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Lepidozia cupressina (Marchantiopsida, Lepidoziaceae) in sub-Saharan Africa, with a note on the taxonomic status of *L. chordulifera*

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Abstract – A taxonomic history of *Lepidozia cupressina* (Sw.) Lindenb. (*Jungermannia cupressina* Sw.) is presented and its diagnostic characters and variability in sub-Saharan Africa are thoroughly discussed. Three subspecies are currently distinguished in this region, namely subsp. *cupressina*, subsp. *africana* (Steph.) Pócs, *stat. et comb. nov.*, which occurs in the East African Indian Ocean islands and in the Eastern Arc of continental East Africa, as well as on the island of St. Helena in the Atlantic Ocean, and subsp. *natalensis* (Steph.) Pócs which is restricted to southern Africa. The other two subspecies, subsp. *pinnata* (Hook.) Pócs and subsp. *quinquefida* (Steph.) Pócs, are merged with the type subspecies of *L. cupressina*. A key to the recognition of the subspecies of *L. cupressina* is provided. *Lepidozia chordulifera* Taylor, a temperate species widely distributed in southern South America, is taxonomically assessed and some of its diagnostic traits are illustrated. It is considered to be conspecific with *L. cupressina* subsp. *cupressina.* Thanks to this taxonomic conclusion the range extension of *L. cupressina* in southern South America, including the Falkland Islands, is sanctioned and, additionally, distribution of this species is extended to subantarctic South Georgia and the northern maritime Antarctic. The current geographical range of *L. cupressina* is reviewed and mapped and it may be designated as a bipolar temperate species with numerous transitional stations in the tropical mountains. In the Southern Hemisphere *L. cupressina* is a typical Afro-American oreophyte.

Africa / Antarctica / bipolar species / distribution patterns / Europe / Hepaticae / nomenclature / phytogeography / South America / taxonomy

INTRODUCTION

In the second half of the last century, bryophyte taxonomy entered into the phase of critical regional or global taxonomic revisions of genera and families. As a result very many species names have been reduced to synonymy with the oldest names of accepted species. Sometimes the level of species inflation had been very high. For example, Touw (1974) showed that in the case of some predominantly exotic moss genera, an average of about 73% of taxa described before 1930 proved to be identical to accepted species. Taxonomic conclusions affect not only the data

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on bryophyte biodiversity of various areas, but also the distribution pattern of the species concerned. The lumping of some species known from narrower areas may definitely change the biogeographical status of the final species. This case is well illustrated by the history of *Lepidozia cupressina* (Sw.) Lindenb. which is discussed in the present account.

The Lepidoziaceae is one of the richest liverwort families and has always presented a serious challenge for hepaticologists. Many species of various lepidozioid genera are notoriously variable and different phenotypes were often described as distinct species, which subsequently proved to represent only fragments of variability of the species concerned. Hence names of such species are usually accompanied by long lists of heterotypic synonyms. In addition to the traditional taxonomic problems, "recent molecular phylogenies of the Lepidoziaceae indicate that the current classification is incongruent with the phylogeny" (Cooper, 2013), and the "composition of subfamilies and genera remains unsatisfactorily resolved" (Cooper *et al*., 2011).

REMARKS ON THE TAXONOMIC HISTORY OF *LEPIDOZIA CUPRESSINA*

Olof Swartz (1760-1818) was a Swedish botanist who, in contrast to most contemporary botanists, collected plants in exotic regions and studied them by himself. In 1784-1786, he travelled to Jamaica and Hispaniola in the West Indies and to north-eastern South America. During this trip he made a large botanical collection, which was the base of his famous *Flora Indiae Orientalis* (Swartz, 1797-1806), but earlier he described many new species of vascular plants and cryptogams in a separate work (Swartz, 1788). One of these was *Jungermannia cupressina* Sw. based upon the specimens collected in the mountains of Jamaica.

The original description of *Jungermannia cupressina* was written by Swartz (1806) himself, who showed its affinity to *J. reptans* L. (*Lepidozia reptans* (L.) Dumort.), from which it differed in its suberect, pinnately branched stems and convex, imbricate leaves. The species was subsequently accepted by Schwägrichen (1814), Weber (1815), and Sprengel (1827). The latter author extended the geographical range of *J. cupressina* to New Zealand because he considered *J. pendulina* Hook. to be conspecific with it and Lehmann (1829) reported it from Table Mountain in the Western Cape Province in South Africa.

Jungermannia cupressina was again redescribed by Lehmann (1832) who recognised the specimens from New Zealand and South Africa as separate varieties, var. *pendulina* (Hook.) Lehm. and var. *capensis* Lehm. Additionally, the species was reported from Trinidad as another separate variety, var. *tenera* Lehm. Finally, J.G.C. Lindenberg (in Gottsche *et al*., 1844) transferred *J. cupressina* to *Lepidozia* (Dumort.) Dumort. as *L. cupressina* (Sw.) Lindenb. and at the same time *J. cupressina* var. *pendulina* was reinstated as a distinct species, *L. pendulina* (Hook.) Lindenb., which is endemic to New Zealand (Engel & Glenny, 2008). Likewise, *J. cupressina* var. *capensis* was raised to species level as *L. truncatella* Nees, which only a century later was considered to be identical to *L. cupressina* (Arnell, 1953).

Because *Lepidozia cupressina* is a highly variable and protean species throughout its wide geographical range, some its phenotypes were recognised as separate infraspecific taxa in Central and South America and Africa. The plants from Trinidad and Barbados in the West Indies were recognised as a separate variety,

L. cupressina var. *tenera* (Lehm.) Gottsche, Lindenb. *et* Nees (Gottsche *et al*., 1844), and two more varieties were described from South America, namely var. *tenuicuspis* Spruce from Peru (Spruce 1885) and var. *dubia* C.Massal. from Isla Grande de Tierra del Fuego (Massalongo, 1885). Moreover, Herzog (1940) intended to recognise a form, f. *minor* Herzog, from Patagonia in Argentina, but this name was invalidly published. Interestingly, despite its remarkable plasticity, *L. cupressina* has had for a very long time no heterotypic synonyms in the rank of species in the Neotropics. However, Pócs (1984) reduced *L. wallisiana* Steph. and *L. muenchiana* Steph. to synonymy with it. The morphological variation of *L. cupressina* in Africa is analysed in detail below.

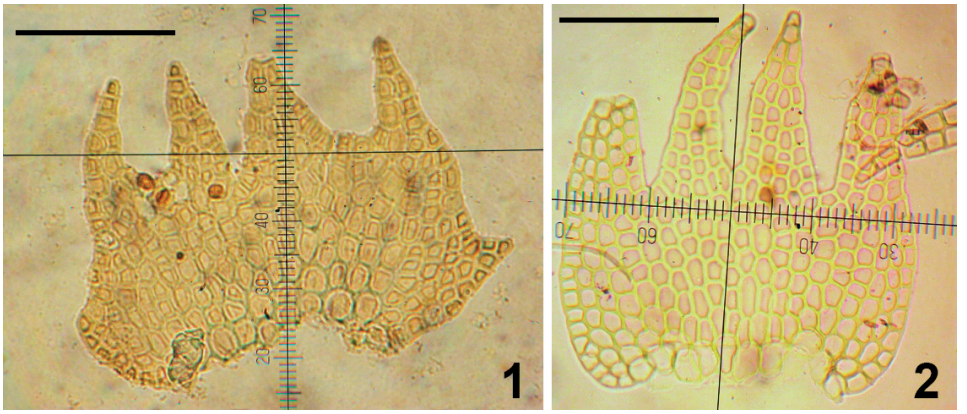
In Europe, *Lepidozia cupressina* was discovered relatively early and it was described as *Jungermannia reptans* var. *pinnata* Hook. (Hooker, 1815). This variety was subsequently raised to species level as *L. pinnata* (Hook.) Dumort. Pearson (1900) was the first to suggest the conspecificity of this species with *L. cupressina* but his idea did not gain wide acceptance and *L. pinnata* was considered to be endemic to Europe and Macaronesia. The conspecificity of *L. cupressina* and *L. pinnata* was accepted by Fulford (1966) and Grolle (1971), who formally synonymised these names.

DIAGNOSTIC TRAITS OF *LEPIDOZIA CUPRESSINA*

Lepidozia cupressina is a distinct species and in Europe it does not pose any problems with identification. It is characterised by a set of traits, which together, make it distinct from other species in the large and morphologically very diverse genus *Lepidozia* (Dumort.) Dumort. It is readily known by its imbricate, asymmetrical and almost transversely inserted leaves. The pinnate or irregularly spreading plants have the *Frullania*-type terminal branching with an acutely bilobed first basal appendage (hemiphyll). They are broadly ovate to rotundate-quadrate and deeply concave, divided into four strongly incurved, acuminate, triangular lobes to half or less the leaf length, with semi-cordate and auriculate dorsal leaf bases crossing and, in most cases, concealing the stem. The underleaves are similar to the lateral leaves, but are less asymmetric and only somewhat smaller. The margins of the leaves and underleaves are entire or toothed on the ventral side. This spurlike structure is found, among others, on the type material of *L. cupressina* (Figs 1-2) and in the plants described as *L. wallisiana* from Central and South America (Fulford, 1966; Pócs, 1984). A characteristic feature of the species is the usually thick-walled leaf cells with a smooth or striate-verruculose cuticle. The plants are very variable in size, procumbent to suberect, cream-coloured to nearly white, sometimes yellow-green to pale or greyish-green.

