



Phylloporia spathulata sensu stricto and two new South American stipitate species of *Phylloporia* (Hymenochaetaceae)

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Abstract

During a taxonomic revision of species belonging to *Phylloporia*, some collections from the Atlantic Forest of southern Brazil previously determined as *P. spathulata* had morphological discrepancies in comparison to the type material of this taxon. Both molecular phylogenetic and morphological analysis revealed them to be two distinct species, described here as *Phylloporia elegans* sp. nov. and *P. nodostipitata* sp. nov. They mainly differ from *P. spathulata* by having reviving basidiomata with smaller pores and basidiospores. *Phylloporia nodostipitata* develops caespitose basidiomata with a knotted and flexuous stipe and a tomentose pileal surface. *Phylloporia elegans* develops solitary basidiomata with a cylindrical and straight stipe and a plagiotrichoderm pileal surface. Both species are described, illustrated, discussed and compared with *Phylloporia spathulata* based on a study of the type. *Phylloporia spathulata sensu stricto* is presented based on its basionym type material.

Key words: Hymenochaetales, morpho-ecological type, neotropics, polypore taxonomy, phylogeny

Introduction

During the last forty years, the taxonomic study of *Phylloporia* Murrill has undergone an upheaval. From a genus with only one species, *P. parasitica* (Murrill 1904: 141), in which basidiomata emerge on the abaxial surface of living leaves, it has become a morphologically heterogeneous genus with 39 currently accepted species. Currently, the genus is characterized by having thick-walled and pale yellow basidiospores usually up to 5 µm length, the absence of setae, and by its ability to grow on living plants (Wagner & Ryvarden 2002, Zhou & Dai 2012, Decock *et al.* 2013, 2015, Gafforov *et al.* 2014, Liu *et al.* 2015, Yombiyeni *et al.* 2015, Zhou 2015 a, b).

Since its morphological delimitation was re-established (Johansen & Ryvarden 1980, Ryvarden 1991) and the first molecular phylogeny of the genus (Wagner & Ryvarden 2002), some new species of *Phylloporia* have been described from different ecosystems around the world based on morphological, molecular and ecological data (Valenzuela *et al.* 2011, Zhou & Dai 2012, Decock *et al.* 2013, Yombiyeni *et al.* 2015, Gafforov *et al.* 2014, Liu *et al.* 2015, Zhou 2015 a, b). Many of these papers present phylogenetic reconstructions with several clades representing new species, as well as other unnamed clades and a few doubtfully placed taxa. For example, *Phylloporia resupinata* (Douanla-Meli & Ryvarden 2007: 416) grouped with *Fomitiporella* Murrill (Decock *et al.* 2013, Zhou & Dai 2012, Gafforov *et al.* 2014, Zhou 2015) and *Coltricia stuckertiana* (Spegazzini 1899: 163) Rajchenb. & J.E. Wright (1998: 119) clustered within the *Phylloporia* clade (Valenzuela *et al.* 2011, Decock *et al.* 2013). Such clades are clear evidence that the diversity of *Phylloporia* is rather underestimated (Decock *et al.* 2013).

So far, only two taxa with stipitate basidiomata have been recorded in the neotropics: *P. verae-crucis* (Berkeley ex Saccardo 1888: 89) Ryvarden (1991: 195) and *P. spathulata* (Hook. in Kunth 1822: 9) (Ryvarden 1991: 196) (Wagner &

Ryvarden 2002, Ryvarden 2004, Valenzuela *et al.* 2011). While *P. verae-crucis* seems to be restricted in its geographic range (Ryvarden & Guzmán 1993, Wagner & Ryvarden 2002, Guzmán 2004, Ryvarden 2004), *P. spathulata*, originally described from Ecuador, has been the name widely applied to monomitic stipitate specimens collected throughout South America. According to the literature currently available, this species has a broad morphological variability and a pantropical distribution (Wagner & Ryvarden 2002, Aime *et al.* 2003, Ryvarden 2004, Gibertoni & Drechsler-Santos 2010, Rajchenberg & Robledo 2013).

Contrary to the current delimitation of *P. spathulata*, recent phylogenetic evidences suggests that *Phylloporia* species are host-specific, with little morphological variability and restricted geographic distribution (Valenzuela *et al.* 2011, Zhou & Dai 2012, Gafforov *et al.* 2014, Zhou 2013, 2015 a, b). Therefore, it is worthwhile to review those *Phylloporia* species currently accepted with broad morphological variation, nonspecific substrate associations, and broad distributions, such as *P. fruticum* Berkeley & M. A. Curtis (1869: 310) Ryvarden (1972: 235), *P. pectinata* Klotzsch (1833: 485) Ryvarden (1991: 196), *P. ribis* Schummacher, H. C. F. (1803: 386) Ryvarden (1978: 371), *P. chrysites* Berkeley (1856: 176) Ryvarden (1972: 235) and *P. spathulata*. Moreover, previous analyses based on the 28S gene region showed a larger than expected diversity of neotropical species of *Phylloporia* with stipitate basidiomata (Decock *et al.* 2013, Zhou 2015b), suggesting that the current morphological delimitation of *Phylloporia spathulata sensu lato* should be revised (Yombiyeni *et al.* 2015). In light of these findings, the objective of this study has been to re-examine the type material of *P. spathulata* and compare it to some South American stipitate specimens previously determined as such.

Materials and methods

Examined material was from southern Brazil (Santa Catarina State, Brazilian Atlantic Forest Biogeographic Province) and northeast Argentina (Misiones Province, Paranense Forest Biogeographic Province), both areas pertaining to the Paranaense subregion according to Morrone (2001). The collections were originally identified as *P. spathulata* and deposited at FLOR and CORD. The collections were studied and compared with the type specimens of *P. spathulata* (K! 19681), *P. verae-crucis* (K! 174177), and *P. minutispora* Ipuleit & Ryvarden (TAA! Ipuleit F706). Herbaria acronyms followed Thiers B. (continuously updated).

Morphological analysis:—The samples were hand-sectioned, mounted in 3% potassium hydroxide (KOH), KOH plus 1% phloxine (Ryvarden 1991), Melzer's reagent and lactophenol (Largent *et al.* 1977) and examined by light microscope. Measurements of microscopic structures and number of pores/mm followed a standard sampling of forty measures per structure ($n = 40$), with 5% of the measurements excluded from each end and given in parentheses. The description of the pileal surface is according to Clemençon (2012), who classifies "tomentum" in a wide sense in plagiotrichoderm and tomentum, in a strict sense (based on their hyphal arrangement), as following: a) plagiotrichoderm = basal hyphae repent (periclinal), most terminal hyphae obliquely ascending to fully erect (anticlinal); b) tomentum = a relatively thick coating of hyphae irregularly arranged, with loose architecture. Description of sterile elements on the hymenium follows Clemençon (2012), and cystidia shape follows Largent *et al.* (1977).

Basidiospores in *Phylloporia* are usually quite heterogeneous in a single specimen, mostly due to their being somewhat "deflated" or "collapsed," and are sometimes referred to as lenticular (Wagner & Ryvarden 2002). Here, we describe this variability through a tridimensional plane, with descriptions and a sporogram adapted from Dominguez de Toledo (1994). Spore shape is described from both equatorial lateral and adaxial views (*el* = equatorial lateral view; *ead* = equatorial adaxial view; *eab* = equatorial abaxial view; *dp* = distal polar view and *pp* = proximal polar view), including ornamentation, color, content, wall thickness, size (breadth \times width, Q = ratio breadth/width, avg. = arithmetic average) and chemical reactions (Melzer's reagent and KOH). Basidiospore shape follows Largent *et al.* (1977). The color descriptions of basidiomata follow Munsell Soil Color Chart (Munsell Color 1975). The abbreviation *IKI*- means that the structure in question does not react in the presence of Melzer's reagent. Country names and abbreviations follow the United Nations Statistics Division Database (<http://unstats.un.org/unsd/methods/m49/m49alpha.htm>). Basidiomata with the ability to develop new spots of tube layers from older tube layers are called *reviving*, in the sense of Fiasson & Niemelä (1984) and Rajchenberg *et al.* (2015). The term *reviving* is chosen instead of *biennial* or *perennial* for the basidiomata studied in here, because their phenology is still poorly known.

