Nova Hedwigia Vol. 103 (2016) Issue 1–2, 125–143 **Article**

Antrodia neotropica sp. nov. (Polyporales, Basidiomycota): a new South American species of *Antrodia* s.s. from Brazil based on morphological, molecular and ecological data

Gesieli Kaipper-Figueiró[1*], Gerardo Lucio Robledo[2], Mateus Arduvino Reck[1], Aristóteles Góes-Neto[3] and Elisandro Ricardo Drechsler-Santos[1*]

[1] PPG Biologia de Fungos, Algas e Plantas, Departamento de Botânica, Centro de Ciências Biológicas, Universidade Federal de Santa Catarina, Campus Universitário Trindade, CEP: 88040-900, Florianópolis, Santa Catarina, Brazil.

[2] Instituto Multidisciplinario de Biología Vegetal, Universidad Nacional de Córdoba, C.C.495, 5000, Córdoba, Argentina.

[3] Laboratório de Pesquisa em Microbiologia (LAPEM), Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana, Avenida Transnordestina, Feira de Santana, CEP: 44036-900, Bahia, Brazil.

With 4 figures and 3 tables

Abstract: During the revision of the *Antrodia* species from the Atlantic Forest in southern Brazil, some specimens collected on dead branches of *Baccharis* (Asteraceae) were found to represent an undescribed species, *Antrodia neotropica* sp. nov. Morphologically, this new species is characterized by resupinate to effused-reflexed basidiomata with a cream to brown pore surface, a dimitic hyphal system and basidiospores that are cylindrical to subcylindrical, in dorsi-ventral view with an obovoid aspect, and from the side-view present a sigmoid ventral side. Molecular phylogeny inferred from nrITS and nrLSU sequence data confirmed that this species belongs to the *Antrodia* s.s. clade, closely related to European and North American species, *A. serpens* and *A. heteromorpha*. Its relationships within *Antrodia* s.s. as well as biological and morphological characters of *Antrodia* s.s. are discussed.

Key words: antrodia clade, brown-rot polypores, phylogeny, taxonomy.

Introduction

Antrodia P. Karst. comprises in a wide sense, brown-rot polypores, morphologically characterized by resupinate to pileate basidiomata, of seasonal to perennial growth habit, a dimitic hyphal system with clamped generative hyphae, and hyaline, thin-walled

---

*Corresponding authors: gesikaipper@hotmail.com; drechslersantos@yahoo.com.br; e.ricardo@ufsc.br

DOI: 10.1127/nova_hedwigia/2016/0340

www.borntraeger-cramer.de
0029-5035/2016/0340 $ 4.75

and usually cylindrical to oblong-ellipsoid basidiospores which are negative in Melzer's reagent (Gilbertson & Ryvarden 1986, Ryvarden 1991, Ryvarden & Gilbertson 1993, Bernicchia & Ryvarden 2001, Núñez & Ryvarden 2001). However, phylogenetic studies have shown that *Antrodia* is polyphyletic, and several species traditionally treated as *Antrodia* are distributed throughout the phylogeny in different clades closely related to other brown-rot species, such as *Amyloporia* Singer, *Daedalea* Pers. and *Fomitopsis* P. Karst, or with an uncertain position without relationships to a known genus (Kim et al. 2003, Yu et al. 2010, Rajchenberg et al. 2011, Bernicchia et al. 2012, Spirin et al. 2012, Spirin et al. 2013, Ortiz-Santana et al. 2013). The phylogenetic position and circumscription of some of these groups/genera and species remain, so far, unclear.

A re-circumscription of *Antrodia* s.s. and the identity of its type species, *Antrodia serpens* (Fr.) Donk, was recently proposed based on morphological and molecular data (Spirin et al. 2013). *Antrodia* s.s. was defined as a monophyletic group comprising the type and five other species [*A. favescens* (Schwein.) Vlasák & Spirin, *A. heteromorpha* (Fr.) Donk, *A. macra* (Sommerf.) Niemelä, *A. mappa* (Overh. & J.Lowe) Miettinen & Vlasák, *A. tanakai* (Murrill) Spirin & Miettinen], which share a combination of characters distinguishing it from other *Antrodia* s.l. species: short-lived pedunculate basidia, hyphidia, and skeletal hyphae bending into the hymenium as skeletocystidia and spore shape (fusiform distal end), as argued by Spirin et al. (2013). *Antrodia* s.s. species are morphologically quite similar with overlapping features, and species circumscription based solely on morphology becomes more difficult. Therefore, ecological characters, i.e. nutritional strategy (saprobes on dead substrates/parasites on living substrates), substrate type (branch/log/stem/etc, angiosperm/gymnosperm/etc), substrate specificity and distribution become increasingly important (Amalfi & Decock 2013, Spirin et al. 2013).

In this new phylogenetic scenario, species of *Antrodia* s.s. are described as restricted to temperate regions of North America (*A. favescens*), Europe (*A. serpens* type) or circumglobal in the Northern Hemisphere, and widespread in the coniferous forests (*A. heteromorpha*) (Spirin et al. 2013). However, records of *Antrodia* s.s. species are reported from tropical and subtropical regions of the world. In South America, *A. albida* (Fr.) Donk [=*A. heteromorpha fide* Spirin et al. (2013)] has been recurrently reported in the Atlantic Forest of Southern Brazil on angiosperm substrata (Meijer 2006, Drechsler-Santos et al. 2008, Reck & Silveira 2008, Leal & Gugliotta 2008, Trierveiler-Pereira et al. 2009, Baltazar & Gibertoni 2009, Motato-Vásquez & Gugliota 2013, Drechsler-Santos et al. 2014). Macro and microscopic descriptions of these records do not evidence differences with the current circumscription of *A. heteromorpha*. On the other hand, ecological data (geographic distribution, climate, and substrate type) are clearly different and contrasting. This situation confronts us with a recurrent dilemma on the distribution-host specificity relationship within wood-decaying fungi. Are they generalists and widely distributed species or host-specific species with restricted distributions (cryptic species)? It has been shown that some wood-decaying fungi are not widely distributed as it was traditionally believed. Several cases in the recent literature of polypores have shown that some worldwide distributed taxa represent, on the contrary, many distinct species, as in the case of *Fomitiporia punctata* Murrill (Decock et al. 2007, Campos-Santana et al. 2014).

In this study we present ecological, morphological and molecular evidence supporting our hypothesis that *A. albida* records from Brazil correspond to distinct *Antrodia* species; accordingly *Antrodia neotropica* is described below as new species from Southern Brazil, the first *Antrodia* s.s. known from the Neotropical region. The inclusion of a new neotropical member in the genus, recently re-circumscribed as north temperate, leads us again to the question: what is *Antrodia* s.s.? In addition to the phylogenetic concept, new morphological and biological evidences are added to the circumscription of the genus.

Materials and methods

Collections and Morphological studies: The studied specimens were collected in the Serra Geral geological formation, South Brazil, in the Atlantic Forest domain, at two protected areas: Centro de Pesquisas e Conservação da Natureza Pró-Mata (Rio Grande do Sul state) and São Joaquin National Park (Santa Catarina state). All collections were deposited in the herbarium FLOR (UFSC). Specimens from BPI and BAFC herbaria were used as additional study materials for morphological comparison. Herbarium designations follow Thiers (2014). Colors were determined according to Munsell (1975). Basidiomata sections were examined in Melzer's reagent, lactic acid Cotton blue, cresyl blue, KOH 4%, phloxine 1% and lactophenol. All microscopic measurements (n = 40) were made in Melzer's reagent. In presenting the size range of the microscopic elements, 5% of the measurements were excluded from each and are given in parentheses, when relevant. The technique to analyze and to describe the hyphal system follows Teixeira (1995). In the text, the following abbreviations are used for basidiospore measurements: ($\bar{X}$ = arithmetic average) (Q = ratio length/width) ($\bar{Q}$ = arithmetic average of Q). We follow Stalpers (1996) and the Resupinate Russulales species database (http://www.cbs.knaw.nl/russulales/) to define the terminology of the basidiospores shape based on the Q value and symmetry. To observe number of nuclei per basidiospore, a thin section of the tubes was mounted in DAPI solution following Calderoni et al. (2003) [a 0.5% (w/v) solution of DAPI (4,6-diamidino-2-phenylindole) in distilled water was mixed at a ratio of 4:6 with McIlvaine buffer of pH 7 (1:1 mixture of 0.2 M Na_2HPO_4 and 0.1 M citric acid) and observed with a fluorescence microscope].