INFRASPECIFIC VARIATION OF *LEPIDOZIA CUPRESSINA* IN AFRICA

It is a well known fact that the extreme phenotypes of polymorphous species are usually so unlike each other that they have often been described as species in their own right. Only a careful analysis of the variability of many

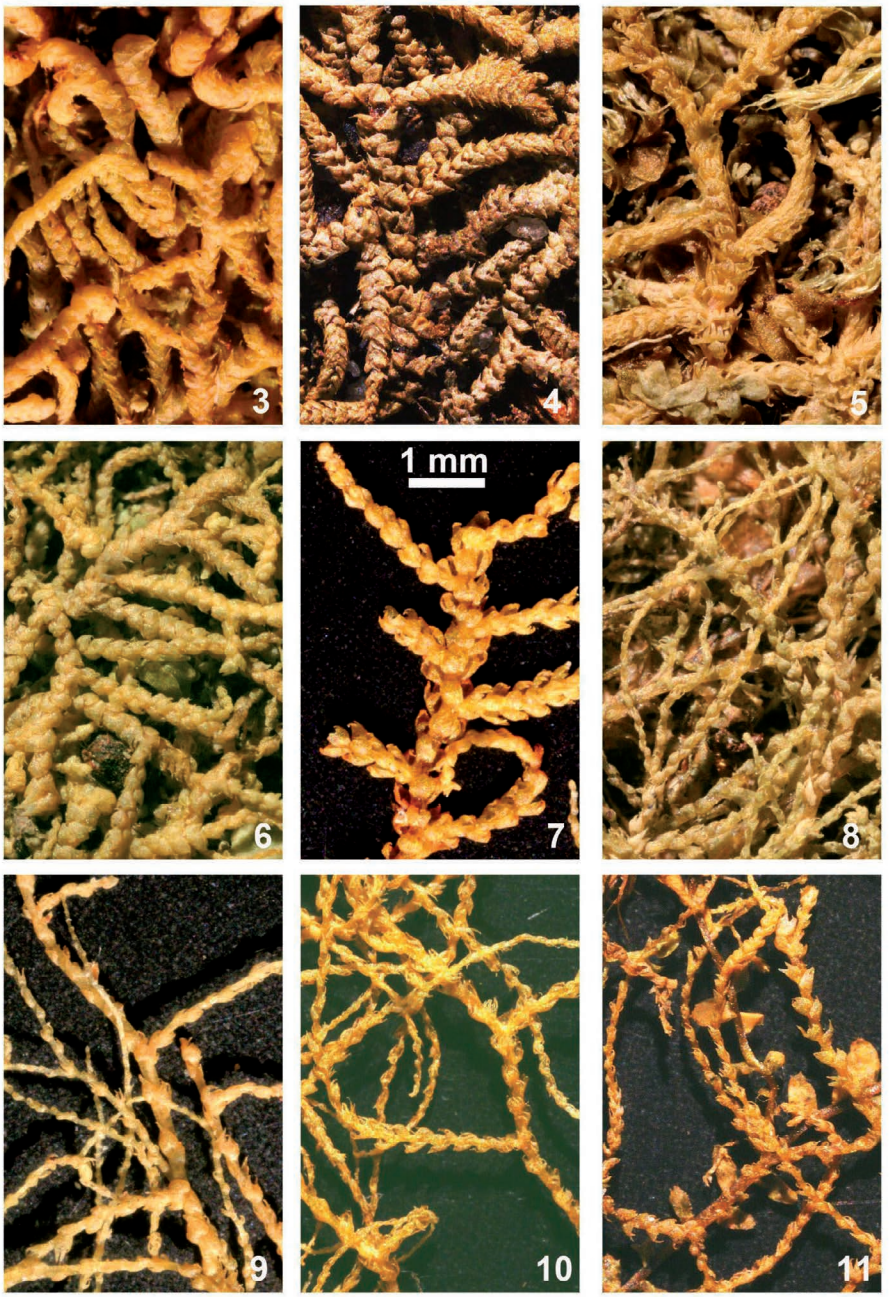


Figs 1-2. *Lepidozia cupressina* subsp. *cupressina*. **1.** Stem leaf. **2.** Underleaf (1-2 from *Swartz s.n.*, BM, isotype of *Jungermannia cupressina*). Scale bar 1 mm for both pictures. (All micrographs T. Pócs).

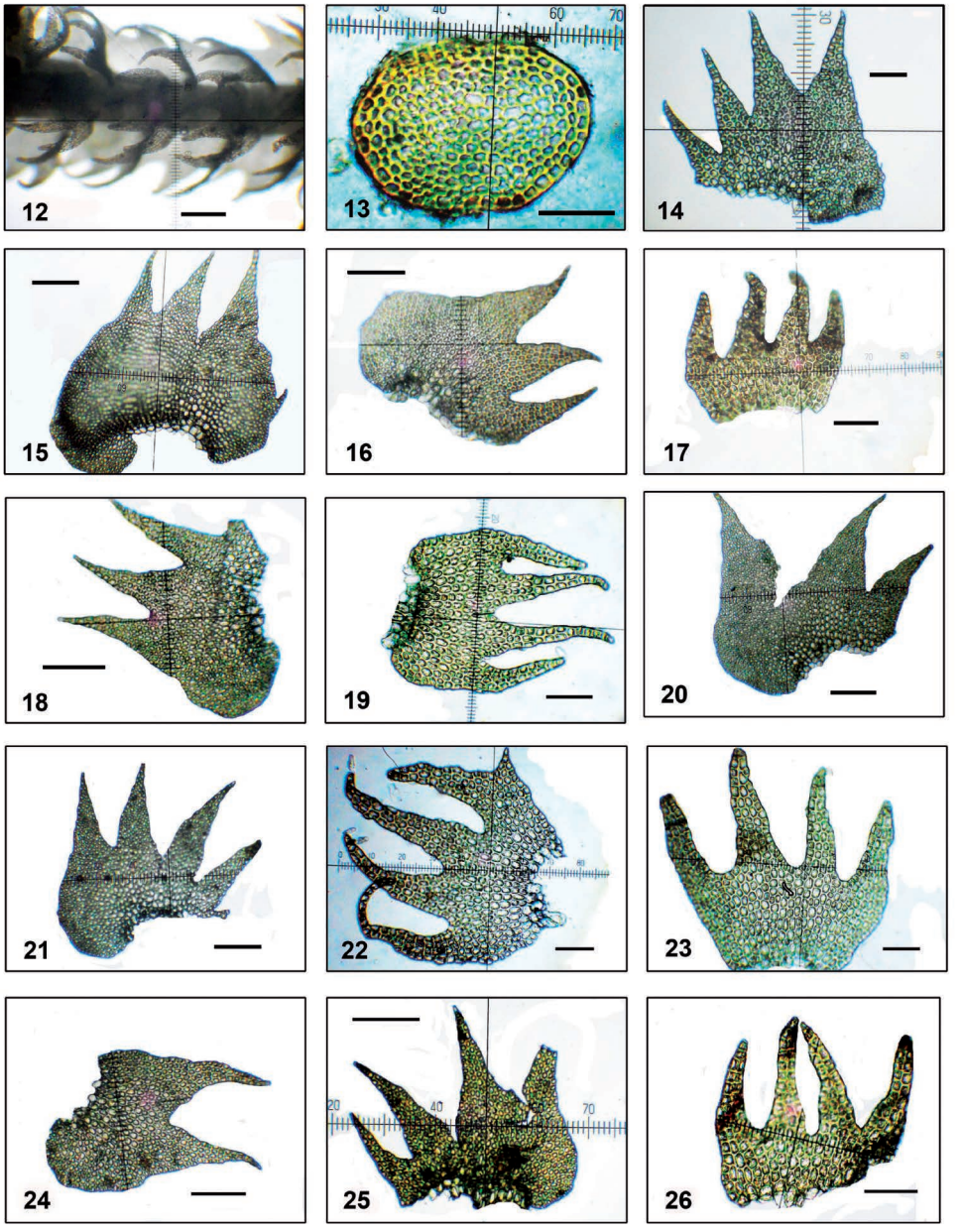
populations of a given species can show that the extremes are interconnected by a long array of intermediates, which provide a strong support for the consideration of such populations as a single entity. In order to avoid an erroneous conclusion with regard to the taxonomic status of *Lepidozia chordulifera*, the variation of African populations of *Lepidozia cupressina* is analysed in detail.

In his synopsis of taxa of the African members of the *Lepidozia cupressina* complex based on studies of the type specimens, Pócs (1984) distinguished no fewer than four subspecies within it. Of these, only two are accepted in the present treatment. The type subspecies has an Afro-American distribution and occurs in Africa mostly in the South and East African mountains, whilst *L. cupressina* subsp. *natalensis* (Steph.) Pócs is restricted to the Cape Floristic Region in South Africa and, possibly, it also occurs in temperate South America. The other two subspecies, *L. cupressina* subsp. *quinquefida* (Steph.) Pócs, which is endemic to the Central and East African mountains, and *L. cupressina* subsp. *pinnata* (Hook.) Pócs which is widely distributed in western Europe, are considered to be no more than ecological modifications which do not merit taxonomic recognition. Moreover, Pócs (1984) suggested that the other two further undescribed subspecies may occur in the Ukaguru and Uluguru Mountains in Tanzania. These plants are actually transitional between *L. cupressina* and *L. africana* Steph. and this observation strongly confirms that the latter cannot be considered to be an independent species and therefore in this paper it is recognised only as a subspecies. This subspecies occurs in the East African Indian Ocean islands, eastern Tanzania and on the Atlantic island of St. Helena (see Figs 3-26).