DNA extraction, PCR amplification and sequencing:—DNA extraction was carried out using dried basidiomata according to Góes-Neto *et al.* (2005). PCR amplification followed the parameters described in Larsson & Larsson (2003) for the 28S (LSU) gene region, using the primer pair LR0R (Cubeta *et al.* 1991) and LR7 (Vilgalys & Hester

1990). All PCR products were purified with Qiagen Kit (Qiagen Inc.) according to the manufacturer's recommendations. Sequencing reactions of PCR products were prepared with the addition of a mix composed of 1 µL BigDye® Terminator v3.1 Cycle Sequencing Kit, 1 µL 5× Buffer, 1 µL primer, 5 µL H₂O q.s.p., to 2 µL of the amplification product. Primers LR0R (Cubeta *et al.* 1991) and LR5 (Vilgalys & Hester 1990) were used for sequencing, which was performed at the Centro de Pesquisas René Rachou in FIOCRUZ (Brazil). Edited and validated sequences were further deposited at GenBank® (<http://www.ncbi.nlm.nih.gov>) and BOLD (Ratnasingham & Hebert, 2007).

Phylogenetic analyses:—A total of 84 specimens representing 35 putative species were included in the phylogenetic analyses. All the LSU sequences of *Phylloporia* species available in GenBank®, as well as some representatives of the sister genera *Fomitiporella* Murrill, *Fulvifomes* Murrill and *Inocutis* Fiasson & Niemelä were retrieved and added to the final matrix. *Inonotus cuticularis* (Bulliard 1785: tab. 210) Karsten (1879: 39) and *Inonotus hispidus* (Bulliard 1789: tab. 462) Karsten (1879: 39) were designated as outgroup (Decock *et al.* 2013). All specimens and sequences used in this study are listed in Table 1. Sequences were assembled and manually corrected with Geneious v. 6.1.8 (<http://www.geneious.com>, Kearse *et al.* 2012) and automatically aligned with Mafft v.7 (Katoh & Standley, 2013) under the G-INS-I strategy. The sequences were also manually inspected, searching for unreliably aligned positions and adjusted whenever necessary, using MEGA 6 (Tamura *et al.* 2013).

TABLE 1. List of taxa, specimens and sequences used in the phylogenetic analyses.

| Taxon | Voucher reference | Origin | Accession Number |
|-----------------------------------|-------------------|-------------|------------------|
| <i>Fomitiporella cavicola</i> | N153 | GBR | AY059052 |
| <i>Fomitiporella umbrinella</i> | CBS 303.66 | USA | AY059036 |
| <i>Fulvifomes fastuosus</i> | CBS 213.36 | Philippines | AY059057 |
| <i>Fulvifomes robiniae</i> | CBS 211.36 | USA | AF411825 |
| <i>Inocutis jamaicensis</i> | Gilb. 14740 | USA | AY059048 |
| <i>Coltricia stuckertiana</i> | Robledo 219 | Argentina | KC136219 |
| <i>Coltricia stuckertiana</i> | MUCL47643 | Argentina | HM635663 |
| <i>Coltricia stuckertiana</i> | Robledo 218 | Argentina | KC136220 |
| <i>Coltricia stuckertiana</i> | Robledo 281 | Argentina | KC136221 |
| * <i>Inonotus cuticularis</i> | 97-97 | Germany | AF518623 |
| * <i>Inonotus hispidus</i> | 92-829 | Germany | AF311010 |
| <i>Inocutis jamaicensis</i> | Gilb. 14740(O) | USA | AY059048 |
| <i>Phylloporia afrospathulata</i> | YOM47 | Gabon | KC136230 |
| <i>Phylloporia afrospathulata</i> | GA06_166 | Gabon | KC136229 |
| <i>Phylloporia bibulosa</i> | Ahmad 27088 | Pakistan | AF411824 |
| <i>Phylloporia cf. fruticum</i> | MUCL 52762 | Mexico | HM635668 |
| <i>Phylloporia cf. fruticum</i> | ENCB TR&RV858 | Mexico | HM635669 |
| <i>Phylloporia cf. fruticum</i> | MUCL 52863 | Mexico | HM635670 |
| <i>Phylloporia chrysites</i> | N.W. Legon (O) | Puerto Rico | AF411821 |
| <i>Phylloporia chrysites</i> | MUCL 52763 | Mexico | HM635665 |
| <i>Phylloporia chrysites</i> | MUCL 52764 | Mexico | HM635666 |
| <i>Phylloporia chrysites</i> | MUCL 52862 | Mexico | HM635667 |
| <i>Phylloporia crataegi</i> | Dai 11014 | China | JF712922 |
| <i>Phylloporia crataegi</i> | Dai 11016 | China | JF712923 |
| <i>Phylloporia dependens</i> | Dai 13167 | China | KP698746 |
| <i>Phylloporia elegans</i> | FLOR 51179 | Brazil | KJ631409 |

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TABLE 1. (Continued)

| Taxon | Voucher reference | Origin | Accession Number |
|--------------------------------------|----------------------|---------------|------------------|
| <i>Phylloporia elegans</i> (H) | FLOR 51178 | Brazil | KJ631408 |
| <i>Phylloporia ephedrae</i> | E. Parmasto TAA 72-2 | Turkmenistan | AF411826 |
| <i>Phylloporia fontanesiae</i> | Li 194 | China | JF712924 |
| <i>Phylloporia fontanesiae</i> | Li 199 | China | JF712925 |
| <i>Phylloporia fulva</i> | GA_657VS | Gabon | KJ743247 |
| <i>Phylloporia gutta</i> | Dai 4103 | China | JF712926 |
| <i>Phylloporia gutta</i> | Dai 4197 | China | JF712927 |
| <i>Phylloporia hainaniana</i> | Dai 9460 | China | JF712928 |
| <i>Phylloporia inonotoides</i> | GA12_855VS | Gabon | KJ743250 |
| <i>Phylloporia inonotoides</i> | GA12_858VS | Gabon | KJ743251 |
| <i>Phylloporia inonotoides</i> | GA12_860VS | Gabon | KJ743252 |
| <i>Phylloporia minutispora</i> | MUCL 52865 | COD | HM635671 |
| <i>Phylloporia minutispora</i> | Ipulet 706 | Uganda | JF712929 |
| <i>Phylloporia nandinae</i> | Dai 10625 | China | JF712931 |
| <i>Phylloporia nandinae</i> | Dai 10588 | China | JF712930 |
| <i>Phylloporia nodostipitata</i> | FLOR 51237 | Brazil | KJ631411 |
| <i>Phylloporia nodostipitata</i> | FLOR 51175 | Brazil | KJ631413 |
| <i>Phylloporia nodostipitata</i> | FLOR 51153 | Brazil | KJ631414 |
| <i>Phylloporia nodostipitata</i> (H) | FLOR 51173 | Brazil | KJ631412 |
| <i>Phylloporia nouraguensis</i> | MUCL/FG-11-400 | French Guiana | KC136222 |
| <i>Phylloporia nouraguensis</i> | MUCL/FG-11-409 | French Guiana | KC136223 |
| <i>Phylloporia nouraguensis</i> | MUCL/FG-11-404 | French Guiana | KC136224 |
| <i>Phylloporia oblongospora</i> | Zhou 179 | China | JF712932 |
| <i>Phylloporia oreophila</i> | Cui 2219 | China | JF712933 |
| <i>Phylloporia oreophila</i> | Cui 9503 | China | JF712934 |
| <i>Phylloporia osmanthi</i> | Yuan 5655 | China | KF729938 |
| <i>Phylloporia pectinata</i> | R. Coveny 113 | Australia | AF411823 |
| <i>Phylloporia resupinata</i> | Douanla-Meli 476 | Cameroon | JF712935 |
| <i>Phylloporia ribis</i> | Strain 82-828 | Germany | AF311040 |
| <i>Phylloporia rzedowskii</i> | MUCL 52868 | Mexico | HM635672 |
| <i>Phylloporia rzedowskii</i> | MUCL 52860 | Mexico | HM635674 |
| <i>Phylloporia rzedowskii</i> | MUCL 52861 | Mexico | HM635675 |
| <i>Phylloporia rzedowskii</i> | MUCL 52859 | Mexico | HM635673 |
| <i>Phylloporia</i> sp. | FG-11-462 | French Guiana | KC136228 |
| <i>Phylloporia</i> sp. | FG-11-506 | French Guiana | KC136227 |
| <i>Phylloporia</i> sp. | FLOR 51239 | Brazil | KJ631407 |
| <i>Phylloporia</i> sp. | FLOR 51258 | Brazil | KJ631406 |
| <i>Phylloporia</i> sp. | MUCL 52864 | Ecuador | HM635676 |

