



## ***Aegis boa* (Polyporales, Basidiomycota) a new neotropical genus and species based on morphological data and phylogenetic evidences**

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### **Abstract**

The new genus, *Aegis* Gómez-Montoya, Rajchenb. & Robledo, is described to accommodate the new species *Aegis boa* based on morphological data and phylogenetic evidences (ITS – LSU rDNA). It is characterized by a particular monomitic hyphal system with thick-walled, widening, inflated and constricted generative hyphae, and allantoid basidiospores. Phylogenetically *Aegis* is closely related to *Antrodiella aurantilaeta*, both species presenting an isolated position within Polyporales into Grifola clade. The new taxon is so far known from Yungas Mountain Rainforests of NW Argentina.

**Key words** – *Grifola* – Neotropical polypores – *Tyromyces*

### **Introduction**

Polypore diversity of NW Argentina was reviewed by Robledo & Rajchenberg (2007). The area is mainly dominated by the Yungas Rainforests, a tropical and subtropical cloud montane forest developed on the oriental slope along the Andes that, in Argentina, harbours 50% of the country's biodiversity (Brown et al. 2001). Little information has been produced in the last years on this group of fungi, with the exception to those associated to the above timber-line *Polylepis* (Rosaceae) woodlands formation (Robledo et al. 2006) and some species in the Hymenochaetales (Amalfi et al. 2014). During surveys in this biogeographic formation specimens of a *Tyromyces* like species were found. On the basis of morphological features of their basidiomata relationships with *Tyromyces chioneus* (Fr.) P. Karst. or with *Skeletocutis amorpha* (Fr.) Kotl. & Pouzar and their respective related species in the *Tyromyces* clade (Zhao & Cui 2014, Wu et al. 2016) were expected. Nevertheless, molecular analyses suggested that these specimens group conforming an independent lineage strongly related to *Antrodiella aurantilaeta* (Corner) T. Hatt. & Ryvarden.

The aim of this paper is to describe a new genus and species to accommodate these specimens, based on morphological and molecular studies.

### **Materials & Methods**

## Morphological studies

Studied specimens are deposited at FCOS, Micoteca of FungiCosmos Foundation. Macroscopic observations follow Robledo & Urcelay (2009). Microscopic observations were made in Melzer's reagent (IKI), 3% potassium hydroxide (KOH), phloxine, lactic acid Cotton Blue (CB; CB+ = cyanophilous) and Cresyl blue (CrB; CrB+ = metachromatic). Number of pores/mm and measurements of microscopic structures were based on a sampling of thirty measures per structure (n = 30). Basidiospore shape description follows Ferreira-Lopes et al. (2016). The following abbreviations are used for basidiospores measurements:  $\bar{X}$  = arithmetic average,  $Q$  = ratio length/width,  $\bar{Q}$  = arithmetic average of  $Q$ . The hyphal system structure was analyzed using a NaOH in which handmade sections were incubated in warm (50°C) NaOH 3% solution during at least 24 hours and later mounted in NaOH 3% plus Congo red (Gómez-Montoya et al. 2017).

## DNA extraction, amplification and sequencing

We followed Ferreira-Lopes et al. (2016) for DNA extraction from dry basidiomata. The primer pairs ITS8-F / ITS6-R (Dentinger et al. 2010) were used to amplify the ITS regions and LROR / LR5 (Vilgalys & Hester 1990, Cubeta et al. 1991) to amplify the LSU regions. PCR conditions used followed Gómez-Montoya et al. (2017).

## Phylogenetic analyses

ITS and LSU sequences newly generated in this study were deposited in GenBank (Table 1). DNA sequences were aligned using Muscle v.3.6 (Edgar 2004), later manually inspected and corrected using BioEdit V7.0.1 editor (Hall 1999). Indels were coded as binary characters using the software Fast Gap 1.2 (Borchsenius 2009). The best fit model of nucleotide evolution to the dataset was selected by AIC (Akaike Information Criterion) using jModelTest2 v.1.6 (Darriba et al. 2012) in the CIPRES Science Gateway platform (Miller et al. 2010). Bayesian analysis was performed by using MrBayes version 3.2.6 (Ronquist et al. 2011) with 5 million Metropolis-coupled Markov chain Monte Carlo (MCMCMC) generations with four chains, and two independent runs, the analysis was run for 5 million generations, after a burn-in of 20000 of the trees, nodes support was tested by posterior probabilities (PP), obtained from a 50% majority rule consensus.