In contrast, Damsholt (2002) recognised in Norwegian populations of *Lepidozia cupressina* three varieties, mostly on the basis of the size and colour of the plants. Apart from the type variety, he distinguished var. *tenera*, which are small plants with dorsal leaf bases seldom crossing the stem and narrow lobes, and var. *dissitifolia* (Jörg.) Damsh., which are large plants, having distant leaves with patent lobes and relatively thin-walled leaf cells. Examination of much more material revealed the high malleability of *L. cupressina*, even within the same population, so the taxonomic value of these varieties is dubious and possibly such phenotypes are conditioned environmentally.



Figs 3-11. Dorsal and ventral views of shoots of *Lepidozia cupressina* subsp. *cupressina* and transitions to subsp. *natalensis* and subsp. *africana*. **3, 6, 7.** *L. cupressina* subsp. *cupressina* (3 from *Frahm et al. 723* [Peru]; 6 from *Pócs 6960/O* [Tanzania]). **4-5.** *L. cupressina*, transitions to subsp. *natalensis* (from *Vorster 1539b* [Republic of South Africa] (7 from *Pócs 7753* [Democratic Republic of Congo]; **8-11.** *L. cupressina*, transitions to subsp. *africana*; 8-9 from *Pócs & Sharma 6599/G* [Tanzania]; 10-11 from *Pócs & Lawrence 6871/F* [Tanzania]). Scale bar 1 mm for all pictures. (All macrophotos T. Pócs).



Figs 12-26. Side branch, main stem cross-section, stem leaves and underleaves of *Lepidozia cupressina* subsp. *cupressina* and transitions to subsp. *africana*. **12-24.** *L. cupressina* subsp. *cupressina* (12, 16 from *Pócs et al. 90018/U* [Tanzania]; 13 from *Pócs et al. 88016/AR* [Tanzania]; 14 from *Frahm et al. 723* [Peru]; 15 from *Pócs et al. 89228/R* [Tanzania]; 17-18 and 21-23 from *Pócs et al. 90067/N* [Tanzania]; 19-20 from *Pócs et al. 90083/G* [Tanzania]; 24 from *Pócs et al. 88079/M* [Tanzania], (half-leaf at base of *Frullania* type branching). **25-26.** *L. cupressina*, transition to subsp. *africana*. Stem leaf and underleaf (from *Pócs et al. 88016/AR* [Tanzania]). Scale bars 100 µm (13, 17, 19, 22, 23, 26) and 200 µm (12, 14-16, 18, 20, 21, 24, 25). (All microphotos T. Pócs).

In Africa, *Lepidozia* species (apart from those belonging to the former genus *Sprucella* Steph.) can be classified into two groups: (1) those having strongly asymmetric leaves with their auriculate dorsal bases crossing the stem midline and possessing *Calypogeia*-type oil bodies resembling bunches of grapes – *L. cupressina* (see Figs 51, 53-55) is a typical representative; (2) the other group consisting of several species with less asymmetric leaves not having an auriculate dorsal base and not crossing the stem midline. They have oil bodies of the *Bazzania*-type, consisting of one to few much larger segments (see Figs 52, 56-57, Kis & Pócs, 1997).

According to the subgeneric classification of *Lepidozia* (Schuster *in* Engel & Schuster, 2001) the first group of species, including *L. cupressina* and *L. ulothrix* (Schwägr.) Lindenb., can be classified into *Lepidozia* subg. *Notholepidozia* R.M.Schust., whereas the second group of species, including *L. pearsonii* Spruce, *L. reptans* and *L. stuhlmannii* Steph., may be positioned in the type subgenus. *Lepidozia* subg. *Notholepidozia* is typically southern temperate in distribution, whilst *L.* subg. *Lepidozia* is more widespread.

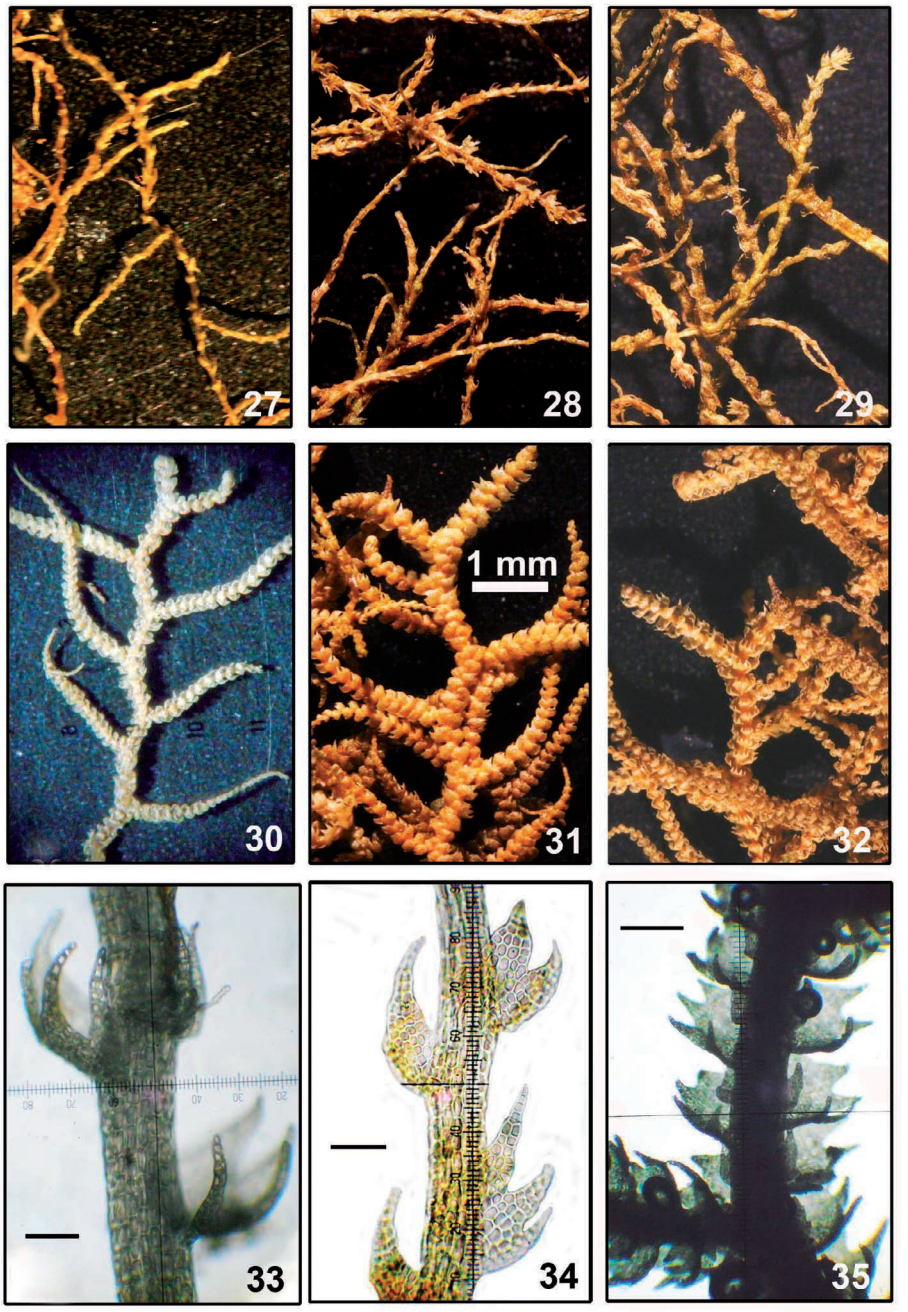
The currently recognised African subspecies of *Lepidozia cupressina* can be distinguished in the following key:

1. Main stem quite irregularly branched, when well developed, only up to 150 μm (10-12 cells) thick; leaves distant, with bases hardly concealing the stem; underleaves small, with low discus, more or less as wide as the stem; ventral leaf base never calcarate ..... *L. cupressina* subsp. *africana*
1. Main stem pinnately branched, when well developed, 200-400 μm (18-25 cells) thick; leaves usually imbricate (except for shade forms) and concealing the dorsal side of stem; underleaves much broader than the stem, with discus usually higher than the length of lobes; ventral leaf and underleaf base in many cases calcarate 2
    2. Main stem straight; ventral lobe of leaves erect; ventral leaf base calcarate or not ..... *L. cupressina* subsp. *cupressina*
    2. Main stem zigzagged; ventral leaf lobe turned forward; ventral leaf base always calcarate ..... *L. cupressina* subsp. *natalensis*