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TABLE 1. (Continued)

| Taxon | Voucher reference | Origin | Accession Number |
|-------------------------------|-------------------|-------------|------------------|
| <i>Phylloporia</i> sp. | MUCL 53433 | Mexico | KC136231 |
| <i>Phylloporia</i> sp. | Robledo 351 | Argentina | KC136226 |
| <i>Phylloporia</i> sp. | Robledo 429 | Argentina | KJ651913 |
| <i>Phylloporia</i> sp. | Robledo 526 | Argentina | KJ651914 |
| <i>Phylloporia</i> sp. | Robledo 527 | Argentina | KJ651915 |
| <i>Phylloporia</i> sp. | Robledo 968 | Argentina | KJ651916 |
| <i>Phylloporia</i> sp. | Robledo 1134 | Argentina | KJ651917 |
| <i>Phylloporia</i> sp. | Robledo 1220 | Argentina | KC136225 |
| <i>Phylloporia</i> sp. | Robledo 1467 | Argentina | KJ651918 |
| <i>Phylloporia</i> sp. | Robledo 1610 | Argentina | KJ651919 |
| <i>Phylloporia</i> sp. | Robledo 1624 | Argentina | KJ651920 |
| <i>Phylloporia</i> sp. | Robledo 1790 | Argentina | KJ651921 |
| <i>Phylloporia</i> sp. | Urcelay 625 | Argentina | KT223570 |
| <i>Phylloporia spathulata</i> | Chay 456 | Mexico | AF411822 |
| <i>Phylloporia terrestris</i> | Yuan 5738 | China | KC778784 |
| <i>Phylloporia ulloai</i> | MUCL 52866 | Mexico | HM635677 |
| <i>Phylloporia ulloai</i> | MUCL 52867 | Mexico | HM635678 |
| <i>Phylloporia ulloai</i> | MUCL 52870 | Mexico | HM635679 |
| <i>Phylloporia weberiana</i> | Dai 9242 | China | JF712936 |
| <i>Phylloporia yuchengii</i> | YG033 | Uzbequistan | KM264324 |
| <i>Phylloporia yuchengii</i> | YG051 | Uzbequistan | KM264325 |

*Outgroup.

H: holotype.

The final alignment and the resulting phylogenetic trees were deposited in TreeBASE (<http://www.treebase.org/treebase/index.html>) under S18446. Maximum Likelihood (ML) and Bayesian Inference (BI) searches were applied to the dataset. The best fit model of nucleotide evolution was obtained according to BIC (Bayesian Information Criterion), as implemented in the software jModelTest 2.1.4 (Guindon & Gascuel 2003, Darriba *et al.* 2012). The base frequencies, the rates of nucleotide substitutions, gamma shape parameter and proportion of invariant sites were all estimated by the same software. A Maximum Likelihood (ML) with analysis was carried out as implemented in RAxML v.8.1.24 (Stamatakis, 2014), available in the CIPRES science gateway (Miller *et al.* 2010, <http://www.phylo.org/>). GTR + I + G were used as nucleotide evolution model. The analysis first involved 100 ML searches, each one starting from one randomized stepwise addition parsimony tree, under a GTR+GAMMA+I model, with all the other parameters estimated by the software. To assess the reliability of the nodes, multi-parametric bootstrapping replicates under the same model were computed, allowing the program to halt bootstrapping automatically by the autoMRE option. The BI was performed in the software MrBayes 3.2.6 (Ronquist & Huelsenbeck 2003), as implemented on the CIPRES Science Gateway 3.1 (Miller *et al.* 2010). BI was implemented by two independent runs, each one starting from random trees, with four simultaneous independent chains and performed 1×10^6 generations, keeping one tree every 1000th generation. Four rate categories were used to approximate the gamma distribution, and the nucleotide substitution rates were fixed to the estimated values. A total of 20% of the sampled trees were discarded as burn-in and checked by the ESS (Effective Sample Size), PSRF (Potential Scale Reduction Factor) and convergence criterion (frequencies of average standard deviation of split <0.01) in Tracer v.1.6 (Rambaut *et al.* 2014), while the remaining ones were used to reconstruct a 50% majority-rule consensus tree and to estimate Bayesian posterior probabilities

(BPP) of the branches. A node was considered to be strongly supported if it showed a BPP ≥ 0.95 and/or BS $\geq 90\%$, while moderate support was considered BPP ≥ 0.9 and/or BS $\geq 70\%$.