Individual datasets were combined in a Nexus file comprising 101 entries representing 82 putative species. Nodes with Bayesian Posterior Probability (BPP)  $\geq 0.95$  were considered strongly supported, while nodes with  $0.94 \geq \text{BPP} \geq 0.7$  were considered moderately supported.

**Table 1** List of taxa and sequences used in the phylogenetic analyses and their corresponding GenBank numbers. O= Outgroup; T= Type. Newly generated sequences are indicated in bold.

Species	Voucher reference	GenBank Accession Numbers	
		ITS	LSU
<i>Abortiporus biennis</i>	FD-319	KP135300	KP135195
<b><i>Aegis boa</i></b>	Robledo 1384	<b>MF919318</b>	<b>MF377539</b>
	Robledo 1685 (T)	<b>MF377538</b>	<b>MF377540</b>
<i>Antrodia heteromorpha</i>	Dai12755	KP715306	KP715322
<i>Antrodia hyalina</i>	Miettinen_X1322	JQ700283	JQ700283
<i>Antrodia tanakae</i>	Yuan1106	KP715313	KP715329
<i>Antrodiella aurantilaeta</i>	Yuan5956	KC485523	KC485540
	Yuan20	FJ613653	-
	voucher 2529	KY769581	-
<i>Antrodiella faginea</i>	Larsson11977	JN710514	JN710514
<i>Antrodiella foliaceodentata</i>	MiettinenX1238	JN710515	JN710515
<i>Antrodiella ichnusana</i>	MiettinenX131	JN710516	JN710516
<i>Antrodiella lactea</i>	Yuan5757	KC485532	KC485550

**Table 1** Continued.

Species	Voucher reference	GenBank Accession Numbers	
		ITS	LSU
<i>Antrodiella nanospora</i>	Yuan5755	KC485531	KC485549
<i>Antrodiella romellii</i>	MiettinenX154	JN710520	KC485543
<i>Antrodiella semisupina</i>	KHL11977	JX109842	JX109842
<i>Antrodiella stipitata</i>	strainFD-136	KP135314	KP135197
<i>Bjerkandera adusta</i>	BRNM 77194	KT305935	KT305935
<i>Ceriporia lacerata</i>	FP-55521T	KP135024	KP135202
<i>Ceriporia purpurea</i>	KKN-223	KP135044	KP135203
<i>Ceriporia aurantiocarnescens</i>	Yuan2066	JX623902	JX644042
<i>Ceriporiopsis aneirina</i>	Dai 12657	KF845952	KF845945
	HHB-15629	KP135023	KP135207
<i>Ceriporiopsis gilvescens</i>	BRNM 667882	FJ496685	FJ496719
	Yuan 2752	KF845953	KF845946
<i>Ceriporiopsis guidella</i>	HUBO 7659	FJ496687	FJ496722
<i>Ceriporiopsis pseudogilvescens</i>	Niemelä 7447	FJ496680	FJ496700
<i>Climacocystis borealis</i>	KHL13318	JQ031126	JQ031126
<i>Climacodon septentrionalis</i>	AFTOL-ID 767	AY85408	AY684165
<i>Corioloropsis caperata</i>	LE(BIN)-0677	AB158316	AB158316
<i>Dacryobolus montanus</i>	Yuan5758	KC344412	KC344413
<i>Daedalea quercina</i>	Miettinen12662	JX109855	JX109855
<i>Earliella scabrosa</i>	PR1209	JN165009	JN164793
<i>Fomitopsis pinicola</i>	AFTOL-ID770	AY854083	AY684164
<i>Gelatoporia subvermispora</i>	strain_FD-354	KP135312	KP135212
<i>Grammothelopsis subtropica</i>	Cui9041	JQ845096	JQ845099
<i>Grifola frondosa</i>	zw-clarku005	AY218415	AY218413
	AFTOL-ID 701	AY854084	AY629318
<i>Grifola sordulenta</i>	AFTOL-ID562	AY854085	AY645050
<i>Hornodermoporus martius</i>	Cui4055	KX081082	KX081145
<i>Hypochnicium lydoniae</i>	NL041031	JX124704	JX124704
<i>Junghuhnia nitida</i>	isolate3135	JN710560	JN710560
<i>Loweomyces fractipes</i>	RP 197	KP859304	KP859309
	X1250	JN710568	JN710568
<i>Loweomyces spissus</i>	MCW 468/13	KX378867	KX378867
	MCW 471/13	KX378868	KX378868
<i>Loweomyces tomentosus</i>	MCW 366/12	KX378870	KX378870
<i>Loweomyces wynneae</i>	DD 846/08	KX378865	KX378865
<i>Melanoporia nigra</i>	isolate_X1735	KC543172	KC543172
<i>Meripilus giganteus</i>	FP-135344	KP135307	KP135228
<i>Microporus xanthopus</i>	Cui8242	JX290074	JX290071
<i>Mycoacia fuscoatra</i>	KHL13275	JN649352	JN649352
<i>Mycoacia nothofagi</i>	KHL13750	GU480000	GU480000
<i>Mycorrhaphium adustum</i>	isolate8024	JN710573	JN710573
<i>Obba valdiviana</i>	Gates FF484	HQ659236	HQ659236
<i>Obba rivulosa</i>	KCTC6892	FJ496693	FJ496710
<i>Oligoporus balsameus</i>	Cui8207	KF699118	KJ684974
<i>Oligoporus lacteus</i>	Cui12206	KR605820	KR605763
<i>Oligoporus guttulatus</i>	L-8050	KC585360	KC585189
<i>Oligoporus rennyi</i>	TN7389(H)	JX109849	JX109849
	KEW57	AY218416	AF287876

