Phylogenetic evidence for an expanded circumscription of *Gabura* (*Arctomiaceae*)

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Abstract
Since the advent of molecular taxonomy, numerous lichen-forming fungi with homoiomerous thalli initially classified in the family *Collemaetaceae* Zenker have been transferred to other families, highlighting the extent of morphological convergence within Lecanoromycetes O. E. Erikss. & Winka. While the higher level classification of these fungi might be clarified by such transfers, numerous specific and generic classifications remain to be addressed. We examined the relationships within the broadly circumscribed genus *Arctomia* Th. Fr., which has been the recipient of several transfers from *Collemaetaceae*. We demonstrated that *Arctomia insignis* (P. M. Jørg. & Tønsberg) Ertz does not belong to *Arctomia* s. str. but forms a strong monophyletic group with *Gabura fascicularis* (L.) P. M. Jørg. We also confirmed that *Arctomia borbonica* Magain & Sérus. and the closely related *Arctomia insignis* represent two species. We formally transferred *A. insignis* and *A. borbonica* to the genus *Gabura* Adams. and introduced two new combinations: *Gabura insignis* and *Gabura borbonica*. We reported *Gabura insignis* from Europe (Scotland and Ireland) for the first time. While material from Europe and North America is genetically almost identical, specimens from Madagascar, South Africa and Reunion Island belong to three distinct phylogenetic lineages, all of which are present in the latter area and may represent distinct species. In its current circumscription, the genus *Gabura* may contain up to six species, whereas *Arctomia* s. str. includes only two species (*A. delicatula* Th. Fr. and *A. teretiuscula* P. M. Jørg.). The *Gabura insignis* group is shown to have an unexpectedly large, subcosmopolitan distribution. With the extended sampling from *Arctomiaceae* Th. Fr., the placement of *Steinera sorediata* P. James & Henssen in the genus *Steinera* Zahlbr. is confirmed and the presence of a new *Steinera* species from Chile is highlighted.

Key words: biogeography, Ireland, lichenized fungi, Scotland, species delimitation

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Introduction
Within the Lecanoromycetes O. E. Erikss. & Winka, the subclass Ostropomycetidae Reeb *et al.* has a high diversity of ascomata, thallus forms, symbiont preferences and ecological habits. Relationships among orders inside Ostropomycetidae have been difficult to resolve (e.g. Baloch *et al.* 2010; Resl *et al.* 2015). Phylogenetic revision of the Lecanoromycetes (Miadlikowska *et al.* 2014) placed the *Arctomialae* S. Stenroos, Miädl. & Lutzoni as a sister group to the Ostropales Nannf. with weak support, as part of a relatively well-supported clade which also contains *Trapeliales* B. P. Hodk. & Lendemer. Resl *et al.* (2015) performed a series of topological hypothesis testing and rejected the sister group relationship of *Arctomialae* and *Ostropales*. Instead, the authors recognized *Arctomialae* as part of the order *Baeomycetales* Lumbsch, Huhndorf & Lutzoni based on its sister relationship to *Xylographaceae* Tuck. and *Trapeliales* M. Choisy ex Hertel. within a large clade that includes *Baeomycetales* Dumort. and *Hymeneliaceae* Körb. A recent revision of the orders and families within the Lecanoromycetes, based on a temporal banding approach (Kraichak *et al.* 2018), confirmed this topology and reduced the *Arctomialae* into synonymy with *Baeomycetales*.