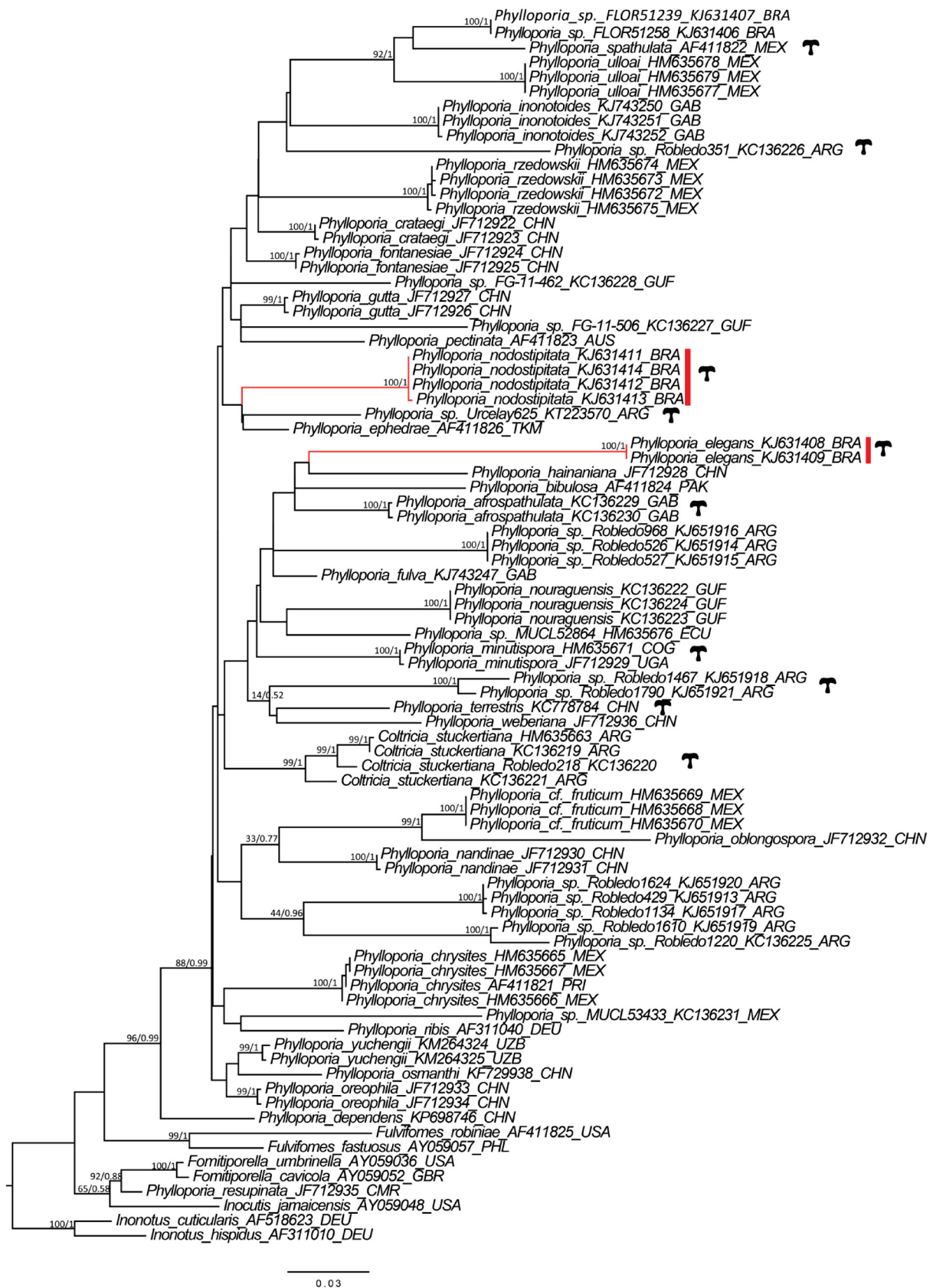


FIGURE 1. Best-scored ML tree representing the phylogenetic relationships within *Phylloporia*, based on 28S rDNA. *Phylloporia elegans* sp. nov. and *P. nodostipitata* sp. nov. are indicated by red bars. Support values of coincident clades from both Maximum Likelihood and Bayesian Inference analyses are respectively indicated, even when not significantly supported. T = stipitate habit.

Results

Molecular analyses (Figure 1):—The final gapped aligned matrix of the 28S (LSU) region was 891 bps long, with 350 variable characters, of which 300 characters were parsimony informative. According to the preceding analyses, TrN+I+G was chosen as the best-fit substitution model to the dataset in the Bayesian Inference, with the following base frequencies A(0.23), C(0.19), G(0.33), T(0.25), a gamma distribution shape parameter of 0.52 and a proportion of invariant sites of 0.38. The nucleotide substitution rates estimated according to this model were A/C= 1.0, A/G=11.36, A/T=1.0, C/G=1.0, C/T=20.92 and G/T = 1.0. The two independent runs of Bayesian analysis converged to stable values of the convergence criterion after 1800000 generations, and the posterior inspection of the runs' log files in Tracer showed that the discarded 20% of burn-in to construct the consensus tree was a suitable value. In the ML searches, GTR+I+G was chosen as the best-fit substitution model for Maximum Likelihood analyses. RAxML found 399 distinct patterns in the alignment, with a proportion of gaps and completely undetermined characters of 4.0%; the multiparametric BS search in ML analysis stopped after 360 replicates. The strict consensus tree of BI and the most likelihood tree of ML (-lnL= -7979.267647) were nearly congruent, and thus only the best-scored ML tree is presented (Fig. 1), with BPP and BS values plotted on the branches.

The topology of the resulted trees corroborated the previous studies (Valenzuela *et al.* 2011; Decock *et al.* 2013; Zhou 2014; 2015 a, b) focusing on molecular phylogeny of the genus (all of them also used only 28S as a marker), where the terminal branches received significant support, however the major clades were barely supported, making it difficult to infer the interspecific phylogenetic relationships within the genus. The *Phylloporia* clade was retrieved with strong support in both analyses (BPP = 0.99 and BS = 96), while the clade that recovered *Phylloporia* as sister group of *Fulvifomes* also received significant support (BPP = 0.99 and BS = 68). The representative specimens of *Inocutis*, *Fomitiporella*, as well the *Phylloporia resupinata* sample (JF712935) clustered in a clade with significant support (BPP = 0.99 and BS = 100). Within the *Phylloporia* clade, forty-two terminal clades, each one representing a distinct phylogenetic lineage, some of them undescribed, received significant support (Fig. 1). The specimen *Phylloporia dependens* (Y. C. Dai 2015: 183) (KP698746) was recovered as the basal lineage in both phylogenetic reconstructions (BPP = 0.99 and BS = 96). The phylogenetic analysis recovered the stipitate specimens from southern Brazil in two distinct unrelated terminal clades, both with maximum support (BPP = 1 and BS = 100) and are unequivocally placed within *Phylloporia*. The first one (representing *Phylloporia elegans* sp. nov.) grouped with the unique specimen of *P. hainaniana* (Y.C. Dai & B.K. Cui 2010: 170), a species from Asia, in an unsupported clade (BS = 16). *Phylloporia afrospathulata* (Yombiyeni & Decock 2015: 1000) and *P. bibulosa* [(Lloyd) Ryvarden 1972: 235] grouped together with *P. elegans* in a more inclusive clade, despite being barely supported. *Phylloporia nodostipitata* sp. nov. in its turn, appears within a poorly supported, more inclusive clade (BS = 3) with *P. ephedrae* [(Woron.) Parmasto 1985: 377] (AF411826), collected in Asia (Turkmenistan), and an undescribed species of *Phylloporia* (Urcelay 625, KT223570), from Argentina.

Taxonomy

Phylloporia spathulata sensu stricto (Hook.) Ryvarden (1991: 196) (Figures 2 A, 3 A–C)

Mycobank:—MB460305

Diagnosis:—Basidiomata seasonal, laterally stipitate, pileus dull, dark yellowish brown, azonate, pileal surface tomentose, 7–9 pores/mm, basidiospores elongate to cylindrical in equatorial lateral view, of 3–4 × 2–2.5 µm (avg. 3.0 × 1.9 µm).

Description:—Basidiomata seasonal, eccentric to laterally stipitate, solitary with conrescent pilei; pileus spathulate to reniform, applanate to convex, up to 0.7 x 0.7 cm and 1 mm thick; pileus surface as a tomentum, appearing adpressed velutinate, mostly dull, concentrically sulcate, without black striations, mostly azonate, dark yellowish brown (10 YR 4/4–4/6), 0.7 × 0.6 cm, up to 0.3 mm thick, separated from the context by a resinous and very thin dark line (up to 0.1 mm); context compact, slightly lighter in color than the superior portion, up to 0.3 mm thick; tube layer yellowish brown (10 YR 5/4–5/6), up to 0.4 mm; margin rounded, entire, up to 1 mm thick, concolorous with the pileal surface, slightly lighter towards the hymenophore; hymenophore not decurrent, yellowish brown (10 YR 5/4–5/6), pores circular, dissepiment entire, slightly fimbriate, (6–)7–9 pores/mm. Stipe probably attached to living roots, cylindrical, slender, slightly flexuous to erect, tomentose, concolorous with the pileus, up to 2.5 cm length by

0.25 cm in diameter; stipe surface a tomentum, the same as the pileal surface in color and texture; stipe context the same as the pileus context in color and texture.

Hyphal structure monomitic (dimitic d1–d2 *sensu* Corner 1991). Generative hyphae simple-septate, slightly thick to thick-walled with wide lumen, alternately branched, almost hyaline to yellowish, darkening slightly in KOH, 1.5–3 μm wide, to thick-walled with narrow lumen (capilar), dark brownish in KOH, alternately branched, simple-septate, (3–)4–6(–7) μm wide, dominating in the tubes. Basidia 4-sterigmate, broadly clavate to clavate, hyaline to faintly yellow in KOH, up to 10 x 4 μm . Basidioles not seen. Cystidia not seen. Basidiospores (Figure 3 A–C) elongate to cylindrical in equatorial lateral view, often with one or more flattened sides, looking somewhat square or trapezoidal in equatorial adaxial view; smooth, pale yellow in KOH/lactophenol; thick-walled; 3–4 x 2–2.5 μm (avg. 3.0 x 1.9 μm), Q = 1.19–2.00, Q avg. = 1.62, IKI–.