DNA extraction and sequencing: For extraction of total genomic DNA from dried basidiomata, the protocol of Doyle & Doyle (1987) adapted by Góes-Neto et al. (2005) was used. The primer pairs ITS6-R - ITS8-F and LR0R - LR7 were used to amplify, respectively, the ITS (ITS1-5.8S-ITS2) and LSU (28S) regions through polymerase chain reaction, according to the cycle parameters described in Dentinger et al. (2010) and Vilgalys & Hester (1990) respectively. Sequencing was performed with BigDye Terminator 3.1 Cycle Sequencing Kit following manufacturer procedures, using the same primers cited above for the ITS and the LR0R-LR5 primer pair for the LSU at FIOCRUZ-MG (Brazil) as part of the FungiBrBol project (www.brbol.org). The generated sequences and their respective chromatograms were manually checked and edited with Geneious 6.1.8 (Kearse et al. 2012).

Phylogenetic analyses: A total of 38 specimens representing nine putative species (including the outgroup), both newly generated in this study or downloaded from Genbank, were used to build a combined ITS/LSU dataset (Table 1). The automatic alignment of each region was carried out with MAFFT (Katoh & Standley 2013), following the Q-INS–i and G-INS-i criteria (for ITS and LSU, respectively), and then manually inspected and adjusted, as necessary, with MEGA 6 (Tamura et al. 2013). Moreover, potentially ambiguous regions were identified with GBLOCKS 0.91b (Castresana 2000) in the phylogeny.fr platform (Dereeper et al. 2008), allowing all parameters for a less stringent selection (i.e. allow smaller final blocks, allow gap positions within the final blocks, allow less strict flanking positions). The final alignment was deposited in TreeBASE (http://www.treebase.org/treebase/index.html) under ID S18270. Maximum Likelihood (ML) and Bayesian Inference (BI) searches were applied to the dataset, which was divided in four partitions: ITS1, 5.8S, ITS2 and nucLSU. The best fit model of nucleotide evolution to each partition was obtained

Table 1. List of species, collections, and sequences used in the phylogenetic analyses. Two-letter codes after vouchers (specimen/strain) denote country of origin (ISO 3166).

Species **Voucher specimen/strain**	**Locality**	**Host tree**	**ITS**	**LSU**	**Authors**
Antrodia favescens					
Vlasák Jr 0412/4J (JV)	US	*Juniperus virginiana*	KC543129	KC543129	Spirin et al. 2013
FP103468-sp.	US		KC585268	KC585268	Ortiz-Santana et al. 2013
FP103723-sp.	US	*Acer rubrum*	KC585269	KC585269	Ortiz-Santana et al. 2013
L10040-sp.	US	*Quercus*	KC585270	KC585270	Ortiz-Santana et al. 2013
L-11015-sp.	US	*Liriodendron tulipifera*	KC585271	KC585271	Ortiz-Santana et al. 2013
L-12838-sp.	CR	Hardwood	KC585272	KC585272	Ortiz-Santana et al. 2013
Mad4875R	US	*Pinus strobus*	KC585273	KC585273	Ortiz-Santana et al. 2013
MD195	US	*Betula*	KC585274	KC585274	Ortiz-Santana et al. 2013
CBS30882	US	Unknown	DQ491414	DQ491414	Kim et al. 2007
FP105979			EU232189	EU232272	Unpublished
Antrodia tanakai					
Miettinen X688	FI	Unknown	KC543134	KC543134	Spirin et al. 2013
Miettinen X1369	FI	Unknown	KC543142	KC543142	Spirin et al. 2013
Antrodia macra					
Otto Miettinen X1292	FI	Unknown	KC543139	KC543139	Spirin et al. 2013
Otto Miettinen X806	FI	Unknown	KC543135	KC543135	Spirin et al. 2013
Antrodia heteromorpha					
CBS200.91	CA	*Abies balsamea*	DQ491415	DQ491415	Kim et al. 2007
FP101702-sp	US	*Tsuga canadensis*	KC585275	KC585275	Ortiz-Santana et al. 2013
FP133176	US	*Picea mariana*	KC585276	KC585276	Ortiz-Santana et al. 2013
FP133496	US	conifer	KC585277	KC585277	Ortiz-Santana et al. 2013
FP71189-R	US	*Tsuga canadensis*	KC585278	KC585278	Ortiz-Santana et al. 2013
HHB14162-T	US	*Picea*	KC585279	KC585279	Ortiz-Santana et al. 2013
L14570	CA	*Picea glauca*	KC585280	KC585280	Ortiz-Santana et al. 2013
L15692	US	conifer	KC585281	KC585281	Ortiz-Santana et al. 2013
Otto Miettinen X1366	FI	*Corylus avellana*	KC543141	KC543141	Spirin et al. 2013
Otto Miettinen X1379	FI	*Picea abies*	KC543144	KC543144	Spirin et al. 2013
Otto Miettinen X1387	RU	-	KC543145	KC543145	Spirin et al. 2013
Otto Miettinen X1438	CA	-	KC543148	KC543148	Spirin et al. 2013
Otto Miettinen X1440	CA	-	KC543149	KC543149	Spirin et al. 2013
Otto Miettinen X686	FI	-	JQ700268	JQ700268	Spirin et al. 2013b
Antrodia serpens					
Otto Miettinen X1163 epitype	PL	*Fagus silvatica*	KC543137	KC543137	Spirin et al. 2013

Otto Miettinen X1370	SK	-	KC543143	KC543143	Spirin et al. 2013
Antrodia mappa					
4132 Tuomo Niemela 2669 (H)	CA	-	KC543130	KC543130	Spirin et al. 2013
Penttilã 11756 (H)	FI	*Papulus tremula*	KC543113	KC543113	Spirin et al. 2013
L3377	US	Conifer	KC585377	KC585377	Spirin et al. 2013
Antrodia neotropical					
GKF 43 FLOR 0054183	BR	*Baccharis uncinella*	KT970443	KT970452	Present study
GKF 44 FLOR 0054184 **holotype**	BR	*Baccharis uncinella*	KT970444	KT970453	Present study
GKF 46 FLOR 0054186	BR	*Baccharis uncinella*	KT970445	KT970454	Present study
***Antrodia* sp.**					
Otto Miettinen X1321	ID		KC595892	KC595892	Ortiz-Santana et al. 2013
Fomitopsis pinicola (**outgroup)**			AY854083	AY854083	

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) 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/). The analysis first involved 100 ML searches, each one starting from one randomized stepwise addition parsimony tree, under a GTRGAMMA model, with no proportion of invariant sites and all other parameters estimated by the software. To access the reliability of the nodes, multi-parametric bootstrapping replicates under the same model were computed, allowing the program halts bootstrapping automatically by the autoMRE option. The BI was performed in the software Mr. Bayes 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 20.000.000 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. Of all trees sampled, 25% were discarded as burn-in and checked by the 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 ≥ 90%, while moderate support was considered BPP ≥ 0.9 and/or BS ≥ 70%. *Fomitopsis pinicola* (Sw.) P. Karst. was defined as the outgroup, based on previous papers that showed it as a sister group of *Antrodia* s.s. (Ortiz-Santana et al. 2013).

Results

Molecular phylogeny: A total of 12 new sequences were generated during this study. Six of them were not used in the analysis, since they represent ITS sequences from specimens which we could not generate the complementary LSU. The combined ITS/LSU dataset included sequences from 38 specimens that represent nine putative taxa, resulting in an aligned matrix of 1531 bp (including gaps); all pertinent information about the four partitions are summarized in Table 2. In the BI analysis, ten of the internal branches (ingroup) appear to be strongly supported, while two are only

Table 2. Summary of ITS rDNA, LSU rDNA datasets.

	Datasets			
Properties	**ITS 1**	**5.8S**	**ITS 2**	**nLSU**
Length (bp)	225	170	219	917
Model selected	TPM2+G	JC	TPM3+G	TrN+G
Likelihood score	–782.4256	–242.9024	–764.5923	–1768.6496
Base frequencies	equal	equal	equal	
Freq. A=				0.27
Freq. C=				0.19
Freq. G=				0.3
Freq. T=				0.24
Proportion of invariable sites	–	–	–	–
Gamma shape	0.72	–	0.3	0.03

moderately supported. In the ML reconstruction, ten of the internal branches appear to be strongly supported, while only one is moderately supported. Only the topology from the ML analysis is exhibited while both BS and BPP values are shown on the branches (Fig. 1). The bootstopping criteria of RAxML indicated 660 pseudoreplications as sufficient to access the internal branch support.