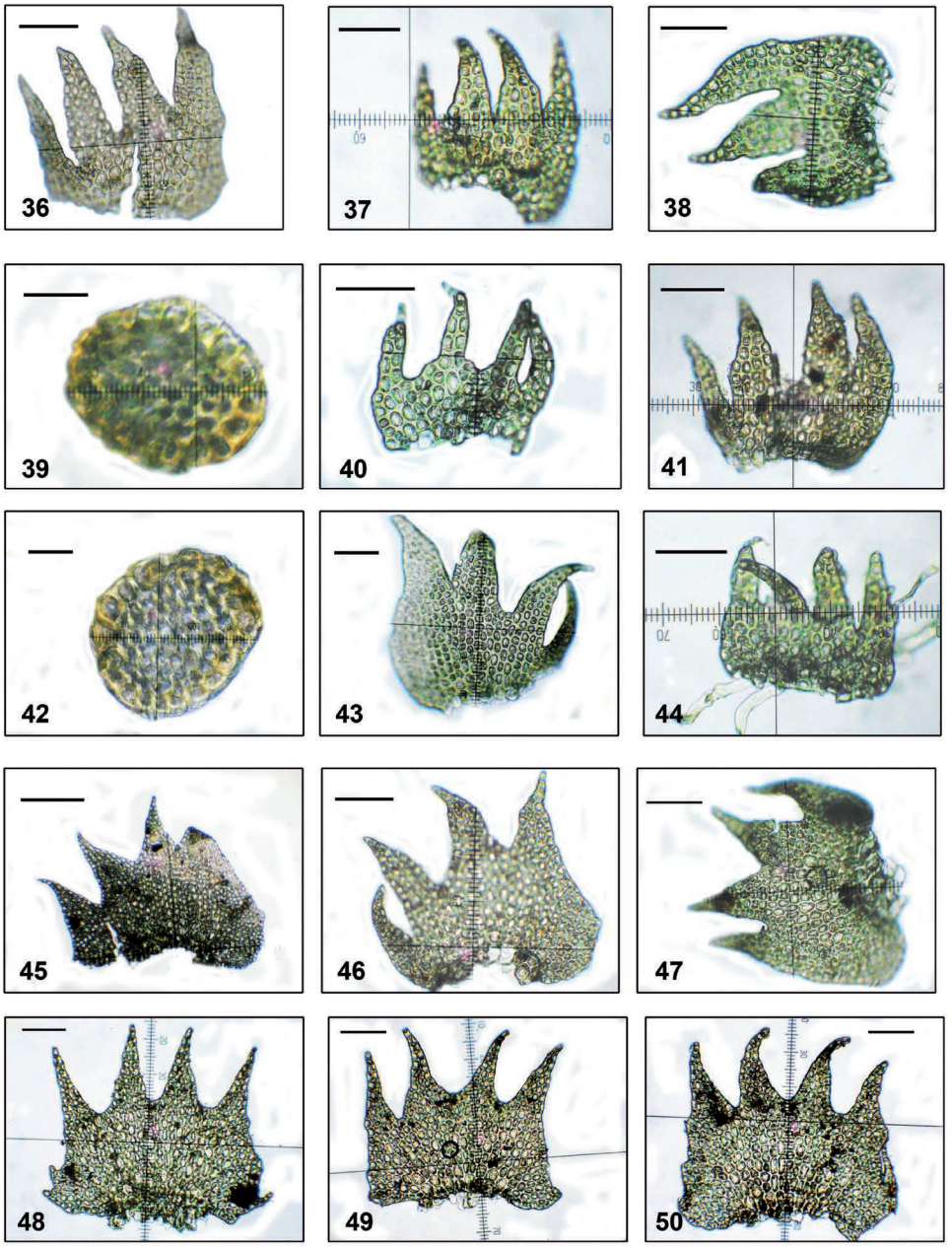
TAXONOMIC STATUS OF *LEPIDOZIA CHORDULIFERA*

Lepidozia chordulifera Taylor was described from specimens collected by Charles Darwin during the *Beagle* Expedition of 1831-1835 in the Chonos Archipelago in western Patagonia of Chile. When describing the species, Taylor (1846) compared it to *L. cupressina* from which it was said to be distinct in the leaves more closely imbricate, with dentate bases, and smaller leaf cells. During the course of the present study we examined the original material from the Taylor herbarium at FH and from the Hooker herbarium in BM.

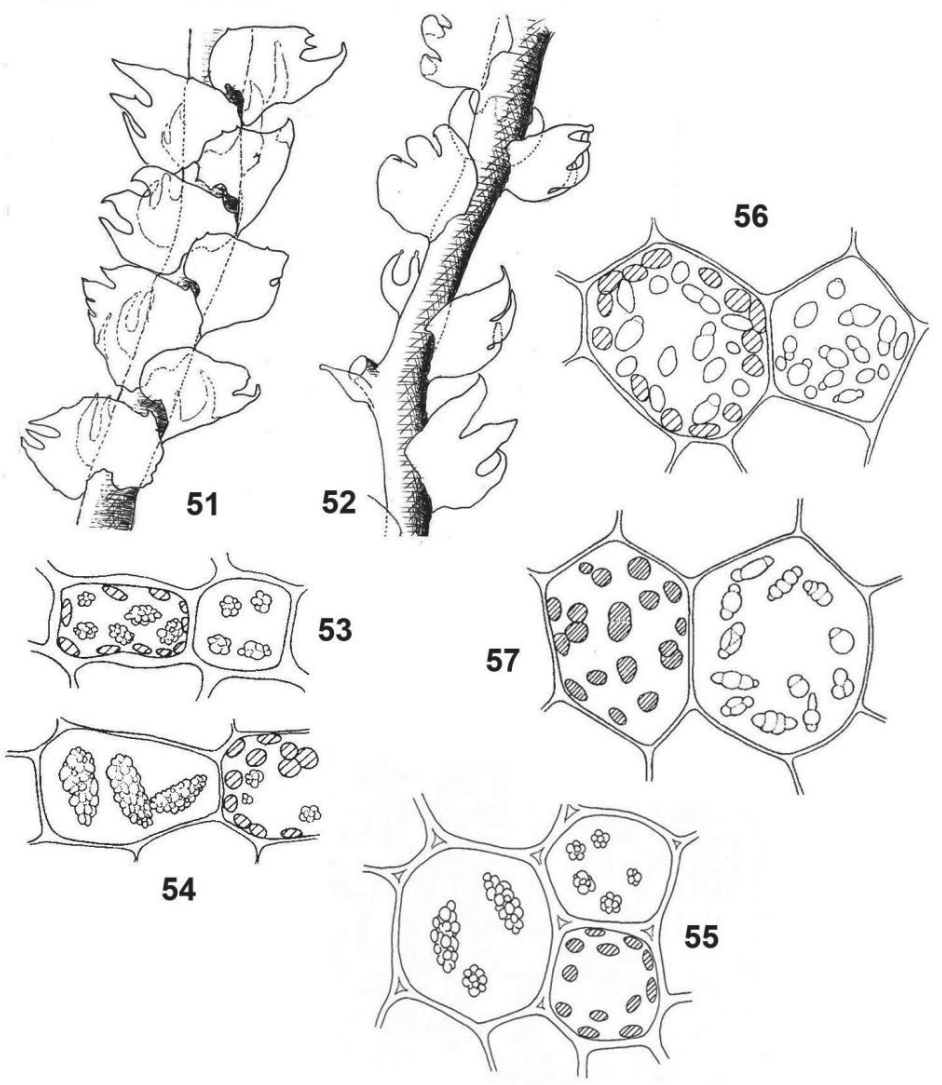
The plants are fairly small and slender, olive-whitish, growing in loose, interwoven mats. The stems are ascending, to 5 cm long, regularly pinnately branched, with branches attenuate, becoming flagelliform and microphyllous at the tips, which are usually bent abruptly downwards. The leaves (Figs 51, 53, 54, 58-60) are obliquely inserted, closely imbricate, erecto-patent, quadrate to wider than longer, semi-cordate at the base and usually crossing and concealing the stem, slightly concave, 0.3-0.4 × 0.3-0.5 mm, asymmetric, quadrifid to the middle or less,



Figs 27-35. Shoots of *Lepidozia cupressina* subsp. *africana*, *L. cupressina* subsp. *natalensis* and transitions to subsp. *natalensis* in dorsal and ventral views. **27-29** and **33-34.** *Lepidozia cupressina* subsp. *africana* (27 from *B. & T. Pócs 86108/M* [Tanzania]; 28-29 from *Pócs et al. 87183/L* [Tanzania]; 33 from *Kis 9422/AL* [Réunion]; 34 from *Renauld 36* [Mauritius], G, type of *L. africana*). **30-32, 35.** *L. cupressina* subsp. *natalensis* (30-32 from *Rehmann 31* [Republic of South Africa], G, JE, PC, type of *L. natalensis*). Scale bars 1 mm (27-32), 100 μm (33-34) and 200 μm (35). (All microphotos T. Pócs).