**Table 1** Continued.

Species	Voucher reference	GenBank Accession Numbers	
		ITS	LSU
<i>Perenniporia medulla-panis</i>	KHL11943	JX109840	JX109840
<i>Perenniporiella neofulva</i>	MUCL45091	FJ411080	FJ393852
<i>Phanerochaete chrysosporium</i>	BKM-F-1767	HQ188436	GQ470643
<i>Phanerochaete velutina</i>	LE_RUS298547	KP994360	KP994385
<i>Phlebia acerina</i>	Strain-FCUG568	AF141615	AF141615
<i>Phlebia rufa</i>	FCUG2397	AF141628	AF141628
	FBCC297	LN611092	LN611092
<i>Phlebia setulosa</i>	PH5105	GU461313	GU461313
	HHB-6891	KP135382	KP135267
<i>Phlebia subserialis</i>	FCUG 1434	AF141631	AF141631
<i>Phlebia tremellosa</i>	ES2008-2(GB)	JX109859	JX109859
	F15198	DQ384584	DQ384584
<i>Phlebia unica</i>	KHL 11786	EU118657	EU118657
<i>Piloporia sajanensis</i>	HK 17250	JX109853	JX109853
	Manninen 2733a	HQ659239	HQ659239
<i>Podoscypha multizonata</i>	Jahn 751012	EU118663	EU118663
<i>Podoscypha venustula</i>	LR_40821	JX109851	JX109851
<i>Polyporus tuberaster</i>	WD2382	AB474086	AB368104
<i>Pouzaroporia subrufa</i>	BRNM710172	FJ496662	FJ496724
	BRNM710164	FJ496661	FJ496723
<i>Postia alni</i>	MiettinenX1400	KC595932	KC595932
<i>Postia caesia</i>	HHB-14891	KC585376	KC585206
<i>Postia floriformis</i>	Cui10292	KM107899	KM107904
<i>Postia subcaesia</i>	MiettinenX1340	KC595944.	KC595944.
<i>Rickiopora latemarginata</i>	isolate RP 56	KU521768	KU521768
	isolate RP 58	KU521769	KU521769
	isolate RP 110	KU521770	KU521770
<i>Sebipora aquosa</i>	Miettinen8680	HQ659240	HQ659240
<i>Skeletocutis amorphia</i>	Miettinen 110381	FN907913	FN907913
<i>Steccherinum fimbriatum</i>	KHL11905	EU118668	EU118668
<i>Steccherinum ochraceum</i>	KHL11902	JQ031130	JQ031130
<i>Stereum hirsutum</i> (O)	KUC20121102-16	KJ668449	KJ668300
	NBRC 6520	AB733150	AB733325
<i>Trametopsis aborigena</i>	Robledo1236	KY655336	KY655338
	Robledo1238	KY655337	KY655339
<i>Trametopsis brasiliensis</i>	Meijer 3637	JN710510	JN710510
<i>Trametopsis cervina</i>	PRM 900574	AY684175	AY855907
	TJV_93_216T	JN165020	JN164796
<i>Tyromyces chioneus</i>	Cui 10225	KF698745	KF698756
	Miettinen 7487(H)	HQ659244	HQ659244
<i>Xanthoporus syringae</i>	X339	JN710606	JN710606