The overall topology of our reconstructions was very similar to the topology presented by Spirin et al. (2013) and by Ortiz-Santana et al. (2013) for the *Antrodia* s.s. clade. Within the ingroup, two main clades can be identified. One clade is composed of three specimens of *A. mappa*, which was resolved as a basal lineage with maximum support values in both analyses. The second clade includes all the other species, with low support values (BPP = 0.73, BS = 45). Within this lineage, the two specimens of *A. macra* are clustered in a basal clade with maximum support values while the two specimens of *A. tanakai* formed a clade (BPP = 0.9, BS = 95) that is related (BPP = 0.82, BS = 47) to *A. favescens*. The latter presented a high genetic heterogeneity within the specimens, represented by relatively long branches that led to some terminals in both analyses. The specimens identified as *A. heteromorpha* formed a strongly supported clade that is related (BPP = 1, BS = 100) to the clade formed by *A. serpens*, *Antrodia* sp. and the new *Antrodia* species, which is strongly supported (BPP = 1, BS = 97). Within this clade, all the branches received maximum or strong support values, with the new species appearing closely related to one specimen identified as *Antrodia* sp. (X1321). Phylogenetic reconstructions recovered the south Brazilian collections GKF43, GKF44 and GKF46 as a strongly supported terminal clade (BPP = 0.99, BS = 99). These combined molecular phylogenetic findings allied to the morphological studies, as well as ecological features, led us to conclude that these specimens represent a distinct species. Looking for available previous old names described for the region by Rick, Bresadola and Spegazzini (Rajchenberg 1987, Rajchenberg & Wright 1987, Ryvarden 1988) no options were found (see discussion), and hence the species is described as new and discussed below.

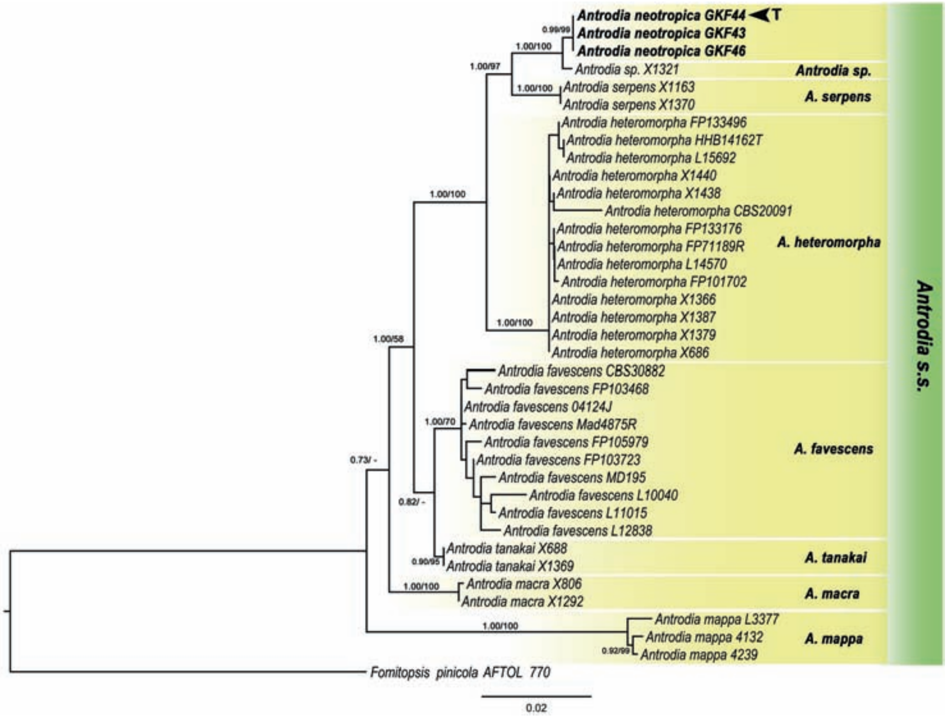

Fig. 1. Phylogram of *Antrodia* s.s. recovered from ITS (ITS1, 5.8S, ITS2) and nucLSU regions, inferred by Maximum likelihood analysis (log likelihood –3715.940706). Support values along branches are Bayesian posterior probability (≥0.7) and Maximum likelihood (≥50).

Taxonomy

Antrodia neotropica Kaipper-Figueiró, Robledo & Drechsler-Santos, **sp. nov.**
Figs 2–3

MycoBank MB809618

Typification: BRAZIL, SANTA CATARINA STATE: municipality of Urubici, Parque Nacional de São Joaquim, on dead tree of *Baccharis uncinella* DC., 21 oct 2013, G.Kaipper-Figueiró GKF 44 (holotype FLOR0054184).

Etymology: *neotropica*, referring to the potential Neotropical distribution of the species, so far known only from Southern Brazil.

Basidiomata seasonal, resupinate to rarely effuse-reflexed, clustered in several regular and adjacent spots on wood, not easily separated from substratum, up to 20 cm long, 4 cm wide and 2.5 mm thick, with a soft, leathery consistency when fresh, leathery to corky upon dried; margin up to 0.5–2.0 mm wide, narrow, whitish, regular, fimbriate to cottony, sterile, present in both young and old basidiomata. Pore surface whitish

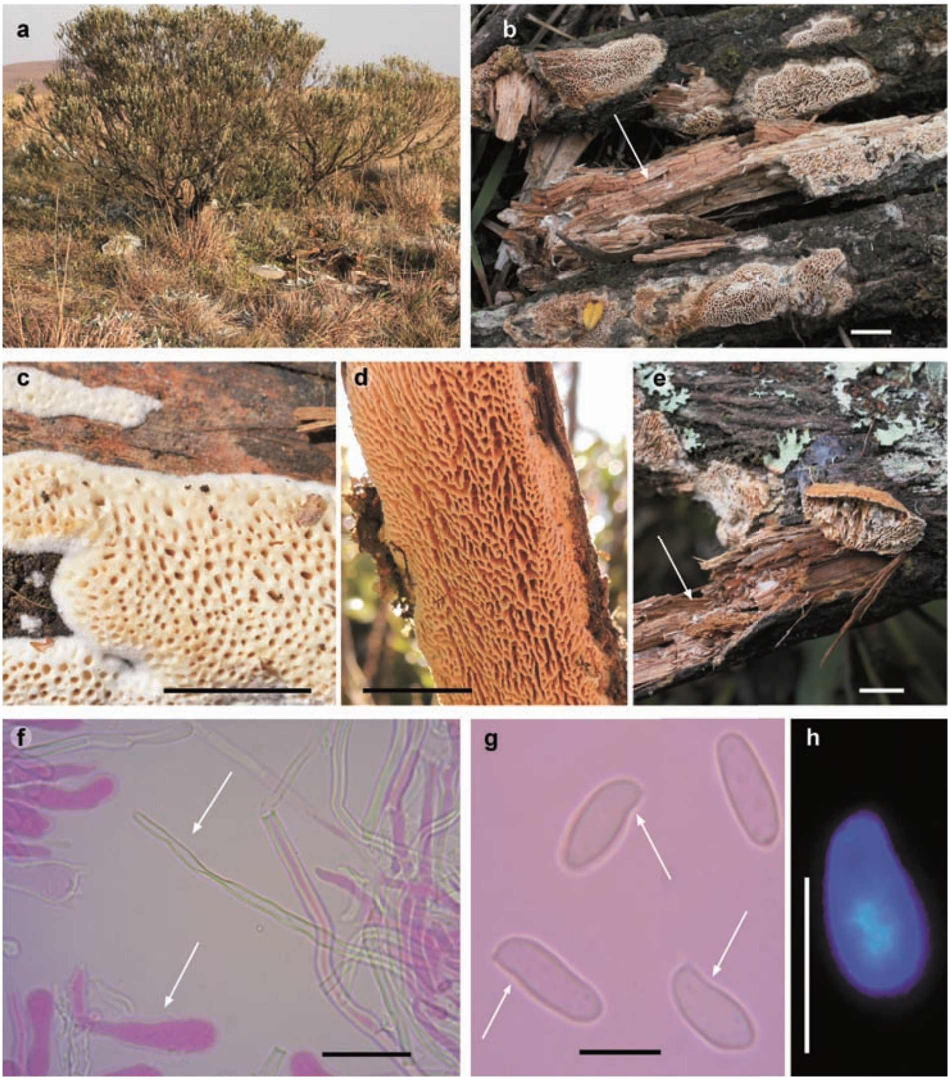

Fig. 2. *Antrodia neotropica*. A–E. Macroscopic features in situ. A. Typical habitat and host/substrate (*Baccharis uncinella*); B. General view of basidiomata and aspect of brown-rot caused on wood (white arrow) (DS1103, FLOR 0054203); C. Young resupinate and whitish basidiome with round pores (GKF053, FLOR 0054191); D. Mature, resupinate and pale brownish basidiome with elongate and lacerate pores (GKF 049, FLOR 0054189); E. Resupinate to effused-reflexed basidiome and aspect of brown-rot caused on wood (white arrow) (DS1098, FLOR 0054200). B–E scale bars = 1 cm. F–H. Microscopic features (scale bars = 10 µm). F. Basidium, basidiole with clamp at the base (white arrows) and skeletal hyphae apex (white arrows) (GKF 053, FLOR 0054191); G. Basidiospores in light microscope showing apiculous and supra-apicular depression (white arrows) (DS1107, FLOR 0054205); H. binucleate basidiospore in fluorescence microscope (holotype).