Substrate and distribution:—Possibly on living root of unknown angiosperm; type locality Amazonian Phytogeographic Province, possibly neotropical in distribution.

Specimens examined:—ECUADOR. Province of Loja: elevation 1,060 m. a. s. l., approx. 3° 59' S, 79° 12' W, A. von Humboldt 246 (K! 19681, Holotype of *Phylloporia spathulata*).

Other specimens examined:—MEXICO. Veracruz: elevation 5,610 m. a. s. l., approx. 22° 28' N, 93° 36' W, August 1854, *Berkeley* (K! 174177, Isotype of *Phylloporia veracruzis*); UGANDA. Kabarole: Kibale National Park, approx. 0° 30' 0" N, 30° 24' 0" E, 26th October 2002, *Ipulet F706* (TAA!, holotype of *Phylloporia minutispora*).



FIGURE 2. A) *P. spathulata* (Holotype); B) *P. elegans* (Holotype); C) *P. nodostipitata* (FLOR 51154), on the upper-right corner, detail of *P. nodostipitata* pileus and stipe in section. Photographs by Gerardo L. Robledo (A, B) & Valéria F. Lopes (C).

Phylloporia elegans Ferreira-Lopes, Robledo & Drechsler-Santos *sp. nov.* (Figures 2 B, 4 A–E)

Mycobank:—MB 805726

Diagnosis:—Basidiomata seasonal to reviving, stipitate, dark yellowish brown pileus covered by short plagiotrichoderm, 8–12(–13) pores/mm and basidiospores broadly ellipsoid to ellipsoid (2.5–3.5 x 2–3 μm).

Etymology:—*Elegans* (Lat.): referring to its slender stipe and delicate basidioma.

Holotype:—BRAZIL. Santa Catarina: Itapoá, Reserva Particular do Patrimônio Nacional Volta Velha, elevation 20 m. a. s. l., –26° 04' 56" S, –48° 38' 56" W, on living roots of a undetermined angiosperm, 18th November 2012, *Robledo 2545* (FLOR 51178). GenBank accession number (LSU; KJ631408).

Description:—Basidiomata seasonal to reviving, stipitate, solitary to laterally fused at the base of the stipe; pileus circular to semicircular, spathulate to flabeliform, infundibuliform, up to 1.5 cm wide by 1.5 mm thick; pileus surface a short plagiotrichoderm, shiny, adpressed velutinate to hispid, concentrically zonate and sulcate, sometimes slightly radially wrinkled, dark yellowish brown (10YR 4/4–4/6) at the center, becoming light olive brown (2.5Y 5/4–5/6) towards the margin, in section appearing light olive brown (2.5Y 5/4–5/6), up to 0.5 mm thick, separated from the context by a resinous and very thin dark line (up to 0.1 mm); context compact, slightly lighter in color than the superior portion, up to 0.5 mm thick; tube layer concolorous with the context, up to 0.5 mm, indistinctly stratified when reviving; margin rounded, entire to lobed, 1–2 mm thick, whitish when fresh, becoming yellowish (2.5Y 7/6–7/8) upon drying; hymenophore slightly decurrent, yellowish (2.5Y 7/6) to light olive brown (2.5Y 5/4–5/6), pores inconspicuous, circular to angular, 8–12(–13)/mm, when reviving, with spots of new tube layers growing irregularly upon older parts, dissepiment entire. Stipe attached to living roots, mostly standing straight, eccentric to lateral, bulbous to cylindrical, uneven and appearing knotted, up to 1 cm wide at the base, tapering towards the pileus insertion point, up to 3.0 cm high; stipe surface an adpressed coat of tomentum, dull, dark yellowish brown (10YR 4/4–4/6), up to 1 mm thick, a thin dark line separating it from the context; stipe context compact, shiny, the same as the context of the pileus in color and texture, up to 4 mm wide.

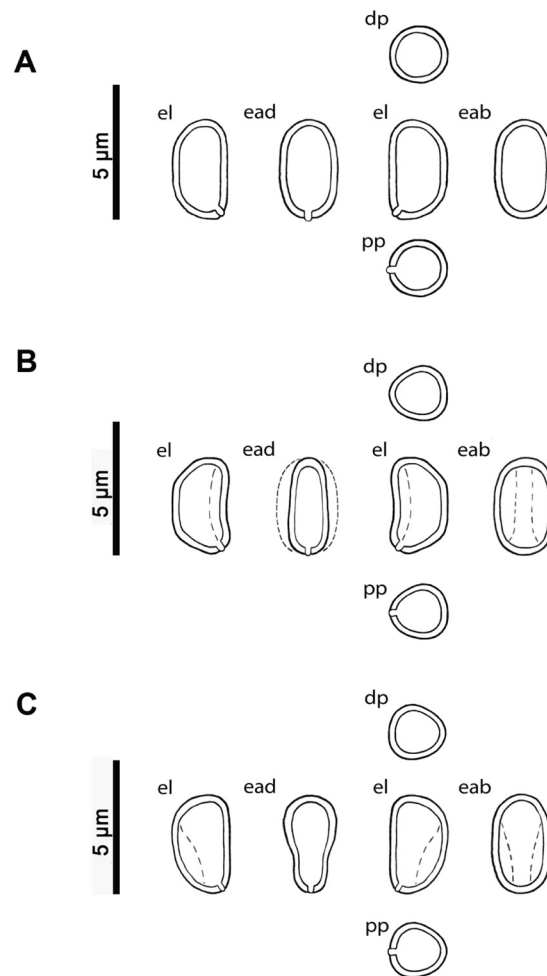


FIGURE 3. Sporogram from the holotype of *Phylloporia spathulata* (K119681), representing three variations of its basidiospores in equatorial and polar view, the dotted lines representing flattened sides (*el* = equatorial lateral view; *ead* = equatorial adaxial view; *eab* = equatorial abaxial view; *dp* = distal polar view and *pp* = proximal polar view). Drawings by Valéria Ferreira Lopes.

Hyphal structure monomitic in all parts (truly monomitic *sensu* Corner 1991). Generative hyphae simple-septate, slightly to moderately thick-walled, with wide lumen, sometimes with portions filled with a bright yellowish resin, pale to golden yellow, more frequent in the plagiotrichoderm; at the hymenophoral trama (2–)2.5–4 µm wide; at the context of pileus and stipe subparallel, (3–)4–6 µm wide; at the plagiotrichoderm (Figure 4 A) often collapsed and with local constrictions towards the apices, 3–5(–6) µm wide, up to 300 µm length, anticlinal, arising from a dark line formed by sclerified brownish agglutinated hyphae, frequently septate and branched; at the stipe tomentum loosely interwoven, mostly unbranched, straight to slightly tortuous, 2–4 µm wide. Hymenium (Figure 4 E). Basidia 4-sterigmate, clavate to barrel-shaped, hyaline in KOH, 7–8 × 4–5 µm, basidioles shorter. Cystidia rarely present, subulate, hyaline in KOH, thin-walled, 12–13 × 3–4(–5) µm. Basidiospores (Figure 4 B–D) broadly ellipsoid to ellipsoid in equatorial lateral view, subglobose in equatorial adaxial view, sometimes with either one flattened side on the equatorial or in the polar view, or in both; smooth; pale yellow in KOH/lactophenol; occasionally guttulate; thick-walled; 2.5–3.5 × 2–3 µm (avg. = 3.0 × 2.4 µm), Q = 1.50–1.75/Q avg. = 1.28, thick-walled, IKI–.