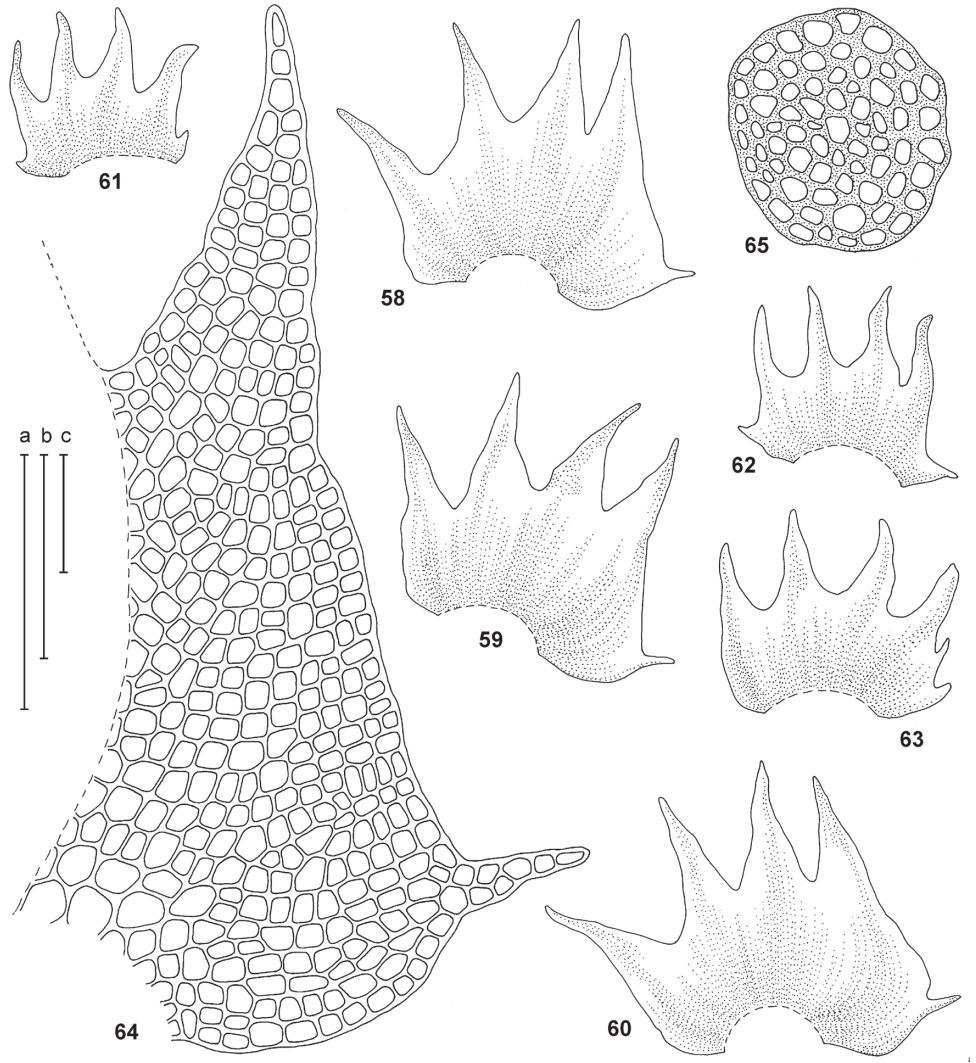


Figs 36-50. Main stem section, stem leaves and underleaves of *Lepidozia cupressina* subsp. *africana* and *L. cupressina* subsp. *natalensis*. **36-44.** *Lepidozia cupressina* subsp. *africana* (36-41 from *Kis 9422/AL* [Réunion]; 42-44 from *De Sloover 17876* [Réunion]. **45-50.** *L. cupressina* subsp. *natalensis* (all from *Rehmann 31* [Republic of South Africa], G, JE, PC, type of *L. natalensis*). Scale bars: 50 µm (39, 42) and 100 µm (36-38, 40-41, 43-50). (All microphotos T. Pócs).



Figs 51-57. Comparison of *Lepidozia cupressina* and *L. stuhlmannii,* representing *Lepidozia* subg. *Notholepidozia* and *L.* subg. *Lepidozia*, respectively. **51, 53, 54.** Dorsal view of shoot and oil bodies of *Lepidozia cupressina* subsp. *cupressina*. **55.** Oil bodies of *L. cupressina* subsp. *africana*. **52, 56, 57.** Dorsal view and oil bodies *L. stuhlmannii* (51, 53, 54 from *Pócs 8448/P* [Tanzania]; 55 from *Szabó 9475/H* [Réunion]; 52 from *Pócs 6976/X* [Tanzania]; 57 from *Pócs 89229/J* [Tanzania]; 51-52 by T. Pócs; 53-57 reproduced from Kis & Pócs, 1997).

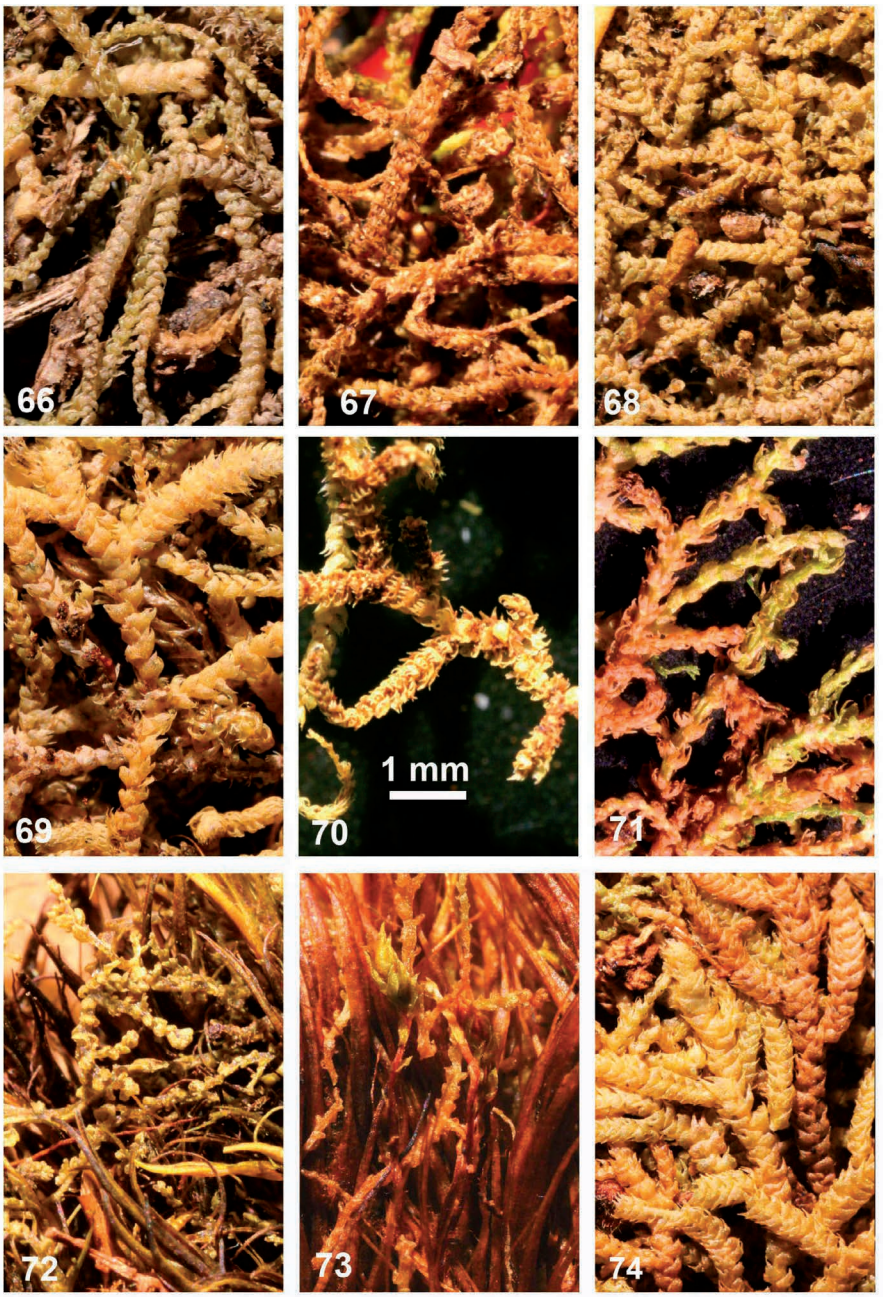
with narrowly triangular, unequal, acuminate lobes that are 4-8 cells wide at the base and have a short uniseriate tip of 3-4 cells. The dorsal margins are convex, entire or furnished with 1 or 2 sharp teeth (Fig. 64). The ventral margins are entire or toothed on well developed leaves. The leaf cells are quadrate or rounded-quadrate, thick-walled, verruculose or nearly so, 10-20 × 18-28 μm. The underleaves are similar to the lateral leaves, nearly as wide or slightly wider than the stem, quadrifid, divided



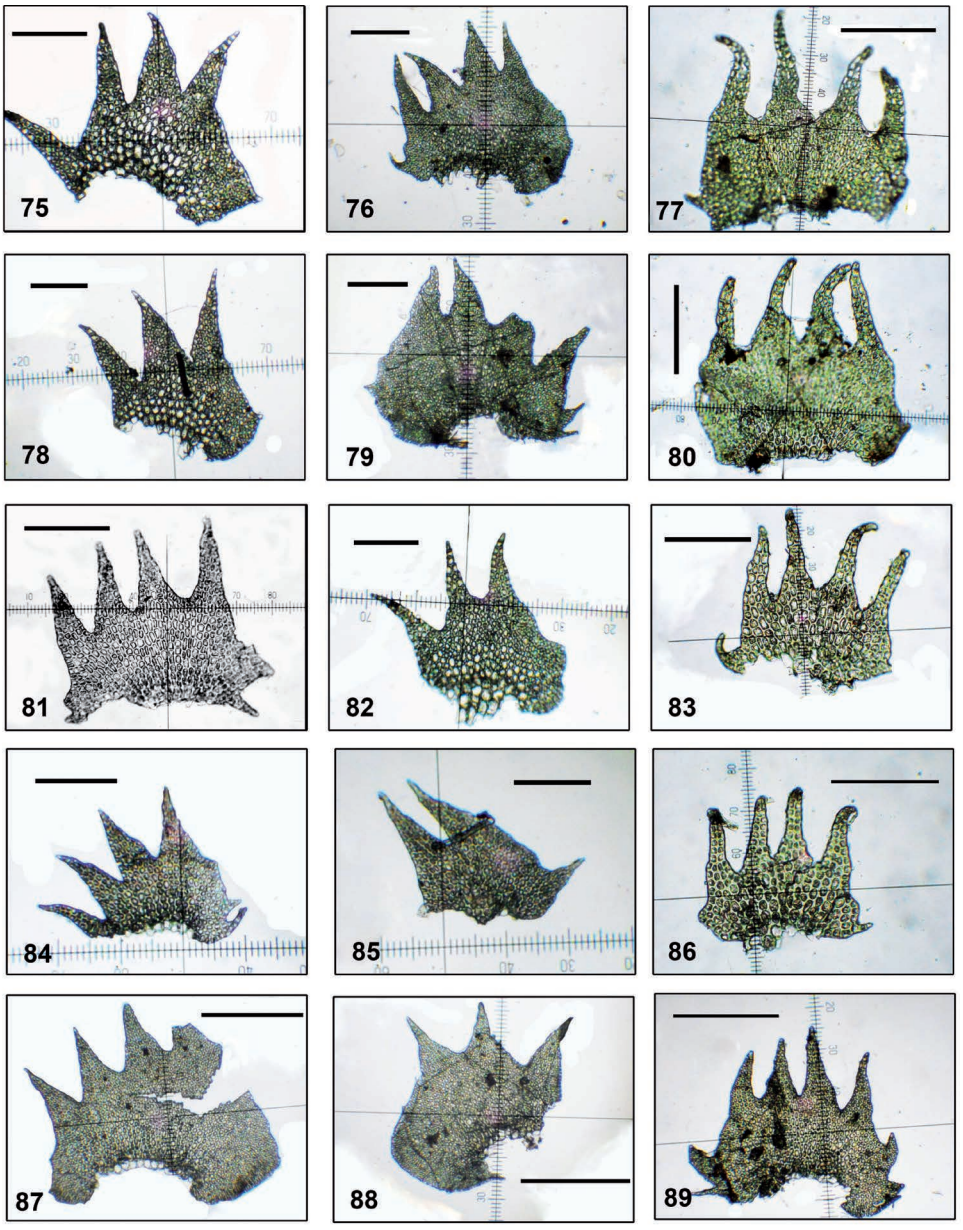
Figs 58-65. *Lepidozia cupressina* subsp. *cupressina*. **58-60.** Leaves. **61-63.** Underleaves. **64.** Leaf areolation on the dorsal side. **65.** Stem cross-section. (All from *Darwin s.n.,* BM-Hooker, isotype of *L. chordulifera* by H. Bednarek-Ochyra).