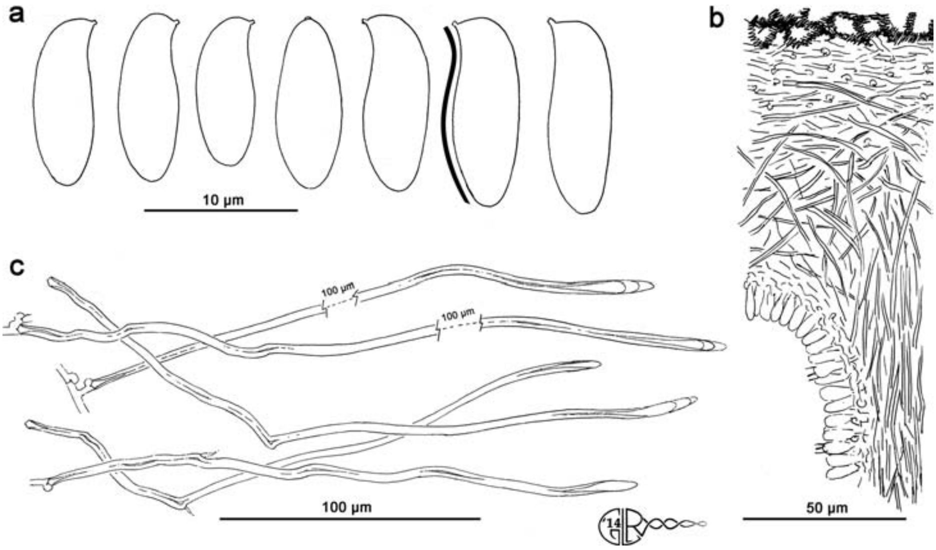

Fig. 3. Microscopic features of *Antrodia neotropica*. Holotype. G.Kaipper-Figueiró 44 (FLOR 0054184). A. Basidiospores. B. Schematic section through basidiome showing a basal layer dominated by generative hyphae arranged more or less in parallel, an intermediate layer of interwoven skeletal hyphae, and finally the trama dominated by skeletal hyphae arranged in parallel. C. Skeletal hyphae.

(when primordial), cream to brownish when mature (HUE 10 YR, 6/6), buff upon dried. Pores 1–2/mm (10–16/cm), round to angular, at first regular and with entire thick dissepiments (Fig. 2C), then irregular, elongated to lacerated, sinuous to straight, with thin dissepiments, mainly when the basidiomata is vertically oriented located on vertical substrata (Fig. 2E). Subiculum up to 0.5 mm thick, white to cream colored; tubes concolorous with pore surface, up to 2.0 mm thick.

Hyphal system dimitic in the subiculum and trama of the tubes. Generative hyphae with clamps, hyaline and thin walled to slightly thick-walled and then yellowish to slightly greenish yellow in KOH, sinuous, 2.5–3.0 µm wide, dominant in the basal layer against the substrate (Fig. 3B); skeletal hyphae unbranched, straight to slightly sinuous and geniculated at the base, then occasionally with lateral aborted processes, loosely interwoven in the subiculum, dominant through trama of the tubes where they are more or less arranged in parallel (Fig. 3B), 2.5–4.0 µm wide, evenly thick-walled with walls up to 2.0 µm with a capillary lumen (almost solid), hyaline, yellowish to slightly greenish yellow in KOH, isodiametric and slightly widening at the apex (often collapsed) where walls are thin and 2–3 adventitious septa are present, metachromatic staining dark violaceous blue in CRB, IKI-, CB-. Basidia clavate, 35–50 × 8.5–10 µm, with four sterigmata, basidioles similar to slightly smaller than basidia, hyphidia present 35–50 × 2–3 µm, straight or with 2–3 small branches at the apex. Basidiospores cylindrical to subcylindrical, in frontal view with a slightly obovoid aspect, i.e, the wider part is closer to the apex, in side-view with a sigmoid ventral side, *i.e.* distinctly concave supra-apicular depression and a tapering apex, (7.0–)8.0–14.0(–15.0) × (4.0–)4.0–5.0(–6.0) µm, ($\bar{X}$ =10.48 × 4.41 µm), Q =1.92–2.74 µm, ($\bar{Q}$ = 2.40 µm) (Fig. 3A, see Discussion), thin-walled fairly distinct, hyaline, IKI-, CB-, binucleate.

Ecology and Distribution: so far restricted to the Atlantic Forest domain of Santa Catarina and Rio Grande do Sul states in Southern Brazil, always in grasslands with sparse shrubs (locally known as "campos sujos"), in a mosaic of distinct phytophysiognomies, near *Araucaria* forests and between 500 and 1800 m of altitude. Most specimens were collected on dead branches of *B. uncinella* DC, which is the case for all specimens from Santa Catarina state, while two collections from Rio Grande do Sul state were found on substrata determined only as *Baccharis* sp. The species causes a brown-rot, easily observed in the substrate (Fig. 2B).

Specimens examined: BRAZIL, SANTA CATARINA STATE: municipality of Urubici, Parque Nacional de São Joaquim, on dead fallen branches of *B. uncinella*, 21 Oct 2013, G. Kaipper-Figueiró GKF043 (FLOR0054183); ibid, 21 Oct 2013, G.Kaipper-Figueiró GKF044 (HOLOTYPE, FLOR0054184); ibid, 21 Oct 2013, G. Kaipper-Figueiró GKF045 (FLOR0054185); ibid, 21 Oct 2013, G.Kaipper-Figueiró GKF046 (FLOR0054186); ibid, 21 Oct 2013, G.Kaipper-Figueiró GKF047 (FLOR0054187); ibid, 21 Oct 2013, G.Kaipper-Figueiró 48 (FLOR0054188); ibid, 21 Oct 2013, G.Kaipper-Figueiró GKF049 (FLOR0054189); ibid, 21 Oct 2013, G.Kaipper-Figueiró GKF050 (FLOR0054190); ibid, 21 Oct 2013, G.Kaipper-Figueiró 53 (FLOR0054191); ibid, 21 Oct 2013, G.Kaipper-Figueiró GKF054 (FLOR0054192); ibid, 16 Feb 2013, E.R.Drechsler-Santos DS0950 (FLOR0054195); ibid, 16 Feb 2013, E.R.Drechsler-Santos DS0952 (FLOR0054192); ibid, 17 Feb 2013, E.R.Drechsler-Santos DS0961 (FLOR00197); ibid, 17 Feb 2013, E.R.Drechsler-Santos DS0963 (FLOR0054198); ibid, 17 Feb 2013, E.R.Drechsler-Santos DS0966 (FLOR0054199); ibid, 12 Jul 2013, E.R.Drechsler-Santos DS1098 (FLOR0054200); ibid, 12 Jul 2013, E.R.Drechsler-Santos DS1100 (FLOR0054201); ibid, 13 Jul 2013, E.R.Drechsler-Santos DS1101 (FLOR0054202); ibid, 13 Jul 2013, E.R.Drechsler-Santos DS1103 (FLOR 0054203); ibid, 13 Jul 2013, E.R.Drechsler-Santos DS1105 (FLOR0054204); ibid, 13 Jul 2013, E.R.Drechsler-Santos DS1107 (FLOR0054205); ibid, 13 Jul 2013, E.R.Drechsler-Santos DS1109 (FLOR0054206); ibid, 14 Sep 2013, E.R.Drechsler-Santos DS1117 (FLOR0054207); ibid, 14 Sep 2013, E.R.Drechsler-Santos DS1118 (FLOR0054208); ibid, 14 Sep 2013, E.R.Drechsler-Santos DS1119 (FLOR0054209); RIO GRANDE DO SUL STATE: municipality of São Francisco de Paula, PROMATA-PUC, on dead fallen branches of *Baccharis* sp.,17 Apr 2013, A.Casale Magnago 628a (FLOR0054193); ibid, 17 Apr 2013, A. asale Magnago 628b (FLOR0054194).