## Results

### Molecular analyses

ITS and LSU dataset comprised 101 taxa. *Stereum hirsutum* was used as outgroup. The alignment of the ITS region included 1024 positions including gaps, whereas LSU region included 880 positions including gaps. GTR+I+G was chosen as the best-fit substitution model to the ITS

dataset in the Bayesian Inference, with the following base frequencies A (0.2640), C (0.1829), G (0.2883), T (0.2648), proportion of invariable sites of 0.5020 and a gamma distribution shape parameter of 0.6030. The nucleotide substitution rates estimated according to this model were A/C=0.9728, A/G=4.5720 A/T=1.5535, C/G=0.5283, C/T=9.9187 and G/T=1.0000. GTR+I+G was chosen as the best-fit substitution model to the LSU dataset in the Bayesian Inference, with the following base frequencies A (0.2377), C (0.277), G (0.2199), T (0.3348), proportion of invariable sites of 0.2670, and a gamma distribution shape parameter of 0.8700. The nucleotide substitution rates estimated according to this model were A/C=1.4525, A/G=3.2371, A/T=1.7110, C/G=0.6561, C/T=4.4622, G/T=1.0000. The two independent runs of Bayesian analysis converged to stable values after 5000000 generations, a total of 20000 sampled trees were discarded as burn-in. The remaining trees were used to construct the 50% majority-rule consensus tree (Figure 1).

Our phylogenetic analysis recovered a similar topology of recent works, where several major recognized clades are strongly supported (e.g. Binder et al. 2013, Zhao et al. 2014, 2015, Wu et al. 2016). The new specimens grouped in a strongly supported clade (BPP=1.0) constituting an independent phylogenetic lineage that is described below as a new genus and species: *Aegis boa*. The new genus clustered together with *Antrodiella aurantilaeta* with a maximum support (BPP=1.0). Both species grouped with *Grifola* with a moderate support (BPP=0.79).

### **Taxonomy**

***Aegis* Gómez-Montoya, Rajchenb. & Robledo, gen. nov.**

Mycobank: MB821875

Etymology – from Greek “aegis”, shield of Pallas Athena, Greek goddess of wisdom and science, which was adorned with the Medusa Gorgon head. In reference to the general shield shape of the basidiomata and the hyphal system mimicking Medusa’s head serpents.

Basidiomata annual, resupinate, effused-reflexed to pileate; pileal surface glabrous to tomentose, usually white to light ivory, azonate; pores round, 5–6 per mm. Context thin, fibrous, white. Hyphal system monomitic with thin- to thick-walled clamped generative hyphae, metachromatic, IKI–. Basidia clavate, with four sterigmata. Basidiospores allantoid hyaline, thin-walled, IKI–.

***Aegis boa* Gómez-Montoya, Rajchenb. & Robledo, sp. nov.**

Figs 2–5

Mycobank: MB821876

Etymology – from Latin “*boa*”= large snake. In reference to the widened and constricted generative hyphae that recall *Boa constrictor*.

