, Caldeira, Schwab, 21.06.1981, (Herb. Schwab-Flora Azorica sub *Madotheca canariensis* Nees); Faial, Mistérios, V. & P. Allorge, 30.06.1937, (PC – Iter Azoricum); Flores, Valleé Cedros, V. & P. Allorge, 03.07.1937, (PC – Iter Azoricum); Flores, Valleé Cedros, V. & P. Allorge, 06.07.1937, (PC – Iter Azoricum); Flores, Ribeira Grande, V. & P. Allorge, 23.07.1937, (PC – Iter Azoricum); Flores, V. & P. Allorge, 14.07.1937, (PC – Iter Azoricum); Flores, Pico do Fransiscão, V. & P. Allorge, 17.07.1937, (PC – Iter Azoricum); Flores, Fajãzinha, V. & P. Allorge, 22.07.1937, (PC – Iter Azoricum); Flores, Fajãzinha, V. & P. Allorge, 22.07.1937, (PC – Iter Azoricum); Flores, Rochão, V. & P. Allorge, 22.07.1937, (PC – Iter Azoricum); Flores, Allorge, 28.07.1937, (MO 2568273); Pico, Mistério da Prainha, Sim-Sim, 09.06.1997, (MADJ 2736); Pico, Furna, V. & P. Allorge, 9.08.1937, (PC – Iter Azoricum); Pico, Serra, V. & P. Allorge, 8.08.1937, (PC – Iter Azoricum); Santa Maria, Pico Alto, V. & P. Allorge, 21.06.1937, (PC – Iter Azoricum); São Jorge, Fajã dos Cubres MH1577, Sérgio & Schumacker, 21.06.1999, (LISU); São Jorge, Fajã dos Cubres, Norte Pequeno, Sérgio & Schumacker, 21.06.1999, (LISU); São Jorge, Fajã dos Cubres, Norte Pequeno, Sérgio & Schumacker, 21.06.1999, (LISU); São Jorge, Fajã dos Cubres, Sérgio, 19.06.1999, (LISU); São Jorge, Norte Grande, Sérgio & Schumacker, 22.06.1999, (LISU); São Jorge, Pedras Brancas, Sérgio & Schumacker, 22.06.1999, (LISU); São Jorge, próximo de Pico da Esperança, vertente norte, 950 m, MH0678, Sérgio & Schumacker, 23.06.1999, (LISU); São Miguel, Lagoa do Congro, Schwab, 05.06.1981, (Herb. Düll 30959); São Miguel, Lagoa do Fogo, Hübschmann, 10.05.1973, [MADJ 2718 ex Herb. Düll 31900 sub *P. chamaedryfolia* (With.) Grolle]; São Miguel, próximo de Furnas, Hübschmann, 04.05.1973, (Herb. Hübschmann sub *P. canariensis* fo. *subintegra*); São Miguel, próximo do Pico da Cruz, Hübschmann, 04.05.1973, (MADJ 2749 ex Herb. Hübschmann 731733 sub *P. canariensis* fo. *subintegra*); São Miguel, próximo do Pico da Cruz, Hübschmann, 18.10.1970, (MADJ 2750 ex Herb. Hübschmann); São Miguel, Lagoa do Congro, Schwab, 5.06.1981, (Herb. Düll 30959 ex Herb. Schwab-Flora Azorica); São Miguel, Parque José do Canto na Lagoa das Furnas, Schwab, 4.06.1981, (Herb. Schwab- Flora Azorica sub *Porella*); São Miguel, Parque próximo do Hotel Terra Nostra, Schwab, 13.06.1981, (Herb. Schwab- Flora Azorica sub *Madotheca canariensis* Nees); São Miguel, Parque do Hotel Terra Nostra, 200 m, Schwab, 4.06.1981, (Herb. Schwab Flora Azorica); São Miguel, Lagoa do Congro, V. & P. Allorge, 31.05.1937, (PC – Iter Azoricum); São Miguel, Cratera das Sete Cidades, V. & P. Allorge, 24.08.1937, (PC – Iter Azoricum); São Miguel, Lagoa Furnas, V. & P. Allorge, 28.05.1937, (PC – Iter Azoricum); São Miguel, Tronqueira, V. & P. Allorge, 1937, (PC – Iter Azoricum); São Miguel, Furnas, V. & P. Allorge, 1937, (PC – Iter Azoricum); São Miguel, Furnas, V. & P. Allorge, 14.06.1937, (PC – Iter Azoricum); São Miguel, Ribeira Quente, V. & P. Allorge, 12.06.1937, (PC – Iter Azoricum); Pico, Furna, V. & P. Allorge, 9.08.1937, (PC – Iter Azoricum); Terceira, Falca, Fontinha, 24.06.1992, (MADJ 2838).
Cape Vert: São Nicolau, Monte Caldeirinha, Lindlar, 24.01.1995, [MADJ 2731 ex BONN sub *P. arboris-vitae* (With.) Grolle]; São Vicente, Monte Verde, Lindlar, 26.01.1995, [MADJ 2730 ex BONN sub *P. arboris-vitae* (With.) Grolle]; São Vicente, Monte Verde, Lindlar, 26.01.1995, [MADJ 2732 ex BONN sub *P. arboris-vitae* (With.) Grolle].
Canary Islands: Hierro, Riscos de Sabinosa, Pitard, 03.1906 (Herb. Pitard- PLANTAE CANARIENSIS 756 sub *Madotheca canariensis* Nees); La Palma, Düll, 20.03.1978, [Herb. Düll 017561 sub P. arboris-vitae (With.) Grolle]; La Palma, Düll, 15.03.1978, (Herb. Düll 17567); La Palma, Düll, 16.03.1978, [MADJ 2725 ex Herb. Düll 017562 sub *P. arboris-vitae* (With.)