*Arctomialae* is the only family of the Ostropomycetidae to associate with cyanobacteria of the order *Nostocales* T. Cavalieri-Smith as their main photobionts (Miadlikowska *et al.* 2014). Morphology-based revisions classified most lichens with jelly-like, homoioomerous thalli in the family *Collemaetaceae* Zenker, until Wedin *et al.* (2009) showed that fungi forming such thalli represent a much broader phylogenetic diversity. Furthermore, it has been shown that the identity of the cyanobiont is likely to influence the thallus structure. For example, Magain & Sérusiaux (2014) demonstrated that in the genus *Fuscopannaria* P. M. Jørg., thalli of the *Kroszia* morphotype involve cyanobionts from a unique clade of *Nostoc* Vaucher ex Bornet ex Flahault,
which is phylogenetically distant from other *Fuscoannaria* photobionts. Recently, several species classified elsewhere have been transferred to *Arctomiaceae* based on molecular evidence, for example *Moelleropsis humida* (Kuhl.) Coppins & P. M. Jørg. (currently *Gregorella humida* (Kuhl.) Lumbsch; Lumbsch et al. 2005). *Collema fasciculare* (L.) F. H. Wigg (currently *Arctomia fasciculare* (L.) Otálora & Wedin; Otálora & Wedin 2013) and *Massalongia intricata* Øvstedal (currently *Steinera intricata* (Øvstedal) Erz; Ertz et al. 2017). Spribille & Muggia (2013) also discussed the possibility of two other *Steinera* species, *S. polymorpha* P. James & Henssen and *S. sorediata* P. James & Henssen, belonging in *Arctomiaceae*.

Otálora & Wedin (2013) recognized *Collema fasciculare* as a member of *Arctomiaceae* under the name of *Arctomia fasciculare*, despite the anatomical differences in comparison to other species of the genus but in the absence of convincing phylogenetic evidence for the recognition of a new genus. Later on, Jørgensen (2014) proposed to resurrect the name *Gabura Adans.* to accommodate *Collema fasciculare* as *Gabura fasciculare* (L.) P. M. Jørg. (spelt as ‘fasciculare’). Currently, the family *Arctomiaceae* contains five accepted genera: *Arctomia* Th. Fr., *Gabura*, *Gregorella* Lumbsch, *Steinera* Zahlbr. and *Wawea* Henssen & Kantvilas. Jørgensen & Palice (2016) suggested that the morphology of *Leptogium insignis* P. M. Jørg. & Tønsberg resembled that of *Gabura fasciculare*, and that this species might also be a member of the genus *Gabura*. However, the formal transfer was never completed due to lack of molecular evidence. *Leptogium insignis* was later transferred to the genus *Arctomia* as *A. insignis* P. M. Jørg. & Tønsberg (Ertz et al. 2017). The geographical distribution of *A. insignis* remains unclear because the species is often confused with the morphologically similar but unrelated *Leptogium brebissonii* Mont., which has been reported from Australia, Brazil, France, Montenegro, Portugal and Tenerife. In contrast, *A. insignis* is found on the west coast of North America, including Alaska, British Columbia, California, Oregon (the type locality) and Washington, where *L. brebissonii* is thought not to occur (Carlb erg 2012). Another new species, *A. borbonica*, morphologically resembling *A. insignis*, was described from Reunion Island by Magain & Sérusiaux (2012). Later, despite the absence of genetic evidence, this species was synonymized with *A. insignis* (as *Leptogium insignis*) by Jørgensen & Palice (2016).

Since many recent studies revealed numerous cases of similar morphotypes representing assemblages of distinct, genetically isolated lineages (e.g. Lücking et al. 2014, 2017; Magain et al. 2017) and because cosmopolitan species seem to be the exception rather than the rule for lichen-forming fungi (e.g. Moncada et al. 2014; Lücking et al. 2017; Magain et al. 2017), the aims of this project were to 1) reconstruct a multilocus phylogeny for the family *Arctomiaceae*; 2) re-evaluate the circumscriptions of genera using monophyly as the grouping criterion; 3) assess the taxonomic validity of *A. borbonica* and *A. insignis*. We present a four-locus phylogeny of the family *Arctomiaceae*, with a focus on the genus *Gabura*. We assessed the generic affinity of *Arctomia insignis* based on expanded taxon sampling. We also tested whether *A. borbonica* represents a distinct lineage sister to *A. insignis*. In addition, we assessed the phylogenetic placement of recently acquired putative specimens of *A. insignis*, and other members of *Arctomiaceae*, in the context of the most comprehensive taxon sampling of the family to date.