Substrate and distribution:—Growing on living angiosperm roots; some specimens were connected to living roots of *Eugenia involucrata* D. C. (Myrtaceae Juss.). So far known from Brazilian Atlantic Forest Biogeographic Province (Santa Catarina State) and Parana Forest Biogeographic Province (northeast Argentina).

Additional specimens examined:—ARGENTINA. Province of Misiones: Department Oberá, *Centro de Investigaciones Antonia Ramos*, elevation 400 m. a. s. l., 27° 19' 58.80" S, 54° 57' 0.00" W, growing on living roots of *Eugenia involucrata* D. C., 24th February 2015, *V. F. Lopes 102* (CORD!); *Idem, Ibidem*, 27th February 2015, *V. F. Lopes 106*, growing on living roots of *E. involucrata*; BRAZIL. Santa Catarina: Itapoá, Reserva Particular do Patrimônio Nacional Volta Velha, elevation 20 m. a. s. l., 26° 04' 56" S, 48° 38' 56" W, growing on living roots, 18th November 2012,

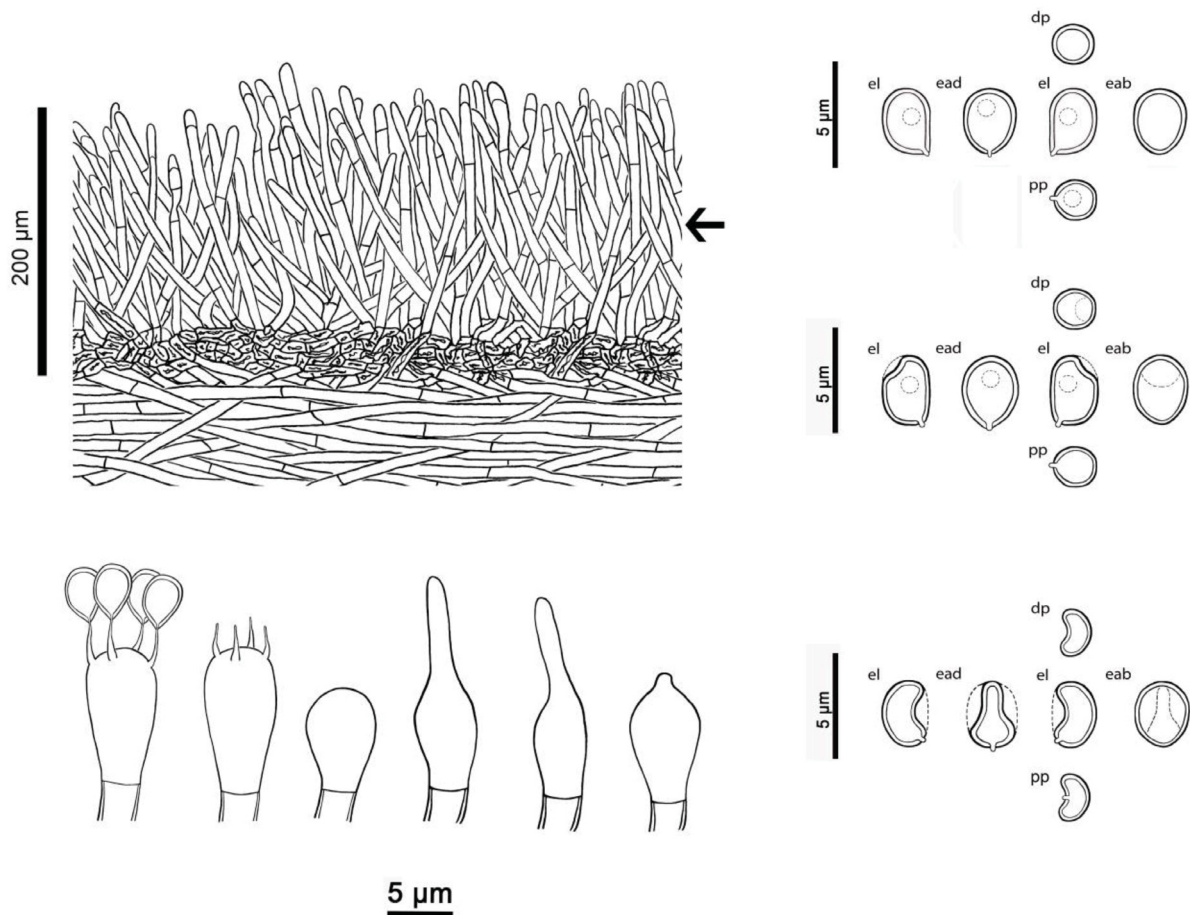


FIGURE 4. *Phylloporia elegans* microscopic features. A) pileus section with black arrow indicating the plagiotrichoderm; B–D) Sporangium from light microscope observations of fresh specimens (FLOR 51179, FLOR 51178), representing three variations of the basidiospores in equatorial and polar view, with dotted lines representing flattened sides; E) Basidia, basidiolae and subulate cystidia, mature and young (*el* = equatorial lateral view; *ead* = equatorial adaxial view; *eab* = equatorial abaxial view; *dp* = distal polar view and *pp* = proximal polar view). Drawings by Gerardo L. Robledo & Valéria Ferreira Lopes.

Robledo 2546 (FLOR! 51179); *Idem, Ibidem*, 28th February 2012, *E. R. Drechsler-Santos 790* (FLOR! 51169); *Idem, Ibidem*, 28th February 2012, *E. R. Drechsler-Santos 792* (FLOR! 51238).

Phylloporia nodostipitata Ferreira-Lopes & Drechsler-Santos *sp.nov.* (Figures 2 C, 5 A–E)

Mycobank:—MB 805722

Diagnosis:—Basidiomata stipitate, seasonal to reviving, with brownish yellow pileus, tomentose pileal surface, knotted and irregularly flexuous stipe, 8–10(–12) pores p/mm and broadly ellipsoid basidiospores [$2.5\text{--}3.5 \times 2\text{--}3$ (–3.5) μm].

Etymology:—*Nodostipitata* (Lat. *nodus*) referring to the knotted and flexuous stipe.

Holotype:—BRAZIL. Santa Catarina: Florianópolis, Unidade de Conservação Ambiental Desterro, elevation 248 m. a. s. l., –27° 31' 52" S, –48° 30' 45" W, 31th March 2012, *E. R. Drechsler-Santos 801* (FLOR! 51173). GenBank accession number (LSU; KJ631412).

Description:—Basidiomata seasonal to reviving, stipitate, rarely solitary to caespitose with multiple pilei or a single, lobed pileus arising from a nodose mass of fused stipes; pileus circular, semi-circular to fan-shaped, flat to infundibuliform, up to 7.0×4.0 cm, new pilei may arise directly from the margin of an older one with no direct insertion of the stipe; pileus surface a cottony tomentum, shiny, concentrically zonate and sulcate, adpressed velutinate to scrupose, brownish yellow (10YR 6/6–6/8) to dark yellowish brown (10YR 3/6–4/6), in aged specimens the tomentum wearing away to expose semicircular dark streaks, tomentum yellowish brown in section (10YR 5/6–5/8), up to 0.5 mm thick, with a dark line up to 0.5 mm thick separating it from the context; context compact, appearing resinous in section, yellow (10YR 7/6–7/8), up to 0.5 mm thick; tube layer up to 1 mm deep, concolorous with the