Holotype – Argentina, Salta, Dpto. Anta, Parque Nacional El Rey, Cerro El Chañar, 1950 m a. s. l., 24° 45’ 46.8” S, 64° 42’ 58.1” W, growing on dead fallen branch, 28 May 2007, *Robledo 1685* (FCOS138, HOLOTYPE, ITS: MF377538, LSU: MF377540).

Basidiomata annual, resupinate to effused-reflexed, with a short reflexed portion; effused portion elliptical, up to 3 × 1.5 × 0.3 cm, pileus elongated, applanate to triquetrous, up to 1 cm wide. Pileal surface white, light beige toward the base and against the substrate, concentrically sulcate, apparently glabrous but finely velutinate under the lens. Margin whitish to light grey, round, incurved upon drying, up to 0.5 mm thick in the effused part. Pore surface whitish. Pores rounded irregular, 5–6 per mm; dissepiments entire. Context homogeneous, whitish to cream, fibrous, up to 0.1 cm thick. Tubes up to 0.2 cm long.

Hyphal system monomitic; generative hyphae with clamps, IKI–, CB–, metachromatic. The context mostly composed of thin-walled, hyaline hyphae, 2–6 µm wide. The trama dominant by notoriously thick hyphae, 6–11 µm wide, hyaline and evenly thick-walled with a wide lumen to slightly yellowish and strongly thick-walled with a capillary lumen to subsolid; often presenting notorious wall-thickenings at the clamps, where lateral subsolid branches observed. Hyphae with strongly thickened walls occurring intercalary (between hyphae of walls not so thickened) or

terminal, often presenting particular widening, inflated portions with lacunar lumen and constrictions. Dissepiment hyphae bearing very small, polymorphic and angular crystals.

Basidia clavate, with a basal clamp connection, hyaline, thin-walled,  $14\text{--}16 \times 4\text{--}5 \mu\text{m}$ , with four sterigmata. Basidiospores allantoid in equatorial lateral view, cylindrical, in equatorial adaxial view, smooth, hyaline, thin-walled, IKI–,  $(4.0\text{--}) 4.0\text{--}4.8(\text{--}5.0) \times (1.0\text{--})1.2\text{--}2(\text{--}2.0) \mu\text{m}$ ,  $\bar{X} = 4.2 \times 1.7 \mu\text{m}$ ,  $Q = 2\text{--}4$ ,  $\bar{Q} = 2.6$ .

Distribution – Known from Yungas Mountain Rainforests in NW Argentina.