Additional Specimens examined: BRAZIL, RIO GRANDE DO SUL STATE: *Trametes subcervina* Bres. (BPI 249300 TYPE); SÃO PAULO STATE: *Antrodia malicola* (Berk. & Curt.) Donk, municipality of Itu, Fazenda São Miguel, 16 May 1987 (BAFC 31275; det. M.Rajchenberg); UNITED STATES, MINNESOTA: Itasca State Park, 11 August 1970 (BAFC 23733; det. R.L.Gilbertson); GEORGIA: Athens, 11 May 1958 (BAFC 23735; det. R.L.Gilbertson); FLORIDA: O'Leno State Park, 15 Sep 1952 (BAFC 23735; det. R.L.Gilbertson).

Discussion

Antrodia neotropica within *Antrodia* sensu stricto: *Antrodia neotropica* is characterized by its seasonal basidiomata, mostly resupinate to slightly effused-reflexed, with a cream to yellowish brown pore surface, a dimitic hyphal system with clamped generative hyphae, and basidiospores that are cylindrical to subcylindrical, slightly obovoid in frontal view, and with a sigmoid ventral side in side-view (i.e. distinctly concave supra-apicular depression and a tapering apex). These micromorphological features placed

A. neotropica into *Antrodia* s.s. sensu Spirin et al. (2013). Phylogenetic analyses (BI and ML) showed *A. neotropica* forming a well distinct, strongly supported clade. Within *Antrodia* s.s., *A. neotropica* groups with an unidentified tropical specimen (*Antrodia* sp. X1321) from Indonesia, for which no morphological information is available. These two taxa grouped with other morphologically closely related species, i.e. *A. serpens* and *A. heteromorpha*, in a well-supported clade (BPP = 1, BS = 100), hereafter called *Antrodia heteromorpha* complex.

Species of the *Antrodia* s.s. have, in general, similar macro and micromorphology and the distinction between these taxa is a difficult task, mainly because of the overlapping of features (Kim et al. 2003, Bernicchia et al. 2012, Spirin et al. 2012, 2013, Cui 2013, Chiu 2007, Yu et al. 2010). However, in most of the cases the geographical distributions are different (Ortiz-Santana et al. 2013, Spirin et al. 2013). Therefore, molecular and ecological characters (type of host and geographic distribution) become important in a necessary perspective of an integrative approach to circumscribe species.

Although *A. neotropica* seems to have slightly larger basidiospores, the basidiopore size overlaps within *A. heteromorpha* complex (Table 3, Fig. 4). However, there are some other morphological differences that can be observed, in addition to the host and geographic distribution that allow its distinction. *Antrodia serpens* differs from *A. neotropica* due to its grayish to pale ochraceous pore surface (whitish when primordial, cream to brownish when mature in *A. neotropica*) (Spirin et al. 2013). Furthermore, *A. serpens* is described as restricted to Southern Europe, usually collected on different species of angiosperms (Spirin et al. 2013). *Antrodia heteromorpha* has similar basidiomata to those of *A. neotropica* but it usually grows on coniferous hosts in North America and Eurasia (Spirin et al. 2013).

Regarding other species of *Antrodia* s.s., *A. favescens* and *A. tanakai* differ macro and microscopically from *A. neotropica*. Macroscopically, they present small pilei growing individually, and the color of pore surface is often ochraceous. Microscopically, both species have irregular crystals on hymenium, encrusted basidia and smaller basidiospores (Fig. 4). Our molecular data reveal that *A. favescens* is closely related to *A. tanakai,* as has been previously shown (Spirin et al. 2013), and are distributed in distinct geographic areas in the North Hemisphere, North America and Eurasia, respectively. *Antrodia macra* differs from *A. neotropica* mainly by their distinctively smaller pores 2–3/mm (Niemelä 1985, Ryvarden & Melo 2014, Spirin et al. 2013) and narrower basidiospores (Table 3, Fig. 4). In addition, *A. macra* is distributed through Europe where it grows exclusively on *Salix* L. and *Populus tremula* L., but has also been reported from Siberia and China (Ryvarden & Melo 2014). *Antrodia mappa* shows morphological differences that distinguish it from all the other species in the genus. Their basidiomata are extremely thin and readily separable, with a fimbriate margin and pores 3–4/mm. Microscopically, although skeletal hyphae can be found in the subiculum of old basidiomata, it has a monomitic hyphal system (Niemelä 1985). The species is only known from Scandinavia and Italy growing on dead conifer wood (Ryvarden & Melo 2014).

The inclusion of *A. neotropica* (first neotropical member) and other tropical taxa (*Antrodia* sp X1321) in the phylogeny of *Antrodia s.s.* contributed to a better

Table 3. Basidiospore size in the *Antrodia* s.s. species. T: type specimen; ✱: average values taken from Spirin et al. (2013); ✚: $\bar{X}$ (arithmetic average) estimated as Median values of size range taken from literature, $\bar{Q}$ = ratio length/width calculated from .

Species	**Basidiospores**		
Specimens/Reference	**Size range**	$\bar{X}$	$\bar{Q}$
Antrodia neotropica			
FLOR0054184 GKF44 (**T**)	(8.0–) 8.0–12.0 (–14.0) × (3.5–) 4.0–5.0 (–5.0)	10.09 × 4.26	2.37
FLOR0054185 GKF 45	(10–) 10.0–13.0 (–14.0) × (4.0–) 4.0–4.5 (–5.0)	11.29 × 4.25	2.67
FLOR0054189 GKF 49	(8.5–) 9.0–11.0 (–12.0) × (4.0–) 4.0–5.0 (–5.0)	10.01 × 4.54	2.23
FLOR0054190 GKF 50	(9.0–) 10.0–12.0 (–12.0) × (4.0–) 4.0–5.0 (–6.0)	10.89 × 4.34	2.53
FLOR0054206 DS 1109	(9.0–) 11.0–14.0 (–15.0) × (4.0–) 4.0–5.0 (–5.0)	12.49 × 4.61	2.74
FLOR0054202 DS 1101	(10–) 10.0–15.0 (–16.0) × (4.0–) 4.0–5.0 (–5.0)	11.96 × 4.68	2.59
FLOR0054194 ACM 628b	(7.0–) 8.0–10.0 (–12.0) × (4.0–) 5.0–6.0 (–6.0)	9.58 × 5.00	1.92
FLOR0054203 DS 1103	(9.0–) 9.0–11.0 (–12.0) × (4.0–) 4.0–5.0 (–5.0)	10.06 × 4.90	2.06
Arithmetic average of individuals		10.48 × 4.39	2.40
Antrodia heteromorpha ✱	(6.4–) 7.6–12.6 (–15.6) × (3.0–) 3.6–5.4 (–6.4)	10.06 × 4.45	2.26
Antrodia serpens ✱	(6.3–) 8.0–12.6 (–14.4) × (2.9–) 3.6–5.3 (–6.0)	9.99 × 4.40	2.27
Antrodia favescens ✱	(6.1–) 6.4–9.4 (–11.4) × (2.5–) 2.8–4.1 (–4.4)	8.02 × 3.39	2.36
Antrodia tanakai ✱	(6.1–) 6.4–10.4 (–12.0) × (2.6–) 2.8–4.3 (–4.7)	8.36 × 3.36	2.41
Antrodia macra ✚			
Niemelä (1985)	9.0 × 3.5	9.0 × 3.5	2.57
Gilbertson & Ryvarden (1993)	9.0–12.0 × 3.5–4.5	10.5 × 4.0	2.63
Ryvarden & Melo (2014)	7.2–11.0 × 2.9–4.5	9.1 × 3.7	2.46
	Arithmetic average of references	9.53 × 3.73	2.55
Antrodia mappa ✚			
Overholts & Lowe (1946)	7.0–12.0 × 2.5–3.0	9.5 × 2.75	3.4
Ryvarden & Melo (2014)	8.0–12.0 × 2.0–3.0	10.0 × 2.5	4.0
	Arithmetic average of references	9.75 × 2.63	3.70

understanding of the species relationships than previously known (Ortiz-Santana et al. 2013, Spirin et al. 2013). Our results show that, despite the two basal clades formed by *A. macra* and *A. mappa*, another two main clades can be recognized. One clade, i.e. *Antrodia heteromorpha* complex, constituted by *A. serpens*, *A. heteromorpha*, *A. neotropica* and *Antrodia sp*. Basidiospore morphology in this clade is mostly identical. *Antrodia serpens* and *A. neotropica* grow, so far, exclusively on angiosperm wood, whereas *A. heteromorpha* on both angiosperm and conifer wood. The second clade, which is related to the last, is constituted by *A. favescens* and *A. tanakai*.