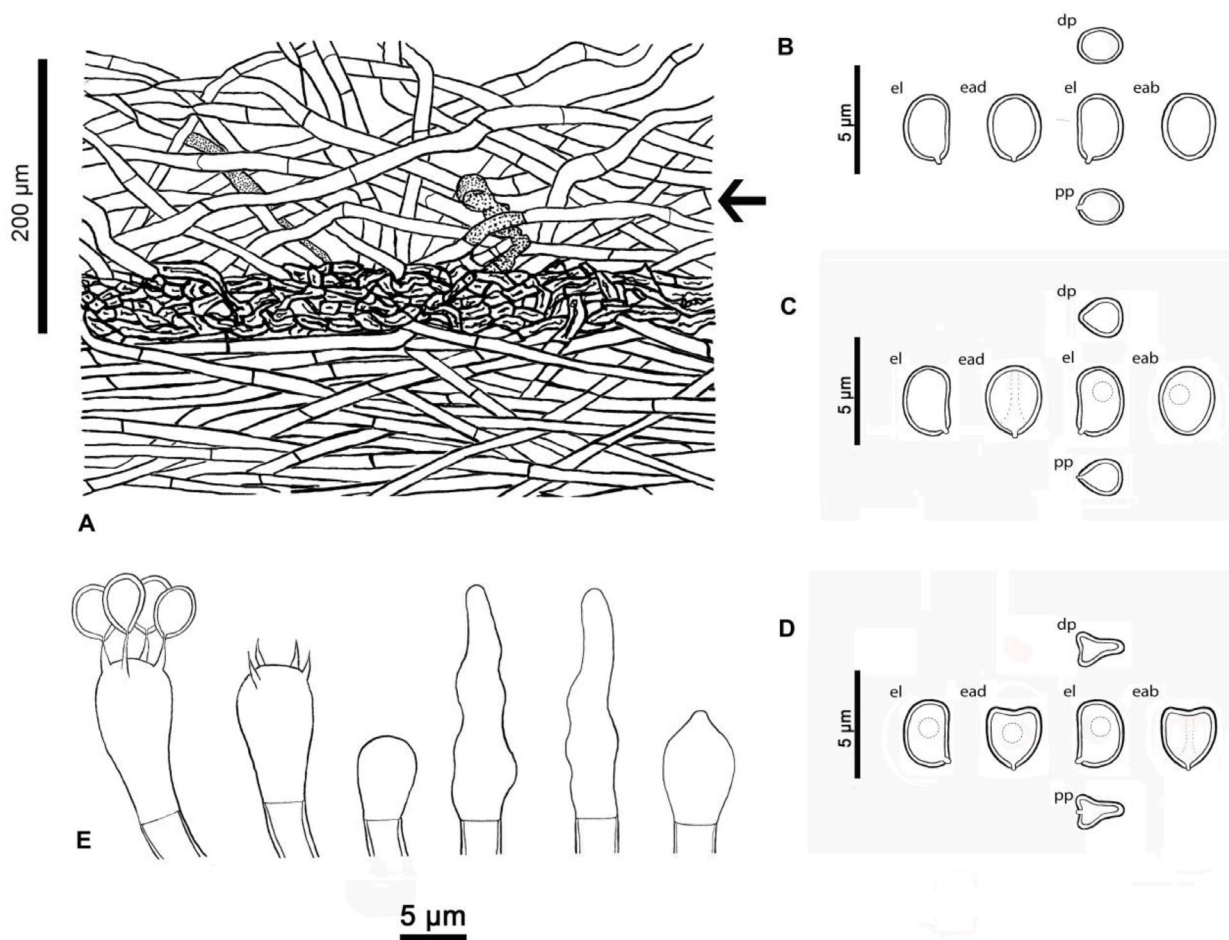


FIGURE 5. *Phylloporia nodostipitata* microscopic features. A) pileus section with black arrow indicating the tomentum; B–D) Sporogram from light microscope observations of fresh specimens (FLOR 51173, FLOR 51154), representing three variations of the basidiospores in equatorial and polar view, with dotted lines representing flattened sides; E) Basidia, basidiole and lageniform cystidia, mature and young (*el* = equatorial lateral view; *ead* = equatorial adaxial view; *eab* = equatorial abaxial view; *dp* = distal polar view and *pp* = proximal polar view). Drawings by Gerardo L. Robledo & Valéria Ferreira Lopes.

context, indistinctly stratified when reviving; margin rounded, entire to lobed, up to 2 mm thick, whitish when fresh, becoming yellowish brown (10YR 5/6–5/8) upon drying; hymenophore slightly decurrent, well delimited by a cottony sterile margin up to 1 mm thick, yellowish brown (10YR 5/6–5/8) becoming light olive brown (2.5Y 5/4–5/6) when mature, pores inconspicuous, circular to angular, 8–10(–12)/mm, with spots of new tube layers growing irregularly upon older parts, dissepiments entire to slightly lacerated. Stipe attached to living roots, mostly prostrate on soil, often with several stipes entirely fused, eccentric to lateral, with a contracted base, strongly flexuous, nodose, uneven, up to 2.5 cm wide at the base and 7.0 cm high; stipe surface as a compressible tomentum, becoming hard and adpressed velutinate to scrupose with age, a thin dark line separating it from the context; stipe context compact, shiny, similar to the context of the pileus in color and texture.

Hyphal structure monomitic in all parts (truly monomitic *sensu* Corner 1991). Generative hyphae simple septate, slightly to moderately thick-walled, with wide lumen, sometimes with portions filled with a bright yellowish resin, pale to golden yellow, more frequent on the context and context of stipe; at the hymenophoral trama 2–3(–5) µm wide; at the context of pileus and stipe (3–)4–6(–7) µm wide; at the tomentum (pileus and stipe, Figure 5 A) loosely interwoven, straight, mostly unbranched, 3–6(–7) µm wide, sometimes with local constrictions. Hymenium (Figure 5 E). Basidia 4-sterigmate, cylindrical to broadly clavate, thin-walled, hyaline in KOH, 10–15 × 4–5 µm. Basidioles spherical to barrel-shaped, thin-walled, hyaline in KOH, shorter. Cystidia rarely present, lageniform to subulate, hyaline in KOH, thin-walled, 17–20 × 3–5 µm. Basidiospores (Figure 5 B–D) broadly ellipsoid to ellipsoid in equatorial lateral view, subglobose in equatorial adaxial view, sometimes with either one flattened side on the equatorial or in the polar view, or in both; smooth; pale yellow in KOH/lactophenol; occasionally guttulate; thick-walled; 2.5–3.5 × 2–3(–3.5) µm (avg. = 3.0 × 2.5 µm), Q = 1.19–1.50, Q avg. = 1.33, IKI–.

Substrate and distribution:—Growing on living angiosperm roots; some specimens were connected to living roots probably of *Psidium cattleyanum* Sabine (Myrtaceae Juss.). So far known only from Brazilian Atlantic Forest Biogeographic Province (Santa Catarina State).

Additional specimens examined:—BRAZIL. Santa Catarina: Florianópolis, Unidade de Conservação Ambiental Desterro, elevation 248 m. a. s. l., 27° 31' 52" S, 48° 30' 45" W, growing on living roots, 25th May 2013, *V. Ferreira-Lopes* 084 (FLOR! 51259); *Idem, Ibidem*, 31th March 2012, *E. R. Drechsler-Santos* 799 (FLOR! 51171); *Idem, Ibidem*, *E. R. Drechsler-Santos* 800 (FLOR! 51172); *Idem, Ibidem*, *E. R. Drechsler-Santos* 801 (FLOR! 51173); *Idem, Ibidem*, *E. R. Drechsler-Santos* 802 (FLOR! 51174); *Idem, Ibidem*, *E. R. Drechsler-Santos* 805 (FLOR! 51175); *Idem, Ibidem*, *E. R. Drechsler-Santos* 806 (FLOR! 51176); *Idem*, Itapoá, Reserva Particular do Patrimônio Nacional Volta Velha, trilha do sambaqui elevation 20 m. a. s. l., 26° 04' 56" S, 48° 38' 56" W, 27th February 2012, *E. R. Drechsler-Santos* 788 (FLOR! 51168); *Idem, Ibidem*, 27th February 2012, *E. R. Drechsler-Santos* 791 (FLOR! 51170); *Idem, Ibidem*, 17th February 2012, *V. Ferreira-Lopes* 79 (FLOR! 51153); *Idem, Ibidem*, 17th February 2012, *V. Ferreira-Lopes* 80, on living roots of *Psidium cf. cattleyanum* (FLOR! 51154); *Idem, ibidem*, on living roots, 2nd February 2013, *A. C. Magnago* 536 (FLOR! 51254); *Idem, ibidem*, *C. A. T. Oliveira* 33 (FLOR! 51237).