Material and Methods

**Taxon sampling and DNA sequence acquisition**

We collected eight specimens morphologically identified as *Arctomia insignis* or *A. borbonica* from the USA (Oregon), Ireland, Scotland, Madagascar, Reunion Island and South Africa, as well as one specimen identified as *G. fasciculare* from Chile. For each of the nine specimens, we sequenced four loci of the mycobiont DNA: the entire ITS regions (internal transcribed spacer 1, 5.8S ribosomal RNA gene and internal transcribed spacer 2; ITS), the nuclear large subunit ribosomal RNA gene (nuLSU), the mitochondrial small subunit ribosomal RNA gene (mtSSU), and the protein-coding RNA polymerase II largest subunit (RPB1), following protocols described in Magain & Sérusiaux (2012, 2015). We also sequenced ITS of the type material of *A. borbonica* (N952), mtSSU and nuLSU for a specimen of *Steinera sorediata* from the type locality, and ITS and mtSSU for two unidentified collections of *Steinera* from Chile. We generated 10 new ITS sequences, nine nuLSU, 12 mtSSU and six RPB1, giving a total of 37 new sequences (Table 1). We downloaded sequences from GenBank representing the diversity of *Baeomyctales* and selected orders from Ostropomycetidae (Kraichak et al. 2018) and added sequences of *Lecanora intumescentes* (*Lecanorales* Nannf.) to root the tree.

We assembled single-locus datasets using Mesquite v. 3.1.1 (Maddison & Maddison 2016). Sequences were aligned using MAFFT v. 7.305b with default settings (Katoh et al. 2002). Substitutions and indels between sequences of the *A. insignis/A. borbonica* group were counted after alignment. After manual exclusion of ambiguously aligned characters, we combined them into two datasets: a three-locus dataset of 63 specimens containing nuLSU (903 characters), mtSSU (605 characters) and RPB1 (654 characters); a four-locus dataset containing, in addition to the three loci, the ITS sequences (653 characters) of eight representatives of the *A. insignis/A. borbonica* group (Table 1). We also assembled a two-locus dataset (ITS and mtSSU with 486 and 790 characters, respectively) for the sequences from the three *Steinera* specimens along with all the sequences for ITS and mtSSU available in GenBank for this genus.

**Phylogenetic and species discovery analyses**

We delimited six subsets for the three-locus dataset (nuLSU, mtSSU, RPB1 1st, 2nd and 3rd codon positions, and the intron of RPB1) and seven subsets for the four-locus dataset (addition of ITS to the six subsets) and ran PartitionFinder2 v. 2.1.1 (Lanfear et al. 2016), searching all models with the greedy algorithm and BIC as the model selection criterion to determine the best partitioning of the data. For the four-locus dataset, four subsets were delimited: the first was composed of ITS and the intron of RPB1 (GTR + G), the second of mtSSU (GTR + I+G), the third of nuLSU and RPB1 1st and 2nd codon positions (GTR + I+G), and the fourth of RPB1 3rd codon positions (GTR + I+G). The same four subsets were delimited in the three-locus dataset, except that ITS was not included.

We ran RAXML v. 8.2.9 (Stamatakis 2006) on the two datasets using the best partition schemes with the GTR+GAMMA model, performing 1000 bootstrap pseudoreplicates and searching for the best maximum likelihood (ML) tree simultaneously. RAXML analysis with similar settings was completed on the two-locus *Steinera* dataset, which was partitioned according to the loci. In addition, we performed a MrBayes v. 3.2.6 analysis (Ronquist & Kluge 2005).
Table 1. Specimens of Ostropomycetidae used in the 3- and 4-locus datasets for phylogenetic and species discovery analyses. Voucher information (for Arctomiaceae) is provided and/or details of the source of the previously published sequences and GenBank reference numbers for each locus. Newly generated sequences are in bold. Details of the outgroup Lecanora intumescentes (Lecanorales) are also provided.

<table>
<thead>
<tr>
<th>Species</th>
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<th>nuITS</th>
<th>nuLSU</th>
<th>mtSSU</th>
<th>RPB1</th>
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<td>JX030032</td>
<td>JX030034</td>
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(Continued)
Huelsenbeck 2003) as implemented on the CIPRES portal (Miller et al. 2010), using the same partition scheme and the best models of nucleotide substitutions as determined by PartitionFinder2. We conducted two runs of four chains for 50 million generations, sampling every 1000th generation, and discarding the first 10 000 trees (20%) as burn-in. We further generated single-locus chronograms for the Gabura clade for the mtSSU (16 taxa, 763 characters) and RPB1 (12 taxa, 653 characters) because they were the two loci with the lowest quantity of missing data. We determined the best sub-

Table 1. (Continued.)