Grolle]; La Palma, Cumbre Nueva, Bornmüller, 08.05.1901, (MADJ 2727 ex BM 518655 ex Herb. Schiffner sub *Madotheca canariensis* (Nees) sensu Schiffn. fo. *integra*]; La Palma, Cumbre nueva, Bornmüller, 08.05.1901, [MADJ 2728 ex JE sub *Madotheca canariensis* (Nees) sensu Schiffn. fo. *integra*]; La Palma, Losada *et al*., 10.02.1990, (MADJ 2821 ex TFC 9125); Tenerife, 1969, (S B3430 HOLOTIPO sub *Jungermannia platyphylla* var. *canariensis*); Tenerife, 1969, (S B3431 HOLOTIPO sub *Jungermannia platyphylla* var. *canariensis*); Tenerife, Anaga, 900 m, Düll, 1978, [Herb. Düll ex DUIS Flora von Makaronesien sub *P. arboris-vitae* (With.) Grolle var. *thuja*]; Tenerife, Anaga, 900 m, Koppe, 01.04.1975, (LISU 161862 sub *P. arboris-vitae*); Tenerife, Anaga, Siegel, 02.09.1980, [MADJ 2693 ex Herb. Mues 2359 sub *P. arboris-vitae* (With.) Grolle]; Tenerife, Anaga, Crundell, 09.04.1979, (Herb. Düll 26405 ex Herb. Crundell 439); Tenerife, Bory, (HB Nees –STR ISOTIPO, HB Web sub *Madotheca canariensis* Nees); Tenerife, Bosque de Esperanza, Düll, 30.12.1973, (Herb. Düll 10007); Tenerife, Casa de la Cumbre, Fontinha & Santos-Guerra, 07.09.1995, (MADJ 2829); Tenerife, Las Mercedes, Bornmüller, 03.1838, (MADJ 2729 ex JE N. ab Esenb., Naturg. d. europ. Leberm., III (I 838), p. 207; cfr. Schiffner in Hedwigia, Bd. XLI (1902), p. 276 (sub *Madotheca canariensis*); Tenerife, Monte de las Mercedes, Fontinha & Santos-Guerra, 07.09.1995, (MADJ 2826); Tenerife, Monte del Agua, Fontinha & Santos-Guerra, 06.09.1995, (MADJ 2822); Tenerife, Monte del Agua, Fontinha & Santos-Guerra, 06.09.1995, (MADJ 2824); Tenerife, Monte del Agua, Fontinha & Santos-Guerra, 06.09.1995, (MADJ 2823); Tenerife, Monte del Agua, Fontinha & Santos-Guerra, 06.09.1995, (MADJ 2825); Tenerife, Pico del Ingles, Fontinha & Santos-Guerra, 07.09.1995, (MADJ 2827); Tenerife, Pijaral, Fontinha & Santos-Guerra, 07.09.1995, (MADJ 2830); Tenerife, Pijaral, Fontinha & Santos-Guerra, 07.09.1995, (MADJ 2832); Tenerife, Pijaral, Fontinha & Santos-Guerra, 07.09.1995, (MADJ 2833); Tenerife, Pijaral, Fontinha & Santos-Guerra, 07.09.1995, (MADJ 2831); Tenerife, próximo de La Laguna, Düll, 05.01.1974, [Herb. Düll 016355 sub *P. arboris-vitae* (With.) Grolle, cf. *macroloba*]; Tenerife, próximo de Puerto de la Cruz, Düll, 30.12.1973, (MADJ 2724 ex Herb. Düll); Tenerife, Tacoronte, Losada & Beltran, 05.05.1986, [MADJ 2820 ex TFC 3878 sub *P. arboris-vitae*]; Tenerife, Casa de la Cumbre, Fontinha & Santos-Guerra, 07.09.1995, (MADJ 2828); Tenerife, Las Mercedes, Bornmüller, 06.1900, (Herb. Bornmüller – *Plantae Exsiccatae Canariensis*).