Biological and morphological characters of *Antrodia* sensu stricto: As pointed out by Rajchenberg (2011) and James et al. (2013), the combination of biological (*e.g.* type of rot, nuclear behaviour and mating system) and morphological characters have been proven to be strong features to characterize and distinguish genera within polypores, corroborating clades recovered by molecular phylogenetics. *Antrodia* s.l. exhibits normal nuclear behaviour with uni- or binucleate basidiospores that display homothallism or bipolar heterothallism in mating systems (Rajchenberg 2011). So

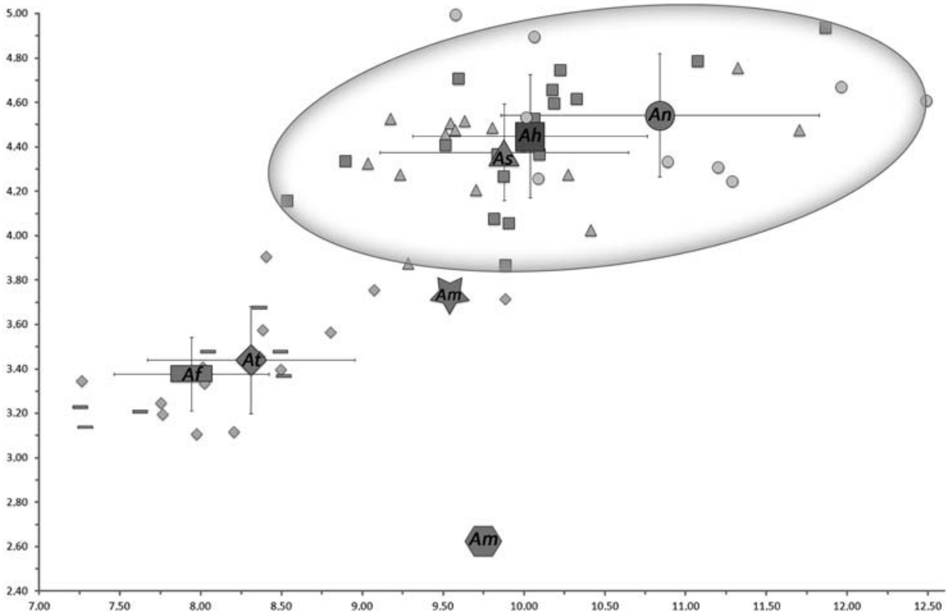

Fig. 4. Comparison of average basidiospore size for specimens and species of *Antrodia* s.s. (see also Table 3). ● = *A. neotropica* (*An*), ■ = *A. heteromorpha* (*Ah*), ▲ = *A. serpens* (*As*), ⬣ = *A. mappa* (*Am*), ★ = *A. macra* (*Am*), – = *A. favescens* (*Af*), ◆ = *A. tanakai* (*At*). Larger symbols represent the arithmetic means of the individuals average. Error bars around larger symbols correspond to Standard Deviation. Shadowed area indicates *A. heteromopha* complex.

far, all species with two nuclei per basidiospore, e.g., *A. heteromorpha* (as *A. albida*), and *A. macra* [as *A. salicina* (Bres.) Niemelä] (Rajchenberg 2011) belong to *Antrodia* s.s. Our results showed that *A. neotropica* presents two nuclei per basidiospore (Fig. 2H), suggesting that it could be a constant feature for *Antrodia* s.s. On the other hand, uninucleate *Antrodia* species, (Rajchenberg 2011) are distributed in different brown-rot genera of the 'core antrodia clade' (Ortiz-Santana et al. 2013, Spirin et al. 2013).

Hyphal system structure. – Detailed analysis of hyphal system in polypores have been used to differentiate genera and species [e.g. *Perenniporia* s.s. Murrill and *Perenniporiella* Decock & Ryvarden (2003), Decock & Stalpers (2006), Robledo et al. (2009)]. Besides the characterization of the hyphal system as dimitic, a detailed morphological analysis, in order to determine the kind of skeletal hyphae, size (length from the septum), branching patterns and distribution throughout basidiome, are important to define *Antrodia* s.s. The presence of skeletal hyphae that penetrate into the hymenium has been reported to occur in several genera of brown-rot polypores (Rajchenberg 2006). Specifically, it is a typical feature for *Daedalea*, in which this kind of hyphae is dominant and a distinct catahymenium can be observed (Rajchenberg 1985, Lindner et al. 2011, Drechsler-Santos et al. 2012). The use of the term "skeletocystidia" for this kind of hyphae in *Antrodia* s.s. should be avoided. The concept of skeletocystidia refers to deuteroplasmatic pseudocystidia, i.e. penetration of the hymenium by differentiated hyphae, as observed in *Stereum* Hill ex Pers. species (Clémençon 2012). Skeletal hyphae in *A. neotropica* are loosely interwoven in the subiculum and more or less arranged in parallel in the trama of the tubes. This pattern of arrangement through basidiomata also has been observed in *Antrodia* s.s. as it has for *A. favescens* and *A. tanakai* (Spirin et al. 2013). However the closest phylogenetic relatives of *A. neotropica,* i.e. *A. heteromorpha* and *A. serpens*, have skeletal hyphae arranged in parallel in the context (Spirin et al. 2013).

It has been suggested that irregular wall thickness of generative hyphae is a specific character present in brown-rot polypores, so far not observed in white-rot polypores (Rajchenberg 1985). This character has been described in *Antrodia* s.l., *Postia* Fr., *Oligoporus* Bref. and *Daedalea* (Rajchenberg 2006, Drechsler-Santos et al. 2012), present in both basidiomata and, typically, in culture. Sometimes these irregular thick-walled generative hyphae are restricted to the basal parts of the basidiomata, mainly in the context areas closest to the substrate or inside the wood (M. Rajchenberg pers. com., G. Robledo pers. observations). Strikingly, this character has not been observed in *Antrodia* s.s., in which generative hyphae are described as thin to evenly slightly thick-walled.

BASIDIA AND BASIDIOSPORE MORPHOLOGY: *Antrodia neotropica* has large clavate basidia (35–50 × 8.5–10 µm). This particular large size of basidia is characteristic for the genus and has been reported in other species (e.g. 27–36 × 6–8.5 µm in *A. heteromopha*, 29–38 × 7–9.5 µm in *A. serpens*). Basidiospore morphology seems to show a pattern for the genus, the supra-apicular depression in combination with the tapering apex on the basidial axis observed in lateral view is a typical feature. This ventral side is defined here as sigmoid (Stalpers 1996), in particular for its double curve shape (Fig. 3A); the term arcuate (arc-like form), previously used in the literature to describe the spores of some *Antrodia* species (Gilbertson & Ryvarden 1986), does not include the definition of the two curves observed in the lateral view. From the dorsi-ventral view, basidiospores are mostly fusoid because of the tapering apexes, subcylindrical to cylindrical (with the thicker part in the middle) to slightly obovoid (with the thicker part displaced to the distal apex). Unfortunately, the different views (side and dorsi-ventral) are not described for other species of *Antrodia* s.s., and basidiospores have been described as ellipsoid. Basidiospores of *Antrodia* s.s. species are mostly thin-walled, however, those of *A. neotropica* are fairly distinct. Detailed observation and characterization of basidiospore morphology, i.e. shapes from distinct points of view, as described by Dominguez de Toledo (1994), should be taken in account as they have been very informative for the taxonomy of other groups of basidiomycetes (Villegas et al. 2005).