<table>
<thead>
<tr>
<th>Species</th>
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<th>mtSSU</th>
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<td>Schmitt et al. 2003b, Lumbsch et al. 2007a</td>
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Results and Discussion

The topologies of the ML trees resulting from the three- and four-
locus datasets match, including branch lengths and bootstrap support (four-locus tree is shown; Fig. 1). Overall, the majority of
branches in the phylogenetic tree of the Ostropomycetidae are highly supported, except for deep relationships including the placement of the family Arctomiaceae in relation to the remaining orders and the relationships among them (although PP support is usually high, bootstrap values are below 70%) (Fig. 1). Contrary to Kraichak et al. (2018), the order Trapeliales is nested in Ostropales, with Protothelella corosalis (Körb.) H. Mayrhofer & Poelt and Thrombium epigaeum (Pers.) Wallr. (Protothelennaceae) placed outside of the clade containing Ostropales and Trapeliales. Our topology does not support the inclusion of Arctomiaceae and Trapeliales in Baeomyctecales. However, our sampling for the latter order does not include all families (Kraichak et al. 2018). Our topology is not in conflict with the phylogeny presented in Otálora & Wedin (2013), where phylogenetic relationships inside the family Arctomiaceae were mostly unresolved due to low bootstrap support.

We recovered a monophyletic family Arctomiaceae with similar internal relationships as reported in Magain & Sérusiaux (2012) and Ertz et al. (2017). Arctomia interfixa (Nyl.) Vain. appears as the first-diverging lineage in the family, and clearly does not belong to Arctomia s. str., as already reported in other studies (Magain & Sérusiaux 2012; Otálora & Wedin 2013). The two monotypic genera Gregorella and Wawea are resolved outside of the clade comprising the remaining genera in the family (Arctomia, Gabura and Steineria).

Within the genus Steineria, S. membranacea Ertz & R. S. Poulsen and S. molybdopla (Nyl.) Zahlbr. form a sister clade to the remaining species of the genus followed by S. sorediata. Two unidentified specimens from Chile (PCC9 and PCC10) cluster with S. intricata (Ertz & R. S. Poulsen) and (Steinera molybdopla (Øvstedal) Ertz and R. S. Poulsen) placed outside of the clade containing Ostropales and Trapeliales. Our topology does not support the inclusion of Arctomiaceae and Trapeliales in Baeomyctecales.
(Henssen 1969; Jørgensen 2003; Otalóra & Wedin 2013). Other characters referred to by Jørgensen (2007), such as the absence of amyloid structures in the ascus apex and fusiform, multiseptate ascospores, are no longer autapomorphic within the family because they are also present in the *Collema fascicularis* group (Otalóra & Wedin 2013).

*Gabura fascicularis* is split into two well-supported and geographically distant groups: one with European specimens (from Spain and Sweden) and the second with specimens from Chile and New Zealand (Fig. 1). The *G. insignis* group is composed of four well-supported clades including *G. insignis* s. str., containing a sequence from the type material (McCune 23460) from Oregon, together with other specimens from Oregon, Scotland and Ireland (Fig. 1). The origin of the type material was erroneously reported as ‘Washington, Lane Co., near mouth of Gwynn Creek on Pacific Ocean’ (Jørgensen & Tønsberg 2010) although it comes from Lane County in Oregon. The second clade is represented by the type specimen of *G. borbonica* (N952) and is sister to *G. insignis* s. str. (Fig. 1). A specimen from Reunion Island previously identified as *Arctomia borbonica* (N1025, Magain & Sérusiaux 2012) and one specimen from Madagascar (L6223) were placed in a separate lineage, whereas another specimen from Reunion Island (N1868) together with a single collection from South Africa (N8003) is part of another separate clade, representing early divergence events within the *G. borbonica/G. insignis* species complex (but with relatively low support; BS = 69, PP = 0.61) (Fig. 1). These four distinct lineages revealed within the *G. insignis* group probably represent separate species. GMYC species discovery analyses of *RBP1*, as well as PTP analysis of the four-locus dataset (15 specimens), suggest the presence of four species in this species complex, whereas GMYC analysis of mtSSU and PTP analysis of the 16-specimen dataset (but with PP = 0.11, Fig. 3C) suggest that they all belong to the same single species (Fig. 3). These analyses are sensitive to sampling, as removal of a single taxon from the mtSSU (data not shown) or from the combined PTP analyses (Fig. 3C & D) resulted in the recognition of several species in the group. In this case, species delimitation results are inconclusive and need to be interpreted with caution.