Madeira Island: Faldas do Pico Jorge, Levada para o Ribeiro Bonito, C. Sérgio & M. Nóbrega 6148; 12.04.1988, (LISU 161857).

Portugal: Mafra?, saxícola,Veiga, (COI 3 sub *P. platyphylla*, *P. arboris-vitae*); Montachique, Cabeço de Montachique, Tavares, 1949, (LISU 148036); Montejunto, Quinta da Serra, Romariz & Mendes, 1947, [LISU 148027 sub *P. arboris-viate* (With.) Grolle]; Sintra, Castelo dos Mouros, Bischler, 09.1991, (MADJ 2838 ex Herb. Bischler 343); Sintra, Cruz Alta, Bischler, 09.1991, (MADJ 2775 ex Herb. Bischler 340); Sintra, Cruz Alta, Bischler, 09.1991, [MADJ 2837 ex Herb. Bischler 338 sub *P. obtusata* (Tayl.) Trev.]; Sintra, Figueiredo & Asakawa, 07.09.1997, (MADJ 2735 ex LISU); Sintra, Welwitsch, 1839, (COI sub *P. thuja*); Sintra, Palácio da Pena, Fontinha, 06.03.1996, (MADJ 2740); Sintra, Palácio da Pena, Fontinha, 06.03.1996, (MADJ 2739); Sintra, Palácio da Pena, Fontinha, 06.03.1996, (MADJ 2747); Sintra, Palácio da Pena, Fontinha, 06.03.1996, (MADJ 2738); Sintra, Pena, Sérgio, 1972, [LISU 148023 sub *Madotheca laevigata* Dum. var. *thuja* Nees, *P. arboris-vitae* (With.) Grolle]; Sintra, Pena, Tavares, 1951, [LISU 148025 sub *P. arboris-vitae* (With.) Grolle]; Sintra, Parque Salazar, Mendes, 1948, [LISU 148030 sub *P. thuja* (Dicks.) Moore, *P. arboris-vitae* (With.) Grolle]; Sintra, Castelo dos Mouros, Melo, 1973, [LISU 148031 sub *P. arboris-vitae* (With.) Grolle]; Sintra, Sá Nogueira, 1954, (LISU 148034); Sintra, Castelo dos Mouros, Sá Nogueira, 1948, (LISU 148035); Sintra, Castelo dos Mouros, I. Tavares, 1941, [LISU 148053 sub *P. thuja* (Dicks.) Moore, *P. arboris-vitae* (With.) Grolle]; Sintra, I. Tavares, 1946, [LISU 148054 sub P. thuja (Dicks.) Moore, *P. arboris-vitae* (With.) Grolle]; Sintra, Pena, Cruz Alta, Sérgio, Schumacker & Bisang, 1987, [LISU 153619 sub *P. arboris-vitae* (With.) Grolle]; Sintra, Castelo dos Mouros, Sérgio, Schumacker & Bisang, 1987, [LISU 