to 0.4-0.5 of the underleaf length (Figs 61-63). The stems consist of an external row of cortical cells that are somewhat larger than the medullary ones, but all cells have uniformly thickened walls (Fig. 65).

Lepidozia chordulifera is a variable species and its various phenotypes were often described as separate species. Fulford (1966) and Engel (1978) distinguished no fewer than six heterotypic synonyms which had been published for new species described from Islas Juan Fernández, Western and Southern Patagonia and Tierra del Fuego.



Figs 66-74. Dorsal and ventral views of shoots of *Lepidozia cupressina* subsp. *cupressina* from southern South America, Subantarctica and Antarctica which were previously identified as *L. chordulifera* (**66-67** from *Engel 10836* [Chile]; **68** from *Engel 2962* [Falkland Is.]; **69-70** from *Engel 10891* [Chile]; **71** from *Newsham 00038* [South Georgia]; **72** from *Lewis Smith 690* [South Orkney Is.]; **73** from *Lewis Smith 00353B* [South Orkney Is.]; **74** from *Hyvönen 3300* [Argentina, Isla Grande de Tierra del Fuego]). Scale bars: 1 mm. (All macrophotos T. Pócs).



Figs 75-89. Stem leaves and underleaves of *Lepidozia cupressina* subsp. *cupressina* from specimens from southern South America which were previously identified as *L. chordulifera* (**75, 78, 82-83** from *Roivainen 532* [Chile, Isla Grande de Tierra del Fuego]; **76-77, 79-81** *Engel 10936* [Chile]; **84-86** from *Engel 2962* [Falkland Is.]; **87-89** from *Engel 12380* [Chile]). Scale bars: 100 μm. The yellow marked part is to be cancelled. (All microphotos T. Pócs.)

The type material of *Lepidozia chordulifera* falls well within the range of variation of *L. cupressina*. The two species share the overall habit of the plants, leaf shape and areolation. The dorsal leaf margins are mostly dentate in *L. chordulifera* but this character is subject to considerable variability in *L. cupressina* throughout its wide geographical range. Because the type material and many studied non-type specimens of *L. chordulifera* from southern South America match well the type and non-type collections of *L. cupressina*, and it is impossible to find any discernible differences between them so these two species are here considered conspecific with *L. cupressina* having priority. It is worth noting that Arnell (1963: 381) considered *L. chordulifera* to be "probably a synonyme (sic!) to *L. truncatella*" which, in turn, is "very near to *L. cupressina*". Unfortunately, these statements were not based upon examination of the type specimens but are merely excerpts from the protologues of the species concerned.

TAXONOMIC CONCLUSIONS

Taxonomic discussion on species and infraspecific taxa presented above is summarised as follows:

Lepidozia cupressina (Sw.) Lindenb. subsp. ***cupressina***

In Gottsche, Lindenb. *et* Nees, *Syn. Hepat*.: 207. 1845 *Jungermannia cupressina* Sw., *Prodr*.: 144. 1788 *Mastigophora cupressina* (Sw.) Trevis., *Mem. Reale Ist. Lombardo Sci., Ser. 3, Cl. Sci. Mat.* 4: 416. 1877. **Type citation**: Jamaica [later Swartz (1806: 1857) wrote: habitat ad radices arborum in montibus summis Jamaicae]. **Isotype**: BM *ex* G 19402!

Lepidozia pinnata (Hook.) Dumort, *Rec. Observ. Jungerm.*: 19. 1835. *Jungermannia reptans* (L.) var. *pinnata* Hook., *Brit. Jung.*: *pl. 75*. 1815 *Lepidozia cupressina* (Sw.) Lindenb. subsp. *pinnata* (Hook.) Pócs, *Proc. Third Meeting Bryol. C. & E. Europe*: 109. 1984. **Type citation**: on the borders of Lough Bray, plentiful. *Mr. Turner*. – Found near Bantry, and in other parts of Ireland, by *Miss Hutchins*, Dr. Taylor, and *Dr. Stokes*. Original material not seen. First synonymised by Grolle (1971: 259).

Lepidozia quinquefida Steph. *in* Mildbr., *Wiss. Ergebn. Deutsch. Zetr.-Afrika Exped.* 2: 123, 1910. **Type citation**: Ruwenzori, Butagu-Tal, Erica-Wald, 3400 m, Mildbraed 2640. **Holotype**: G 00069025!), ***syn. nov.***

Lepidozia truncatella Nees *in* Gottsche, Lindenb. *et* Nees, *Syn. Hepat.*: 209. 1845. **Type citation**: In Promontorio Bonae Spei in montis Tabularis cacumine. **Lectotype** (*designated here*), Ecklon C.F. s.n. G 00281064; prope Zwellendam: Grootvadersbosch (Dr. Pappe). First synonymised by Pócs (1984: 109).

Lepidozia chordulifera Taylor, *London J. Bot.* 5: 371. 1846 *Jungermannia chordulifera* (Taylor) Taylor *et* Hook.f. *in* Hook.f., *Fl. Antarct.* 2: 442. 1847 *Mastigophora chordulifera* (Taylor) Trevis., *Mem. Reale Ist. Lombardo Sci., Ser. 3, Cl. Sci. Mat*. 4: 416. 1877. **Type citation**: [Chile] Chonos Archipelago, n. 461; Darwin, Hook. Herb. **Lectotype** (*designated here*): "*Jungermannia chordulifera* Tayl. (Lepidozea) '461 Chonos Archipelago. Darwin' Hook. Hab. J. D. Hooker June 1844" - FH-Taylor!; **isotype**: BM-Hooker!, ***syn. nov.***

Selected specimens examined of *Lepidozia cupressina* subsp. *cupressina*.

EUROPE. FRANCE. Dép. ***Finistère***, Plougastel-Davulas, 18 Apr 1912, *Camus s.n.* [Schiffner, *Hepaticae Europaeae Exsiccatae* 667] (EGR). IRELAND. ***Kerry***, Killarney, 40-70 m, Sep 1935, *Verdoorn s.n.* (EGR,). GREAT BRITAIN. SCOTLAND. ***West Ross.*** Allt Cleann Chaorachain near Dundonnel, 29 Jun 1973, *Een s.n.* [Soc. d'Échange de Musc. 3268] (EGR). NORWAY. Bergen, 50 m, 1900, *Jörgensen s.n.* [Schiffner, *Hepaticae Europaeae Exsiccatae* 671] (EGR).

NORTH AMERICA. MEXICO. Mirador, *Liebmann* (G 19397).

CENTRAL AMERICA. CUBA. Palenque. *Bisse & Köhler 9510* (HAC). COSTA RICA. ***Alajuela***, 15 km NW of San Rámon, Cerro Azahar, 1400-1500 m, *Liesner et al. 15627* (EGR, U). JAMAICA. Without detailed locality, *Swartz* (BM *ex* G 19402, isotype of *Jungermannia cupressina*).