The four lineages of the *G. insignis/G. borbonica* complex form a monophyletic clade and could represent a single species corresponding to a broadly defined and widely distributed *G. insignis*,

![Phylogenetic tree of Steinera species resulting from the RAxML analysis on a two-locus dataset (ITS, mtSSU) for a total of 45 taxa and 1276 characters. ML bootstrap values are shown above branches. Thick black branches received ML bootstrap support value ≥ 70. Newly sequenced specimens are shown in bold. The tree was rooted according to Fig. 1.](https://www.cambridge.org/core/etext)
as suggested earlier by Jørgensen & Palice (2016) (Fig. 1). However, several lines of evidence suggest that each lineage represents a distinct species. First, there is almost no genetic differentiation among specimens of *G. insignis* from Oregon, Ireland and Scotland, suggesting that this species has low intraspecific genetic variation (Table 2). Furthermore, if the four lineages reflect a biogeographical structure within a species, we would expect to see all populations from Reunion Island clustered together. Instead, *G. borbonica* shares a most recent common ancestor with European and North American representatives of *G. insignis*, while specimens from other lineages of *G. cf. insignis* from Madagascar, Reunion Island and South Africa form the most early-diverging lineage in this clade (Fig. 1). Branch lengths between these four lineages are similar to the branch lengths between species in the closely related genus *Steinera* (Fig. 1), suggesting a similar level of genetic differentiation between these specific-level lineages. Furthermore, a large difference between intraspecific and interspecific variation in all loci suggests the presence of a barcoding gap (Table 2) between these four putative species (with the exception of the mtSSU sequences of *G. borbonica*). This gap indicates that these species are distinct from one another, as suggested by the GMYC analyses on the chronograms of mtSSU (A) and RPB1 (B), and PTP analyses on the four-locus phylogram with 16 specimens (C) or 15 specimens (D). Red branches represent intraspecific branching events, and black branches interspecific branching events. Vertical bars to the right of the trees summarize the best ML species delimitations.

**Fig. 3.** Species discovery results for the genus *Gabura* based on GMYC analyses on the chronograms of mtSSU (A) and RPB1 (B), and PTP analyses on the four-locus phylogram with 16 specimens (C) or 15 specimens (D). Red branches represent intraspecific branching events, and black branches interspecific branching events. Vertical bars to the right of the trees summarize the best ML species delimitations.
insignis 1 and G. cf. insignis 2, which are more similar). As mentioned, G. fascicularis also seems to be composed of two lineages (Fig. 1), probably representing distinct species with a similar strong biogeographical pattern: one clade in Europe (Spain and Sweden) and the other in the Southern Hemisphere (Chile and New Zealand). We also noticed subtle morphological differences in the examined collections although, as clearly demonstrated by the original description of Leptogium insignis (Jørgensen & Tønsberg 2010), considerable variation had already been observed. The monophyletic group of G. fascicularis, G. borbonica, G. insignis and other accessions here referred to as G. cf. insignis 1 and 2 is morphologically heterogeneous. Gabura fascicularis has a subfoliose thallus with numerous erect lobules, abundant and crowded apothecia with very thick rugose thalline margins, and veriform, twisted ascospores, 10–15-septate, 50–95 × 5–6 μm, whereas all G. borbonica, G. insignis and G. cf. insignis 1 and 2 accessions develop subfoliose to granular thalli, often very crumpled, usually with indistinct lobes and produce granular, yellowish to brownish soralia, but never apothecia. Therefore, all the characters of apothecium development and structure, ascus apex and ascospores identified by Otañora & Palice (2016) are applicable, (following Henssen (1969)) to demonstrate the phylogenetic affiliation of the Collema fasciculare group with the Arctoniaceae, are not applicable to the G. insignis/G. borbonica complex. Despite these morphological differences, we refrain from describing a new genus to accommodate these taxa because their sister relationship with G. fascicularis is strongly supported and our sampling did not include many poorly explored territories. Species potentially related to G. fascicularis (Collema leptosporum, C. papanorum and C. uviforme; see Degelius 1974) share a similar morphology. Interestingly, G. borbonica is the most morphologically distinct taxon within the G. insignis group, and easily distinguished from its sister species, G. insignis (see Taxonomic Treatment).