COMMENTS ON *ANTRODIA ALBIDA* FROM BRAZIL: *Antrodia albida* (= *A. heteromorpha*) has been recorded frequently for Southeastern Brazil occurring in different ecosystems (Loguercio-Leite & Wright 1991, Meijer 2006, Drechsler-Santos et al. 2008, Leal & Gugliotta 2008, Reck & Silveira 2008, Baltazar & Gibertoni 2009, Trierveiler-Pereira et al. 2009, Motato-Vásquez & Gugliotta 2013, Drechsler-Santos et al. 2014). This fact could have been consequence of the proposed synonymy of *Trametes subcervina* Bres. with *Antrodia albida* (Ryvarden 1988). The study of the holotype of *T. subcervina* (BPI

249300) showed that macro and microscopical features fit well with *Antrodia malicola*. No differences were observed with original reference specimens of *A. malicola* (including ones from type locality, *cfr* additional specimens examined); consequently, *Trametes subcervina* is regarded as heterotypic synonym of *A. malicola*. As evidenced by Ortiz-Santana et al (2013), this species is placed within the 'core antrodia clade' but it does not belong to the *Antrodia* s.s. clade.

Records from Southeastern Brazil have been characterized by having resupinate whitish basidiomata, angular to elongated pores (1–3/mm), dimitic hyphal system and cylindrical (12.5–15 × 3.75–6.25 µm), hyaline, thin-walled and smooth basidiospores (Leal & Gugliotta 2008). Without more detailed morphological and ecological evidence, besides molecular data, this weak morphological concept led us to keep the record as *A. heteromorpha* complex species as definided here (*A. heteromorpha*, *A. serpens* and *A. neotropica*). Actually, as already observed by Drechsler-Santos et al. (2014), most of *A. albida* records from Brazil should be revised and as has been shown by our results, geographical distribution and host specificity should be considered as important features. *Antrodia albida* records on *Baccharis* spp. probably correspond to *A. neotropica* whereas records from *Pinus* L. plantations and records from other substrates should be carefully checked in order to establish an accurate identification.

Key to *Antrodia* sensu stricto species

1 Hyphal system monomitic, skeletal hyphae present in the subiculum of old specimens ... *A. mappa*
1' Hyphal system dimitic throughout all basidiome ... 2

2 Pores 2–4/mm ... *A. macra*
2' Pores larger, 0.5–2/mm ... 3

3 Basidiospores up to 10 µm long ... 4
3' Basidiospores up to13 µm long ... (Antrodia heteromopha complex) 5

4 Basidiomata white to pale cream when fresh, Eurasian distribution ... *A. tanakai*
4' Basidiomata darker (ochraceous or brownish) when fresh, North American distribution ... *A. favescens*

5 On dead branches of Baccharis sp. (Asteraceae), in Brazil (Neotropics) ... *A. neotropica*
5' On other substrates, North Hemisphere ... 6

6 On gymnosperms ... *A. heteromorpha*
6' On angiosperms ... *A. serpens*

Acknowledgments

Authors thank the staff of the Parque Nacional São Joaquim and PPBio Mata Atlântica during the field expeditions; D.H.Costa-Rezende, V.Ferreira-Lopes, C.A.Salvador-Montoya and A.C.Magnago for their support in the field expeditions; Dr. G.Grilli and N.Gomez Montoya for help to improve the text and figures; herbaria mentioned for the loaning of specimens; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for providing a master's scholarship to GKF; Fiocruz for performing the molecular sequencing; PPGFAP/UFSC and BrBOL for partial financing of the research. Mateus A.Reck thanks CAPES (PNPD Institucional 2011 – 23038.007790/2011-93) for scholarship and funding. This study is part of the project Fungos poliporóides (Agaricomycetes) em Santa Catarina – Políporos SC" (Depto. Botânica/ UFSC n° 2011.0182).

References

AMALFI, M. & C. DECOCK 2013: *Fomitiporia castilloi* sp. nov. and multiple clades around *F. apiahyna* and *F. texana* in Meso- and South America evidenced by multiloci phylogenetic inferences. – Mycologia **105**: 873–887.

BERNICCHIA, A., S.P. GORJÓN, P. VAMPOLA, L. RYVARDEN & A. PRODI 2012: A phylogenetic analysis of *Antrodia* s.l. based on nrDNA ITS sequences, with emphasis on rhizomorphic European species. – Mycol. Prog. **11**: 93–100.

BERNICCHIA, A. & L. RYVARDEN 2001: A new *Antrodia* species (Coriolaceae, Basidiomycetes). – Mycotaxon **79**: 57–66.

BALTAZAR, J.M. & T. GIBERTONI 2009: A checklist of the aphyllophoroid fungi (Basidiomycota) recorded from the Brazilian Atlantic Forest. – Mycotaxon **109**: 439–442.

CALDERONI, M., T.N. SIEBER & O. HOLDENRIEDER 2003: *Stereum sanguinolentum*: Is it an amphithallic basidiomycete? – Mycologia **95**: 232–238.

CAMPOS-SANTANA, M., M. AMALFI, G. ROBLEDO, R.M.B. SILVEIRA & C. DECOCK 2014: *Fomitiporia neotropica*, a new species from South America evidenced by multilocus phylogenetic analyses. – Mycol. Prog: doi: 10.1007/s11557-013-0943-1.

CHIU, H. 2007: Phylogenetic analysis of *Antrodia* species and *Antrodia camphorata* inferred from internal transcribed spacer region. – Antonie van Leeuwenhoek **91**: 267–276.

CLÉMENÇON, H. 2012: Cytology and plectology of the Hymenomycetes. – J. Cramer; 520 pp.

CUI, B.K. 2013: *Antrodia tropica* sp. nov. from southern China inferred from morphological characters and molecular data. – Mycol. Prog. **12**: 223–230.

CASTRESANA, J. 2000: Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. – Mol. Biol. Evol. **17**: 540–552.

DARRIBA, D., G.L. TABOADA, R. DOALLO & D. POSADA 2012: jModelTest 2: more models, new heuristics and parallel computing. – Nature Methods **9**: 8–772.

DECOCK, C., A.S. HERRERA-FIGUEROA, G. ROBLEDO & G. CASTILLO 2007: *Fomitiporia punctata* (Basidiomycota, Hymenochaetales) and its presumed taxonomic synonyms in America: taxonomy and phylogeny of some species from tropical/subtropical areas. – Mycologia **99**: 733–752.

DECOCK, C. & L. RYVARDEN 2003: *Perenniporiella* gen. nov. segregated from *Perenniporia*, including a key to neotropical *Perenniporia* species with pileate basidiomes. – Mycol. Res. **107**: 93–103.

DECOCK, C. & J.A. STALPERS 2006: (1708) Proposal to conserve the name *Perenniporia* against *Physisporus* with a conserved type (Basidiomycota). – Taxon **55**: 227–238.

DENTINGER, B.T.M., S. MARGARITESCU & J.M. MONCALVO 2010: Rapid and reliable high throughput methods of DNA extraction for use in barcoding and molecular systematics of mushrooms. – Mol. Ecol. Res. **10**: 628–633.

DEREEPER, A., V. GUIGNON, G. BLANC, S. AUDIC, S. BUFFET et al. 2008: Phylogeny.fr: robust phylogenetic analysis for the non-specialist. – Nucleic Acids Res.: 1–36.

DOMÍNGUEZ DE TOLEDO, L.S. 1994: Suggestions for describing and illustrating fungal spores. – Mycotaxon **52**: 259–270

DOYLE, J.J. & J.L. DOYLE 1987: A rapid isolation procedure for small quantities of fresh tissue. – Phytochemical Bulletim **19**: 11–15.

DRECHSLER-SANTOS, E.R., M.A. CAVALCANTI, C. LOGUERCIO-LEITE & G. ROBLEDO 2012: On Neotropical *Daedalea* species: *Daedalea ryvardenica* sp. – Nova Kurtziana **37**: 65–72.

DRECHSLER-SANTOS, E.R., C. GROPOSO & C. LOGUERCIO-LEITE 2008: Additions to the knowledge of lignocellulolytic Basidiomycetes (Fungi) in forests from Santa Catarina state, Southern Brazil. – Mycotaxon **103**: 197–200.

DRECHSLER-SANTOS, E.R., C. SALVADOR-MONTOYA, D.H. COSTA-REZENDE, F. MAFALDA-FREIRE, G. KAIPPER-FIGUEIRÓ et al. 2014: Macrofungos do Parque Nacional de São Joaquim: Aspectos preliminares sobre a micodiversidade. – In: CASTILHO, P.V., M.T.R.N. OMENA, M.H. TANIWAKI (eds.): Parque Nacional de São Joaquim: Portal do Conhecimento. Editora Santarém: pp. 23–44, São Paulo

GILBERTSON, R.L. & L. RYVARDEN 1986: North American polypores. Vol. 1. *Abortiporus-Lindtneria*. Fungiflora, 433 p., Oslo.