SOUTH AMERICA. VENEZUELA. ***Mérida.*** Parque Nac. Sierra Nevada, La Aguada, 3300 m, *Pócs & Rico 9736/BT* (EGR, ULA). COLOMBIA. ***Cundinamarca***, Páramo el Palacio, 4000 m, *Cleef 1687* (U). PERU. ***Amazonas***, Prov. Chachapoyas, oberhalb Leimebamba, 2800 m, *Frahm et al. Bryotrop Peru 723* (EGR). BRASIL. ***Santa Catarina***, Serra do Corvo Branco, Urubici-Grão Pará, 1110 m, *Schäfer-Verwimp & Verwimp 13500* (EGR). CHILE. ***Valdivia***, Osorno, *Engel 10936* (EGR); Prov. Arauco, *Engel 12581* (EGR); Prov. Cautin, Villarica National Park, *Engel 11204* (EGR); Parque de Exposiciones Saval, Isla Teja, *Engel 10891* (KRAM). ***Los Lagos***, Parque Nac. Alerce Andino, Tal des Rio Chaicas, Puerto Montt, *Zündorf 21094* (KRAM); W slope near Río Futa in vicinity of Futa, *Engel 10836* (EGR); summit of El Mirador, Cordillera Pelada, 1000 m, *Engel 12380* (EGR). ***Juan Fernandez***, Mas Afuera I., 900 m. *Hatcher & Engel 319* (EGR). ***Chiloé Island***, *Engel 12076*, (EGR). ***Magallanes***, Seno Otway, alt. 170 m, *Hyvönen 2900* (EGR); Cabo de Hornos, I. Navarino w of Puerto Williams, alt. 5-100 m, *Buck 40739* (KRAM); Brunswick Peninsula, Punta Arenas, alt. 300 m, *Imshaug & Harris 38997* (EGR); Isla Grande de Tierra del Fuego, Lago Escondito, alt. 120 m, *Roivainen 532* (EGR). ARGENTINA. ***Neuquén***, Parque Nac. Nahuel Huapi, Paso de Puyehue, alt. 880 m, *Hyvönen 5760* (EGR). ***Isla Grande de Tierra del Fuego***, Bahia Lapataia, alt. 40 m, *Hyvönen 3300* (KRAM); Peninsula Mitre, alt. 30 m, *Hyvönen 3090* (EGR, KRAM); Bahia Valentin, alt. 50 m, *Hyvönen 3174* (EGR). FALKLAND ISLANDS. ***West Falkland,*** West French Peak, alt. 310 m, *Engel 2962* (EGR).

SUBANTARCTICA. SOUTH GEORGIA. Royal Bay, Moltke Harbour, 29 Apr 1902, *Skottsberg s.n.* (S); Cumberland Bay, Harbour, May 1902, *Skottsberg s.n.* (S); above King Edward Point, S side of Mt. Duse, alt. 85 m, *Smith 01366A* (AAS, KRAM); Bird Island, Jordan Cove, alt. 30 m, 15 Dec 1960, *Greene s.n.* (AAS, KRAM); slopes o f Gazella Peak, *Wright 00005D* (AAS, KRAM); small dell at base of slope, Grytviken, *Newsham 00038* (AAS, KRAM).

ANTARCTICA. SOUTH SANDWICH ISLANDS. ***Candlemas Island***. Steaming lake on western shore, alt. *ca* 35 m, *Longton 635* (AAS, KRAM). SOUTH ORKNEY ISLANDS. ***Coronation Island***. Cape Hansen, alt. *ca* 15 m, *Lewis Smith 1852* (AAS, KRAM). ***Signy Island***. Borge Bay, Knife Point, alt. *ca* 15 m, *Lewis Smith 10729 & 19033* (AAS, KRAM); Factory Cove, alt. 50 m, *Lewis Smith 5203* (AAS, KRAM), alt. *ca* 65 m, *Lewis Smith 303* (AAS, EGR, KRAM) and alt. 80 m, *Lewis Smith 690* (AAS, KRAM); south-east shore of Factory Cove, alt. 50 m, *Longton 1165* (AAS, KRAM); east side of Rusty Bluff above Paal Harbour, alt. *ca* 30 m, *Lewis Smith 1839* (AAS, KRAM) and alt. *ca* 35 m, *Lewis Smith 353B* (AAS, KRAM); above Paal Harbour, alt. 75 m, *Lewis Smith 10865* (AAS, KRAM).

AFRICA. BIOKO. NE slope of the Pico Basile along the road to the summit, alt. 2400-2600 m, *Müller B459* (DR). DEMOCRATIC REPUBLIC OF CONGO (formerly ZAIRE). ***Kivu***. Kahuzi-Biega Nat. Park, Lushanja bog SW of Camp Biega, alt. 2400 m, *Frahm 7348* (EGR); Mt. Kahuzi, ridge along summit trail, alt. 3270 m, *Pócs 7753* (EGR). RWANDA. ***Gikongoro.*** Forêt de Nyungwe, Rwasenoko, alt. 2500 m, *Pócs 6123* (EGR). UGANDA. ***Toro***. Rwenzori Mts., near Nyabatiba Hut, alt. 2600 m, *Lye B-128* (EGR). TANZANIA. ***Kilimanjaro***. Kilimanjaro Mts., Osaki Forest St., alt. 1750-1950 m, *Pócs et al.90066/G* (EGR); N of Kibosho village, Lilimankaro Forest Res., alt. 1950 m, *Pócs et al. 90067/N* (EGR); Marangu Route, alt. 2130-2350 m, *Pócs & Orbán 89142/L* (EGR); above Mandara Hut, alt. 2730-2780 m, *Pócs*, *Ochyra & Bednarek-Ochyra 88122/F* [Ochyra & Pócs,

Bryophyta Africana Selecta 17] (EGR, KRAM); Machame Route, alt. 2200-2700 and 2700-3000 m, *Pócs 6976/X & 6977/A* (EGR); Umbwe Route, alt. 2200-2400 m, *Pócs et al. 89228/R & 89229/J* (EGR), alt. 2800-2900 m (as subsp. *quinquefida*) *Pócs 6229/A* (EGR); North Pare Mts., summit of Mt. Kindoroko, alt. 1800-1900 m, *Pócs et al. 90018/U* (EGR); South Pare Mts., Mt. Shengena, alt. 2330-2462 m, *Pócs 90083/G & 9084/L* (EGR). ***Tanga***. West Usambara Mts., Mazumbai University Forest Reserve, alt. 1850-1930 m, *Pócs et al. 88079/M* (EGR); Mazumbai, Sagara Ridge, alt. 1850-1980 m, *Pócs 6960/O* (EGR); Mlomboza summit, alt. 2200-2300 m, *8448/P* (EGR); SW of Kwagoroto summit, *Pócs 8448/P* (EGR); Shagein Peak, alt. 2100 m, *Iversen et al. 86206/M* (EGR); Magamba summit, alt. 2200 m, *Pócs 6954/E* (EGR). ***Morogoro***. Nguru Mts., Dikurura Valley, alt. 1900 m, *Pócs 89120/C* (EGR); Uluguru Mts., Bondwa Peak, alt. 1700-2050 m, *Pócs et al. 6260/M* (EGR) *& 6599/G* (transitional to subsp. *africana*) (EGR); ridge between Lupanga and Kinazi peaks, alt. 1800-1900 m (transitional to subsp. *africana*), *Pócs & Mwanjabe 68366AZ* (EGR); Ukaguru Mts., Mnyera ridge, alt. 2050-2100 m (transitional to subsp. *africana*)*, Pócs & Lawrence 6871/F* (EGR); Mamwira summit, alt. 2100-2260 m (transitional to subsp. *africana*)*, Pócs et al. 88016/AR* (EGR). REPUBLIC OF SOUTH AFRICA. ***Mpumalanga*** (formerly Transvaal). Pelgrimsrus, 1900 m (transitional form to subsp. *natalensis*), *Vorster 1539b* (JE). ***Western Cape***. Table Mountain, *Wilms 2531* (G 447); Echotal, alt. 800 m, *Lübenau 14* (EGR); E slope of Table Mountain, Skeleton Gorge, alt. 700 m, 16 Oct 1996, *Arts s.n.* (EGR); Deloits Cliff, 610 m (transitional form to subsp. *natalensis*), *MacOwen* (G 19055); Cape (transitional form to subsp. *natalensis*), *Drége s.n.* (PRE).

Lepidozia cupressina (Sw.) Lindenb. subsp. ***africana*** (Steph.) Pócs, ***stat. et comb. nov.*** **Figs 27-28, 33-34, 36-44**

Well illustrated by Wigginton (2010), Figs 3-5 sparse and distant branching.

Basionym: *Lepidozia africana* Steph., *Spec. Hep*. 6: 320. 1922. **Type citation**: Insula Mauritius, Renauld 36. **Holotype**: G 00045345!

Lepidozia africana was described on the basis of an extremely delicate specimen. It has been collected several times since, often in tufts of *Sphagnum* or dicranaceous mosses, where it is similarly slender. However, the epigean or epiphytic plants of this species are more vigorous. In the Eastern Arc of continental East Africa both typical "africana" specimens and transitions to *Lepidozia* subsp. *cupressina* occur. These have narrower stems, distant leaves only partly covering the dorsal surface of the stem and small underleaves. Therefore, *L. africana,* which has its own distribution area in the Indian Ocean islands and eastern Tanzania, does merit recognition at the subspecies level. The affiliation of this distinct phenotype to the range of variability of *L. cupressina* is confirmed by the basic auriculate dorsal leaf base and the *Calypogeia*-type oil bodies (roughly segmented, like bunches of grapes). Wigginton (2010) also discovered it on the South Atlantic island of St. Helena, where it seems to be relatively widespread and also occurs in a well developed form and in a shade attenuated form with distant branching and small leaves.

Selected specimens examined of *Lepidozia cupressina* subsp. *africana*. AFRICA. TANZANIA. ***Morogoro***. Uluguru Mts., Lupanga crest, alt. 2100-2140 m, *T. & B. Pócs 86108/M* (EGR); NW ridge of Palata, alt. 1700-1850 m, *Pócs & Crosby 6851/G* (EGR); Kinazi ridge, *Pócs et al. 87183/L* (EGR). MAURITIUS. Sine loco, *Renauld 36* (G 19020, type of *Lepidozia africana*). RÉUNION. Basse Vallée – Puys Ramond, alt. 1000-1400 m, *Pócs 9612/DF & 9613/CX* (EGR); Cirque de Cilaos, sentier du Piton des Neiges, *De Sloover 17876* (EGR); Plaine des Cafres, Piton Mare à Boue, alt. 1500 m, *Onraedt 69R.0482* (EGR); Saint Philippe, NNW ridge of Piton Marmite, alt. 1740 m, *Szabó 9425/H* (EGR); Cirque de Salazie, Plaine des Merles, alt. 1800 m, *Kis 9422/AL 9422/AM* (EGR).