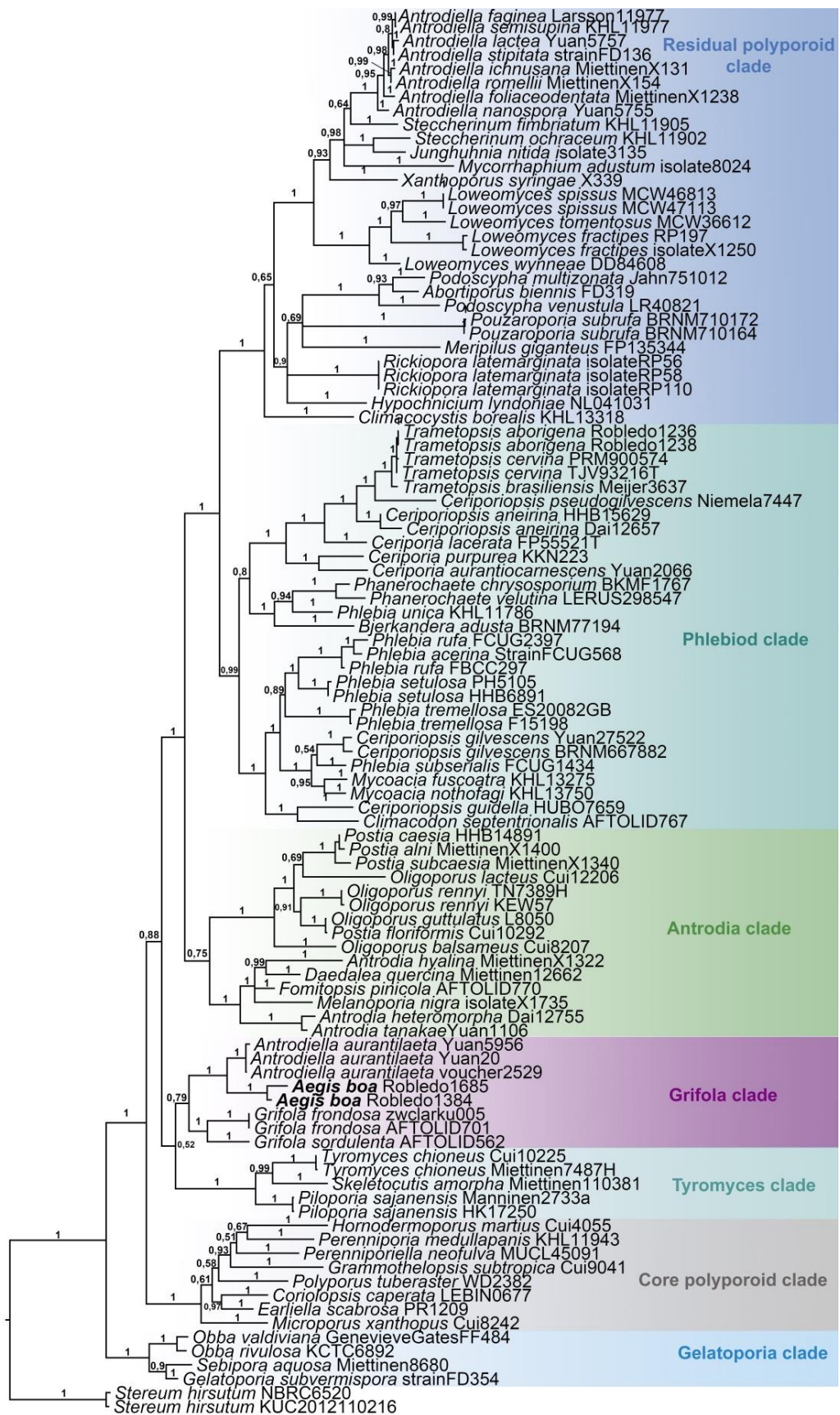
Additional material studied – Argentina, Salta, Dpto. Sta. Victoria, Parque Nacional Baritú, Nogales, between Lipeo and Baritú towns, 1653 m. a. s. l.,  $22^\circ 27' 20.8''$  S,  $64^\circ 44' 34.5''$  W, growing on dead fallen branch, 08 May 2007, *Robledo 1384* (FCOS137).

## Discussion

*Aegis boa* is characterized microscopically by a monomitic hyphal system with clamp connections and particular thick-walled hyphae that presents inflated and widened portions and constrictions, and allantoid basidiospores. Generative hyphae are thin-walled or, more commonly, have slightly thickened walls with a wide lumen. Many hyphae present particular thick-walled clamp connections from where a lateral ramification frequently occurs (Fig. 4). Widened hyphae have very thickened, yellowish walls, with a capillary lumen that closes in the constrictions. Inflated hyphae present moderately thickened walls and a lacunar lumen. Widened portions of generative hyphae are noticeably and easily observed when a thin section is mounted in the light microscope, giving the impression that the material presents vesicles. These hyphae are commonly terminal with rounded apices of thickened to subsolid walls; occasionally they occur in intercalary hyphae, between hyphae with slightly thickened walls. This combination of morphological characters does not match any other polypore genus described so far. In some way, macro- and micromorphological features of *A. boa* are reminiscent of *Tyromyces chioneus* and other *Skeletocutis* Kotl. & Pouzar species in the ‘*Tyromyces* clade’, such as *Skeletocutis amorpha*. The typical crystals of *Skeletocutis*, and the diagnostic branched generative hyphae of *T. chioneus* are, though, absent in *Aegis*.