153620 sub *P. arboris-vitae* (With.) Grolle]; Sintra, Parque da Pena, Lagoa dos Cisnes, Sérgio, 1973, [LISU 160400 sub *P. arboris-vitae* (With.) Grolle]; Sintra, Cruz Alta, Bischler, 1991, (LISU 160402); Sintra, Welwitsch, 1849, [LISU 53165 sub *Bellincinia thuja* Dicks., *P. obtusata* (Tayl.) Trev.]; Sintra, Welwitsch, 1852, [LISU 53177 sub *P. arboris-vitae* (With.) Grolle, *Bellincinia laevigata* (Schrad.) O. Ktze.]; Sintra, Quinta da Penha Verde, Welwitsch, 1852, [LISU 53179 sub *P. arboris-vitae* (With.) Grolle, *Madotheca platyphylloidea* Nees, *Bellincinia laevigata* (Schrad.) O. Ktze.]; Socorro, próximo de Torres Vedras, Luisier, 1908, [LISU 53169 sub *Bellincinia thuja* Dicks., *P. obtusata* (Tayl.) Trev.].

Spain: Cadiz, Algeciras, 13.04.1963, (MADJ 2719 ex Herb. Düll).

*P. obtusata*

Canary Island: without locality, Sir W. J. Hooker, 1843, (JE Hl448 ISOTYPE).

France: Hennebont, Bischler & Boisselier, 08.04.1992, (MADJ 2770 ex Herb. Bischler 426); Le Coudon, 660 m, John, 02.09.1980, (MADJ 2696 ex Herb. Mues 1180).

Madeira Island: Machico, Koppe, 22.03.1970, (STAATL ex Herb. F. & Koppe); Madeira Island, Poiso, Ade, 03.06.1926, (STAATL ex Herb. F. & Koppe); Madeira Island, Ribeiro Frio, Koppe, 09.04.1970, (STAATL ex Herb. F. & Koppe); Bussaco, Cruz Alta, Bischler, 09.1991, (MADJ 2777 ex Herb. Bischler 346); Entre a Pousada dos Vinháticos e Encumeada, C. Sérgio 2377, 13.05.1979, (LISU 161874).
Portugal: Bussaco, Fernandes & Sérgio, 24.06.1965, (COI 91); Coimbra, Sérgio & M. Sim-Sim, 26.06.1996, (MADJ 2698 ex Herb. Mues 2131); Estremadura, próximo de Pataias, Sérgio, 11.12.1996, (MADJ 2834 ex LISU); Fraga da Pena, Sérgio & M. Sim-Sim, 19.07.1995, (MADJ 2716 ex LISU 9789); Santo Tirso, Sérgio, 30.12.1995, (MADJ 2715 ex LISU 10236); Serra da Estrela, Sérgio, Brugués & Cros, 25.01.1995, (MADJ 2955 ex LISU 9583).
Spain: Astúrias, Oviedo, Mues, 02.09.1980, (MADJ 2697 ex Herb. Mues 1179).