The current sampling suggests a complex pattern of genetic diversity within G. insignis, regardless of the ultimate delimitation of this species. Three distinct phylogenetic lineages occurring in the Indian Ocean are present on Reunion Island. The genetic diversity found in this island alone is higher than the diversity between collections from Europe and North America. The only lineage that has been sampled outside of the Mascarenes and Africa (i.e. in Europe and the Pacific Northwest of North America), G. insignis s. str., is one of the most recently diverged lineages within the G. insignis clade. If we were to assume that our sampling reflects the global population structure of the taxon, most of its genetic diversity was detected in the Indian Ocean, suggesting that this is the most probable origin and diversification centre for this group. Under this scenario, a single dispersal event might have led to the spread of the group to Europe and the Pacific Northwest of North America. However, the recent discovery of G. insignis in the British Isles, one of the best-explored areas in the world, underlines the deficiencies in our estimation of lichen distribution ranges. It is unclear whether the specimen from Ecuador reported by Jørgensen & Palice (2016) belongs to G. insignis, G. borbonica, one of the two unnamed early diverging lineages, or if it represents a new distinct lineage.

We refrain from describing new species for the two early diverging lineages in the G. insignis group because they are each represented only by two relatively small, and morphologically cryptic specimens. A lack of obvious diagnostic characters is the reason why these lichens might be overlooked and thus their distributions should be much broader than currently known.

Transferring Arctomia insignis and A. borbonica to the genus Gabura solves the problem of morphological and anatomical heterogeneity in the genus Arctomia (following Henssen (1969)) raised by Jørgensen & Palice (2016). As recircumscribed, the
monophyletic Arctomia s. str. currently encompasses two species, *A. delicatula* and *A. teretiuscula*. All species of the *Collema fasciculare* group transferred to *Arctomia* by Otálora & Wedin (2013) probably represent *Gabura*, but DNA evidence is required before applying any taxonomic changes to this complex group. The two subantarctic species, *Arctomia latispora* Øvstedal and *A. subantarctica* Øvstedal (Øvstedal & Gremmen 2001, 2006), were transferred to the genus *Steinera* (Ertz et al. 2017). Based on the reconstructed phylogeny (Fig. 1), *Arctomia interfixa* does not belong to *Arctomia* s. str. and a new genus should be erected to accommodate this species.

**Taxonomic Treatment**

*Gabura borbonica* (Magain & Sérusiaux) Magain & Sérusiaux comb. nov.

Basionym: *Arctomia borbonica* Magain & Sérus., *Mycocles* 4, 1 6 (2012); type: Reunion, Forêt de Bébour, track starting at gîte de Bélouve toward Piton des Neiges, 21°4′49″S, 55°31′24″E, 1850 m, 9 November 2009, N. Magain & E. Sérusiaux s. n. (holotype LG).

(Fig. 4A–C)
Fig. 5. Gabura insignis (A–F) and Steinera sp. (G & H). A, collection of G. insignis from USA (Oregon; DNA 6282). B, collection from Ireland (DNA 3786); circled area enlarged in E. C, collection from UK (Scotland; DNA 4892); circled area enlarged in F. D, collection from USA (Oregon; DNA 6281); white thallus is a fragment of Peltigera. E, collection from Ireland (DNA 3786); dark brownish lobes with yellowish punctiform soredioid masses are typical of this specimen but can be absent in other accessions of G. insignis. F, collection from UK (Scotland; DNA 4892). G & H, Steinera sp. (Tim Wheeler & Peter Nelson 2507); G, thallus and H, ascospores. Scales: A–C = 1 cm; D = 2 mm; E & F = 1 mm; H = 10 μm.
**Thallus** up to 1 cm across, with distinct c. 1.5–2 mm large lobes, brownish black when dry, with a well-developed linear soredioid margin which may become bluish; lobes with strongly developed wrinkles, somewhat scrobiculate, with extremities erect and corrugated.