Discussion

Based on the examination of the type material of *P. spathulata*, we present a delimitation for *P. spathulata s. s.* The age and condition of the type material prevented the description of its hyphal system with accuracy, since the hyphae were brittle and mostly fractured, though despite this, some meaningful observations were still able to be made. There are clearly two hyphal differentiations: one slightly thick and faintly yellowish with a wide lumen, and the other thick-walled, brownish and simple-septate with a narrow lumen.

In *Phylloporia*, the classification of the hyphal system has been widely accepted in the sense of Johansen & Ryvardeen (1980), which defines skeletal hyphae as thick-walled to solid, unbranched to sparingly branched, and essentially without true septa. By this definition, the basidiomata not having these thick-walled, aseptate hyphae, are considered monomitic. To Corner (1932, 1991), the presence of two kinds of hyphae, with different orientation, form or branching constitutes a dimitic hyphal system, even when both kinds of hyphae are truly septate. Corner (1991) categorizes the dimitic hyphal system in Hymenochaetaceae, depending on septation, branching and length of the skeletal hyphae. The categories are dimitic in first (d1: septate, frequently branched, unlimited growth), second (d2: septate, sparingly branched, unlimited growth), third (d3: aseptate to secondarily septate, sparingly branched, unlimited growth), fourth (d4: aseptate to secondarily septate, sparingly branched to unbranched, not exceeding 1500 µm length) or fifth degree (d5: aseptate to secondarily septate, sparingly branched to unbranched, not exceeding 600 µm length). The hyphal system of *P. spathulata s. s.*, *P. elegans* and *P. nodostipitata* can be considered monomitic in the sense of Johansen & Ryvardeen (1980), since they lack aseptate skeletal hyphae. On the other hand, *P. spathulata s. s.* can be considered dimitic d1–d2, while *P. elegans* and *P. nodostipitata* are monomitic, according to Corner (1991). In this study, we refrain from adopting strictly one of these two hyphal system classifications (Johansen & Ryvardeen 1980, Corner 1991), because the hyphae of *P. spathulata s. s.* are broken due to the age of its type material. Besides, the classification of hyphal system is an issue concerning the whole of the genus *Phylloporia*, which requires a thorough discussion to be undertaken in future studies.

Phylloporia spathulata s. s. shares the laterally stipitate basidiomata, azonate pileus and elongate to cylindrical basidiospores in equatorial lateral view with *P. verae-crucis*, mainly differing by *P. spathulata* having smaller basidiomata (pileus up to 0.7 cm broad vs. pileus of *P. verae-crucis* up to 10 cm broad), slightly larger pores (7–9 p/mm vs. 8–12 p/mm) and smaller basidiospores [$3\text{--}4 \times 2\text{--}2.5$ µm vs. $4\text{--}5 \times 2\text{--}3(3.5)$ µm]. *P. verae-crucis* also has a distinctly brownish orange context. *Phylloporia spathulata s. s.* mainly differs from both *P. elegans* and *P. nodostipitata* by being strictly seasonal, having slightly larger pores (7–9 p/mm vs. 8–10 p/mm), slightly larger basidiospores ($3\text{--}4 \times 2\text{--}2.5$ µm vs. $2.5\text{--}3.5 \times 2\text{--}3$ µm) which are elongate in equatorial lateral view, and the presence of thick-walled, brownish hyphae with a narrow lumen. Although the plant host of the type specimen examined is unknown, it was collected in Ecuador.

The two new South American species described here are morphologically very similar. Both species share similar pore sizes and size of basidiospores (Figures 4 and 5). They mainly differ in the pileal surface: the pileal surface of *P. nodostipitata* is a tomentum formed by loosely interwoven hyphae of undefined growth whereas in *P. elegans* the pileal surface consists of short and anticlinal hyphae, here referred to as a plagiotrichoderm in the sense of Clemençon (2012) (Figure 4 A).

A pileal surface similar to the plagiotrichoderm of *P. elegans* was found in *P. pulla* (Montagne & Berkeley 1844: 332) (Decock & Yombiyeni 2015: 1007), *P. fulva* (Yombiyeni & Decock 2015: 1005) and *P. afrospathulata* Yombiyeni & Decock 2015 (Yombiyeni *et al.* 2015). *Phylloporia pulla* and *P. fulva* mainly differ from *P. elegans* by being sessile and dimitic. *Phylloporia afrospathulata* mainly differs from *P. elegans* in its pilei with grayish concentric lines, involute margin, incompletely dimitic hyphal system and the absence of cystidia (Yombiyeni *et al.* 2015). Regarding their geographical distribution, *P. pulla* appears to be Indo-Malaysian, while *P. fulva* and *P. afrospathulata* are known only from Africa.

Phylloporia verae-crucis is a neotropical species that also has stipitate basidiomata. It mainly differs from *P. elegans* and *P. nodostipitata* by being strictly seasonal, laterally short-stipitate (or pseudo-stipitate), and by the presence of elongate to cylindrical basidiospores which are larger [$4\text{--}5 \times 2\text{--}3(3.5) \mu\text{m}$, avg. 4.2×2.5 , Q avg. = 1.71]. So far, its distribution is restricted to Mexico and Costa Rica (Ryvarden 2004). *Phylloporia nodostipitata* and *P. elegans* should also be compared to *P. minutispora* (Ipulet & Ryvarden 2005: 95). *Phylloporia minutispora* has smaller pores (10–16 p/mm) and slightly smaller basidiospores [$(2\text{--})2.5\text{--}3 \times 2\text{--}2.5 \mu\text{m}$, avg. $2.5 \times 2.0 \mu\text{m}$, Q avg. = 1.26]. Also, *P. minutispora* is known only from Africa (Yombiyeni *et al.* 2015).

P. elegans and *P. nodostipitata* both have the ability to develop spots of young tube layers directly from a degraded tube layer (*i.e.* they revive). *P. elegans*, *P. nodostipitata* and *P. terrestris* (L. W. Zhou: 2015) could also be reviving according to the photographs corresponding to their type material, however, they were described simply as annual (Zhou 2015a). *Phylloporia terrestris* mainly differs by having smaller pores (10–14 p/mm) and the absence of cystidia, as well as being known only from China (Zhou 2015a).

Although the nutritional strategy of the genus *Phylloporia* is still poorly studied, it has been suggested that it is parasitic with high levels of host specificity (Esquivel & Carranza 1996, Wagner & Ryvarden 2002, Dai 2010, Rajchenberg & Robledo 2013, Liu *et al.* 2015, Yombiyeni *et al.* 2015). The currently described species seem to be able to develop basidiomata in different plant organs. This association between habit and the plant organ from which the basidiomata emerge has been referred to as the ‘morpho-ecological type’ (Yombiyeni *et al.* 2015). Species of *Phylloporia* with a ‘stipitate on roots’ morpho-ecological type in the neotropical region up to now includes four species: *P. elegans*, *P. nodostipitata*, *P. spathulata* and *P. verae-crucis*. However, this number will likely increase with the study of collections from the lineages identified as *Coltricia stuckertiana sensu lato*, *Phylloporia aff. spathulata* and *Phylloporia sp.* (KC136225) (Figure 1), as well as other South American collections with stipitate basidiomata currently under revision, all of which will be the subject of future studies.

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