The phylogenetic reconstruction showed that the closest relative of *A. boa* is *A. aurantilaeta*. However, they present morphological differences. *Antrodiella aurantilaeta* develops orange to orange yellow basidiomata and present ellipsoid basidiospores (Corner 1989, Yuan 2013). In addition, *A. aurantilaeta* has a distinctly dimitic hyphal system with long and more or less uniform skeletal hyphae, and distributed in Aaia (Corner 1989, Dai 2012). Both species group with *Grifola* Gray with a moderately support (BPP=0.79). *Grifola* differs morphologically by developing typically multipileate, stipitate or sessile basidiomata, and ovoid to ellipsoid basidiospores. *Grifola* was recovered recurrently with an isolated position in the phylogeny of the polypores (Hibbett & Binder 2002, Binder et al 2013) constituting a family by itself (Justo et al. 2017). The closest relative of *Grifola*, *A. aurantilaeta*, was evidenced and confirmed recently (Yuan 2013, Justo et al. 2017).

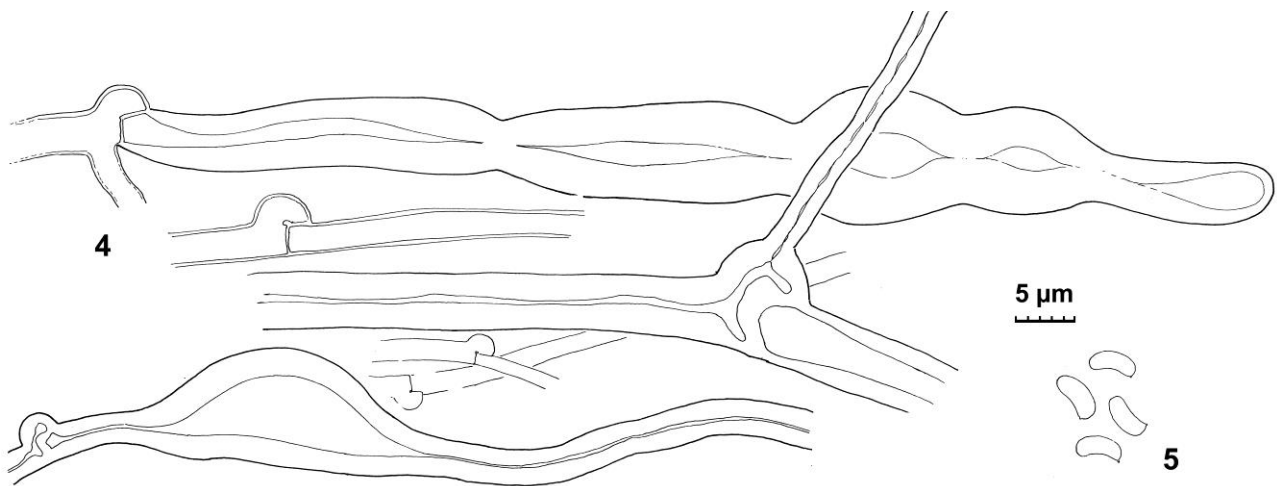
Our phylogenetic analysis recovered the general topology of previous works, with *Grifola*, *A. aurantilaeta* and *Aegis* presenting an isolated position, here called ‘*Grifola*’ clade. Further studies, sampling of species and specimens, and more phylogenetic markers are needed to elucidate whether *A. aurantilaeta* may be congeneric with *A. boa*, and whether both species are part of *Grifolaceae*, currently including only just *Grifola* (Justo et al. 2017). The importance of the inclusion of species and specimens from tropical regions of the world for the interpretation of the phylogenetic scenario of the polypores is evidenced.



**Figure 1** – Strict consensus tree from Bayesian inference of the combined ITS-LSU dataset illustrating the phylogenetic relationships of *Aegis boa* within Polyporales. The new species from which new sequences were obtained in this work are in boldface.



**Figures 2–3** – *Aegis boa*, macroscopic features (Robledo 1685, FCOS138, Holotype). 2 General view of pore surface. 3 Longitudinal section, showing context and tubes. Pictures are copyright of G. Robledo.



**Figures 4–5** – *Aegis boa*, microscopic features (Robledo 1685, FCOS138, Holotype). 4 Generative hyphae. 5 Basidiospores equatorial lateral view. Drawings by G. Robledo.

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