Lepidozia cupressina (Sw.) Lindenb. subsp. ***natalensis*** (Steph.) Pócs **Figs 30-32, 35, 45-50**

Proc. Third Meeting Bryol. C. & E. Europe: 109. 1984 *Lepidozia natalensis* Steph., *Spec. Hep.* 3: 562, 1909. **Type citation**: Cape, Montagu Pass, Rehmannn. **Lectotype** (*designated here*): G 00281064!; **isotypes:** JE!, PC!).

Selected specimens examined of *Lepidozia cupressina* subsp. *natalensis*. AFRICA. REPUBLIC OF SOUTH AFRICA. ***Western Cape***. Montagu Pass, *Rehmann 31 (Hepaticae austro-africanae*) (G, JE, PC, type of *Lepidozia natalensis*); Knysna, *Iverson 1803* (BM); Cape of Good Hope, *Wilms* (G 19048); "Afrique Australe", *J. Hennegart s.n. 1838-1839* (PC *ex* Hb. Drège as *Jungermannia cupressina* β *capensis*).

Lepidozia cupressina subsp. *natalensis* seems at first sight to be a different species due to its zigzagging stem and forward turned first lobe tooth. However, a closer investigation reveals that there are morphological transitions between this taxon and *L. cupressina* subsp. *cupressina.* Since this taxon has a narrow range and is restricted to southern Africa, it seems reasonable to consider it as a subspecies of *L. cupressina.*

A REVIEW OF THE GLOBAL RANGE OF *LEPIDOZIA CUPRESSINA*

Lepidozia cupressina is an excellent example of a species whose geographical range has been variously interpreted, depending on the accepted taxonomic concepts of the species. For a long time its geographical range was considered as a classical example of a montane species, having maximum occurrence in the Neotropics and only occasionally occurring in South and East African mountains. The number of known localities of the species in Central and East Africa has markedly increased in several recent decades with progress in the bryological exploration in this part of the continent (Wigginton & Grolle, 1996; Wigginton, 2009). Gradstein *et al*. (1984) considered it to be a "wide southern temperate element penetrating up to Atlantic Europe". Currently, *L. cupressina* is known from Kenya, Uganda, Rwanda, Democratic Republic of Congo and Tanzania (Wigginton, 2009), and recently it was also found in Bioko in West Africa (Müller & Pócs, 2007) and in Lesotho in southern Africa (Hodgetts *et al*., 1999).

In the Neotropics the species is very widespread in the West Indies, in the Central American isthmus and in northern South America, extending to Bolivia and SE Brazil (Yano, 1984). This type of distribution includes no fewer than 77 species of hepatics (Gradstein, 2013; Ellis *et al*., 2013b,c) and about 80 species of mosses (e.g. Frahm, 1982; Allen & Crosby, 1986; Ochyra *et al*., 1992; Ochyra & Lewis Smith, 1998; Blockeel *et al*., 2010; Ellis *et al*., 2012a,b,c,d, 2013a; Bednarek-Ochyra & Ochyra, 2012a,b, 2013), but probably the final tally of Afro-American bryophyte species will be higher with progress in taxonomic and field studies.

The South American occurrence of *Lepidozia cupressina* was partly resolved by Pócs (1984) who considered *L. wallisiana* to be identical with it, however, Fulford (1966) considered it to be a distinct species. The conspecificity of these species confirmed the occurrence of *L. cupressina* in Colombia, Venezuela, Ecuador, Peru, and Bolivia. Additionally, the range of *L. cupressina* was extended to Costa Rica in Central America as a result of the conspecificity of *L. muenchiana* and *L. cupressina* (Pócs, 1984), and recently the species was also reported from Panama (Stotler *et al*., 1998) and Costa Rica (Dauphin, 2005).

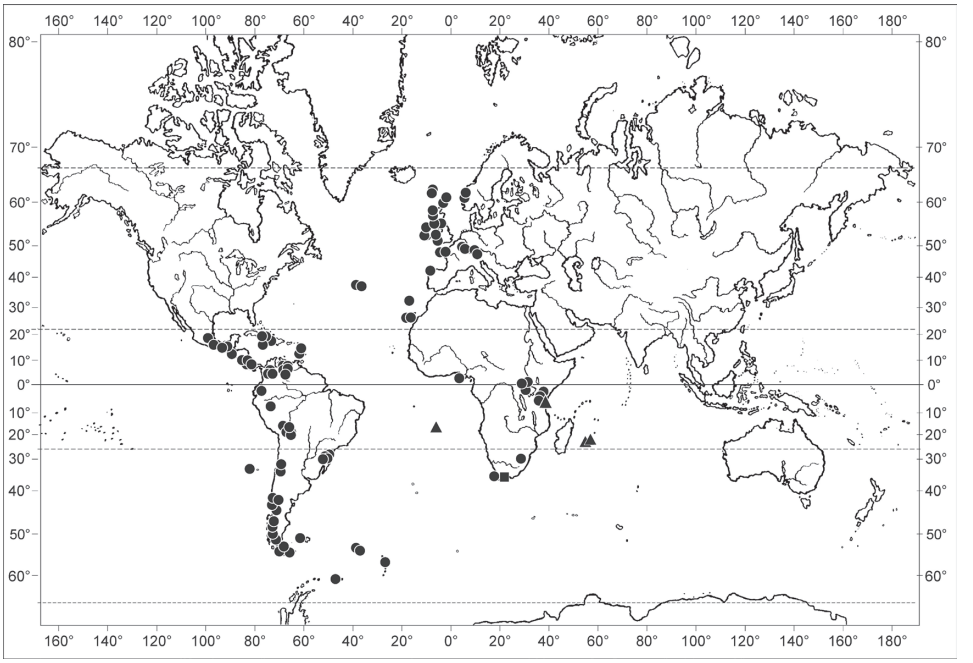


Fig. 90. Global distribution map for *Lepidozia cupressina*: subsp. *supressina* (●), subsp. *africana* (▲) and subsp. *natalensis* (■).

The most problematic was the occurrence of *Lepidozia cupressina* in temperate southern South America, including Western Patagonia (e.g. Reimers, 1926; Stephani, 1900, 1901) and Tierra del Fuego (e.g. Massalongo, 1885; Stephani, 1901). The species was excluded from this region by Engel (1978) and Hässel de Menéndez and Rubies (2009). On the other hand, Gradstein *et al*. (1984) presented the global distribution map for *L. cupressina* which was partly based on the specimens examined and it covered Patagonia and Tierra del Fuego and, additionally, the Falkland Islands, although the species had not been earlier recorded from this archipelago (Engel, 1990). As a result of the taxonomic conclusion on the conspecificity of *Lepidozia cupressina* and *L. chordulifera*, the occurrence of the former in southern South America confirmed. This conclusion is reinforced by examination of many non-type collections of *L. chordulifera* as demonstrated in Figs 3-6. In addition, the range of *L. cupressina* was extended to subantarctic South Georgia from where it was previously reported as *L. chordulifera* (Stephani, 1905) and *L. cuspidata* Steph. (Grolle, 1972), as well as to the northern maritime Antarctic where it is known from the volcanic Candlemas Island in the South Sandwich Islands archipelago and Signy Island in the South Orkney Island (Grolle, 1972; Bednarek-Ochyra *et al*., 2000). *Lepidozia cupressina* is evidently a postglacial immigrant on South Georgia and in the Antarctic, as is the case with many species of mosses and liverworts on subantarctic islands (Birkenmajer *et al*., 1985; Van der Putten *et al*., 2004, 2010).

Considering its current geographical distribution (Fig. 90), *Lepidozia cupressina* may be designated as a bipolar temperate species with numerous transitional stations in the tropical mountains.

The highest concentration of the transitional tropical localities is in the Neotropics from southern Mexico to Bolivia, and in South, East and Central Africa. The species is rare in West Africa, which is less mountainous, and in the East African Indian Ocean islands. In the Atlantic island of St. Helena it is represented only by the separate subspecies, *L. cupressina* subsp. *africana* (Wigginton, 2009, 2010).

In the Northern Hemisphere *Lepidozia cupressina* is restricted in its occurrence to the oceanic part of Europe. It has an optimum occurrence in the British Isles, especially on the western coasts of Ireland, Scotland, Wales and England (Blackstock, 2014) and in the Faroes and SW Norway (Damsholt, 2002). In continental Europe it is much rarer in NE France (Touffet, 1969), NW Spain (Casas *et al*., 1985), Baden-Würtemberg and Nordrhein-Pfalz in Germany (Meinunger & Schröder, 2007), Luxembourg (Werner & Hans, 2003; Werner, 2011), and Belgium (Söderström *et al*., 2002). A highly isolated station of this species in western Bulgaria (Stefanov & Petrov, 1962) proved to be very doubtful and in fact this record was rejected by one of the authors of the original report (Petrov, 1975), although Ganeva and Natcheva (2003) continued to report it from Bulgaria, but as a dubious species. In addition, *L. cupressina* is widespread in Macaronesia, including the Azores, the Canary Islands and Madeira (Eggers, 1982).

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