**Gabura insignis** (P. M. Jørg. & Tønsberg) Magain & Sérusiaux comb. nov.

MycoBank No.: MB 883419

Basionym: *Leptogium insigne* P. M. Jørg. & Tønsberg, *Biblioth. Lichenol.* **104**, 242 (2010); type: USA, Oregon [incorrectly reported as Washington in protologue], Lane Co., near mouth of Gwynn Creek on Pacific Ocean, 44°17′N, 124°06′W, 10 m, on leaning *Alnus* trunk in forest, 23 February 1996, B. McCune 23460 (holotype OSC (seen by TS), isotype BG, not seen).


(Fig. 5A–F)

Short description for the European collections (Ireland and Scotland): thallus with distinct and erect lobes, c. 1.0–1.2 mm across, dark brown, without any bluish tinge, sometimes with punctiform and rarely linear soralia which are yellowish to dark brown, never bluish and not forming a linear soredioid margin; main lobes flat but can be overgrown by erect lobes and soredioid masses in some parts of the thallus.

**Notes.** In Europe, *Gabura insignis* is difficult to see in the field as thalli are minute (c. 2–5 mm across) and never abundant, unlike in western North America. It could be mistaken for a poorly developed *Leptogium brebissonii*, but it has not been found in the collections filed under that name in E (B. J. Coppins, personal communication) or in LG. Interestingly, it was not found in our large collections of *Peltigerales* from Macaronesia (Canary Islands, Madeira and the Azores). This unexpected discovery demonstrates that our understanding of lichen biodiversity is still incomplete, and more fieldwork is necessary even in well-researched territories such as the British Isles.

**Specimens examined.** Ireland: Kerry: S of Killarney, near the Muckross Lake, trees in parkland conditions, 52°01′05″N, 09°30′15″W (coordinates centred on Muckross Castle), alt. 30 m, ii 2014, E. Sérusiaux s. n. (LG DNA 3786).—Great Britain: Scotland: V.C. 104, Isle of Skye, Dunvegan Park, park with various trees, incl. exotic species, 57°26.49″N, 06°35.17″W, alt. 20 m, vi 2015, E. Sérusiaux s. n. (LG DNA 4892).

![Fig. 6. Gabura cf. insignis 1 from South Africa (DNA 8003). A, thallus rather similar to G. cf. insignis 1, with flat dark brown lobes. B, Lobes mainly hidden by the exuberant development of soredioid masses, forming soredioid margins and rarely well-delimited soralia. Scales: A & B = 2 mm.](https://www.cambridge.org/core/doi/10.1017/S0024282919000471)
**Gabura cf. insignis 2**

(FIG. 6A & B)

Thallus up to 1 cm across, with rather flat dark brown lobes, almost hidden by the exuberant (compared to the other species) development of soredioid masses present on the margins and over the wrinkles of lobes, forming soredioid margins, and rarely well-deliminated soralia.

**Specimens examined.** Reunion: Réserve naturelle de la Roche Écrite, piste vers le sommet, 20°58′26″E, alt. 1500 m, 4 xi 2009, N. Maguin & E. Sériaux s. n. (LG DNA 1868).—South Africa: Western Cape: Cape Town, trail to Table Mountain from Kirstenbosch National Botanical Garden, 33.988′S, 18.424′E, 6 vi 2019, R. Vargas (BOL, DUKE DNA NM8003).

**Steineria sorediata**

**Specimen examined.** New Zealand: South Island: Otago, Mt Cargill (type locality), boulders below summit, 2009, D. Galloway 5984a (GZU).

**Steineria sp.**

(FIG. 5G & H)

**Specimens examined.** Chile: Region X: north of Lago General Pinto Cabrera in subalpine Lenga forest and up above treeline at the base of Volcan Yates, 41°48′.982′S, 72°21′.074′W, P. Nelson & T. Wheeler 2479, 2483, 2507 (hb. Nelson).

**Data Accessibility.** Alignments have been deposited in TreeBase and can be accessed at http://purl.org/phylo/treebase/phylows/study/TB2:525138

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R. Vargas

2019,


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