GÓES-NETO, A., C. LOGUERCIO-LEITE & R.T. GUERRERO 2005: DNA extraction from frozen field-collected and dehydrated herbarium fungal basidiomata: performance of SDS and CTAB-based methods. – Biotemas **18**: 19–32.

GUINDON, S. & O. GASCUEL 2003: A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. – Systematic Biology **52**: 696–704.

JAMES, T.Y., S. SUN, W. LI, J. HEITMAN, H.C. KUO et al. 2013: Polyporales genomes reveal the genetic architecture underlying tetrapolar and bipolar mating systems. – Mycologia: doi: 10.3852/13-162.

KATOH, K. & D.M. STANDLEY 2013: MAFFT. Multiple sequence alignment software 7: improvements in performance and usability. – Mol. Bio. Evol. **30**: 772–780.

KEARSE, M., R. MOIR, A. WILSON, S. STONES-HAVAS, M. CHEUNG et al. 2012: Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. – Bioinformatics **28**: 1647–1649.

KIM, S.Y., H.S. JUNG, K.S. KO & H.S. JUNG 2003: Phylogenetic analysis of *Antrodia* and related taxa based on partial mitochondrial SSU rDNA sequences. – Antonie van Leeuwenhoek **83**: 81–88.

LEAL, G.R. & A.M. GUGLIOTTA 2008: Criptógamos do Parque Estadual das Fontes do Ipiranga, São Paulo, SP. Fungos, 9: Meripilaceae. – Hoehnea **35**: 99–110.

LINDNER, D.L., L. RYVARDEN & T.J. BARONI 2011: A new species of *Daedalea* (Basidiomycota) and a synopsis of core species in *Daedalea* sensu stricto. – North American Fungi **6**: 1–12.

LOGUERCIO-LEITE, C. & J.E. WRIGHT 1991: Contribution to a biogeographical study of the Austro-American xylophilous polypores (Aphyllophorales) from the Santa Catarina Island, SC., Brazil. – Mycotaxon **41**: 161–166.

MEIJER, A.A.R. de 2006: Preliminary list of the macromycetes from the Brazilian state of Paraná. – Bol. Mus. Bot. Munic. **68**: 1–55.

MILLER, M.A., W. PFEIFFER & T. SCHWARTZ 2010: Creating the CIPRES science gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE). 14 Nov 2010, New Orleans, Louisiana p. 1–8.

MOTATO-VÁSQUEZ, V. & A.M. GUGLIOTA 2013: Polypores from an Atlantic rainforest area in southeast Brazil: resupinate species. – Braz. J. Bot.: doi 10.1007/s40415-013-0031-4.

MUNSELL color 1975: Munsell soil Colors Charts. – Baltimore.

NIEMELÄ, T. 1985: On Fennoscandian polypors 9. *Gelatoporia* n. gen. and *Tyromyces canadensis*, plus notes on *Skeletocutis* and *Antrodia*. – Karstenia **25**: 21–40.

NÚÑEZ, M. & L. RYVARDEN 2001: East Asian polypores 2. – Syn. Fung. **14**: 170–522.

OVERHOLTS, L.O. & J.L. LOWE 1946: New species of *Poria*. – Mycologia **38**: 202–212.

ORTIZ-SANTANA, B., D.L. LINDNER, O. MIETTINEN, A. JUSTO & D.S. HIBBETT 2013: A phylogenetic overview of the antrodia clade (Basidiomycota, Polyporales). – Mycologia **105**: 1391–1411.

RAJCHENBERG, M. 1985: On *Trametes aethalodes* and other species of *Daedalea* (Polyporaceae). – Canadian Journal of Botany **64**: 2130–2135.

RAJCHENBERG, M. 1987: Type studies of Polyporaceae (Aphyllophorales) described by J. Rick. – Nordic. Journal of Botany **7**: 553–568.

RAJCHENBERG, M. 2006: Polypores (Basidiomycetes) from the Patagonian Andes Forests of Argentina. – Biblio. Mycol. Band. 201. J. Cramer, 300 p.

RAJCHENBERG, M. 2011: Nuclear behavior of the mycelium and the phylogeny of Polypores (Basidiomycota). – Mycologia **103**: 677–702.

RAJCHENBERG, M. & J.E. WRIGHT 1987: Type studies of Corticiaceae and Polyporaceae (Aphyllophorales) described by C. Spegazzini. – Mycologia **79**: 246–264.

RAJCHENBERG, M., S.P. GORJÓN & M.B. PILDAIN 2011: The phylogenetic disposition of *Antrodia* s.l. (Polyporales, Basidiomycota) from Patagonia, Argentina. – Aust. Syst. Bot. **24**: 111–120.

RAMBAUT, A. & A.J. DRUMMOND 2007: Tracer 1.4. Available from http://beast.bio.ed.ac.uk/Tracer

RECK, M.A. & R.M.B. SILVEIRA 2008: Polyporales (Basidiomycota) no Parque Estadual de Itapuã, Viamão, Rio Grande do Sul. – Rev. Bras. de Bio. **6**: 301–314.

ROBLEDO, G., M. AMALFI, G. CASTILLO, M. RAJCHENBERG & C. DECOCK 2009: *Perenniporiella chaquenia* sp. nov. and further notes on *Perenniporiella* and its relationships with *Perenniporia* (Poriales, Basidiomycota). – Mycologia **101**: 657–673.

RONQUIST, F. & J.P. HUELSENBECK 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. – Bioinformatics **19**: 1572–1574, doi: 10.1093/bioinformatics/btg180

RYVARDEN, L. 1988: Type studies in the Polyporaceae – 20. Species described by G. Bresadola. – Mycotaxon **33**: 303–327.

RYVARDEN, L. 1991: Genera of Polypores, nomenclature and taxonomy. – Syn. Fung. **5**: 1–363.

RYVARDEN, L. & R.L. GILBERTSON 1993: European polypores part 1. – Syn. Fung. **6**: 1–387.

RYVARDEN, L. & I. MELO 2014: Poroid fungi of Europe. – Syn. Fung. **31**: 1–455.

SPIRIN, V., O. MIETTINEN, J. PENNANEN, H. KOTIRANTA & T. NIEMELA 2012: *Antrodia hyalina*, a new polypore from Russia, and *A. leucaena*, new to Europe. – Mycol. Prog. **12**: 53–61.

SPIRIN, V., J. VLASÁK, T. NIEMELA & O. MIETTINEN 2013: What is *Antrodia* sensu stricto. – Mycologia **105**: 1555–1576.

STALPERS, J.A. 1996: The aphyllophoraceous fungi II. Keys to the species of the Hericiales. – Studies in Mycology **40**: 1–185.

STAMATAKIS, A. 2014: RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. – Bioinformatics **30**: 1312–1313.

TAMURA, K., G. STECHER, D. PETERSON, A. FILIPSKI & S. KUMAR 2013: MEGA 6: molecular evolutionary genetics analysis. – Mol. Biol. Evol. **30**: 2725–2729.

TEIXEIRA, A.R. 1995: Método para estudo das hifas do basidiocarpo de fungos poliporaceos. – Manual n° 6. São Paulo, Instituto de Botânica; 20p.

THIERS, B. 2014 (continuously updated): Index Herbariorum: A global directory of public herbaria and associated staff. – New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/.

TRIERVEILER-PEREIRA, L., J.M. BALTAZAR & C. LOGUERCIO-LEITE 2009: Santa Catarina Island mangroves 4 xylophilous basidiomycetes. – Mycotaxon **109**: 107–110.

VILGALYS, R. & M. HESTER 1990: Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several species of *Cryptococcus*. – Journal Bacteriol. **172**: 4238–4246.

VILLEGAS, M., J. CIFUENTES & A.E. TORRES 2005: Sporal characters in Gomphales and their significance for phylogenetics. – Fungal Diversity **18**: 157–175.

YU, Z.H., S.H. WU, D.M. WANG & C.T. CHEN 2010: Phylogenetic relationships of *Antrodia* species and related taxa based on analyses of nuclear large subunit ribosomal DNA sequences. – Bot. Stud. **51**: 53–60.

Manuscript submitted January14, 2016; accepted February 1, 2016.