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Taxonomic notes on *Pycnothelia* Dufour and *Gymnoderma* Nyl. (Cladoniaceae) in Madagascan Region

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ABSTRACT
This study was focused on two species of lichen-forming fungi from Madagascan Region whose taxonomy has been controversial over the years, *Cladonia mascarena* Nyl. and *Heterodea madagascarea* Nyl. While some authors considered *C. mascarena* to belong to *Cladonia,* others place it in *Pycnothelia* Dufour. In this study three loci (ITS rDNA, *rpb2* and *ef1α*) were used to determine the phylogenetic placement of *C. mascarena*. Our results show that it belongs to *Pycnothelia* and the combination *Pycnothelia mascarena* (Nyl.) Nyl. is substantiated. In addition, a key to the genus *Pycnothelia* is provided. The morphological study of new specimens of *Gymnoderma coccocarpum* Nyl. and *H. madagascarea* concluded that these taxa belong to a same species, confirming the extension of *Gymnoderma* Nyl. to Africa. The overlooked genus *Baeoderma* Vain. is regarded as a synonym of *Gymnoderma,* and its type species *Baeoderma madagascareum* (Nyl.) Vain. is referred to *G. coccocarpum*.

KEY WORDS
Cladoniaceae,
lichen-forming fungi,
genus concepts,
phylogeny,
Réunion.

RÉSUMÉ
Notes taxonomiques sur Pycnothelia *Dufour et* Gymnoderma *Nyl. (Cladoniaceae) dans la région malgache.*
Cette étude est axée sur deux espèces de champignons formant des lichens de la région malgache dont la taxonomie a été controversée au fil des ans, *Cladonia mascarena* Nyl. et *Heterodea madagascarea* Nyl. Si certains auteurs ont considéré que *C. mascarena* appartenait à *Cladonia*, d'autres la situeraient à *Pycnothelia* Dufour. Dans cette étude, le placement phylogénétique de *C. mascarena* est abordé à l'aide de trois marqueurs génétiques (ADNr de ITS, *rpb2* et *ef1α*). Nos résultats montrent qu'il appartient à *Pycnothelia* et que la combinaison *Pycnothelia mascarena* (Nyl.) Nyl. est justifiée. Une clé du genre Pycnothelia est fournie. L'étude morphologique de nouveaux spécimens de *Gymnoderma coccocarpum* Nyl. et de *H. madagascarea* a permis de conclure que les deux taxons appartenaient à une même espèce, ce qui confirme l'extension du *Gymnoderma* Nyl. à l'Afrique. Le genre négligé *Baeoderma* Vain. est considéré comme un synonyme de *Gymnoderma* et son espèce type *Baeoderma madagascareum* (Nyl.) Vain. est appelée *G. coccocarpum.*

MOTS CLÉS
Cladoniaceae,
champignon lichénisant,
concepts de genre,
phylogénie,
Réunion.

INTRODUCTION

The Madagascan Floristic Region (Madagascar and surrounding archipelagos of the Mascarenes, Seychelles and Comoros) is one of the world's biodiversity hotspots (Mittermeier *et al.* 2011), holding the highest concentration known of endemic species belonging to several taxonomic groups, such as plants, amphibians or mammals (Myers *et al.* 2000). This is the reason why the Madagascan Region has attracted the attention of a large number of biologists. A variety of factors are responsible for the high degree of endemism: some islands have never been connected to continental masses, they are extremely rich in habitats, since they shelter different plant formations (semi-dry sclerophyllous forests, tropical lowland rainforests, cloud forest and subalpine scrub) and high mountains are present in them (Piton des Neiges in Réunion is the highest mountain on islands of the Indian Ocean). In addition, some patches of the original forests are still preserved untransformed, reaching in Réunion up to the 25% of the total surface (Thébaud *et al.* 2009). Nevertheless, our knowledge of the biodiversity of some groups of organisms there is still scarce, such as the lichens. Although numerous lichenologists have focused their attention on the diversity of the Mascarenes and nearby regions (e.g. Nylander 1859; Vainio 1898, 1901; Crombie 1876; Jatta 1905; Lindau 1908; Aptroot 1990, 1991; David & Hawksworth 1995; Schumm & Aptroot 2010; Boom *et al.* 2011), some areas have been poorly collected, particularly the dry tropical regions (Aptroot 2016), while large collections of lichens remain unidentified (Boom *et al.* 2011) because of the complicated taxonomy of many groups. Thus far nearly 600 lichen species have been reported for the Mascarenes (Boom *et al.* 2011) and 500 species for Madagascar (Aptroot *et al.* 2016). Des Abbayes (1956, 1959, 1961a, 1961b, 1966) intensively studied the area and some of his works were dealing with the family Cladoniaceae (des Abbayes 1947, 1948). Afterwards, other authors have also studied the Cladoniaceae in this region (Ahti & Aptroot 1992; Ahti *et al.* 1987; Stenroos 1991; Sipman 2011). Nowadays 41 species of Cladoniaceae are known from the Madagascan Region (Ahti, unpublished), with three genera represented, *Cladia* Nyl., *Cladonia* F.H.Wigg and *Heterodea* Nyl. (Boom *et al.* 2011). *Cladonia*, in general, has a low endemicity degree (Ahti 2000), but in Madagascar and Réunion a considerable number of endemic species exists. One of them is *Cladonia mascarena* Nyl., described by Nylander, although its taxonomic status has been controversial from the very outset. Nylander considered it a subspecies of *Cladonia papillaria* Hoffm. (synonym of *Pycnothelia papillaria*) but later on he gave it the species rank. Vainio (1887) treated this species as a synonym of *Pycnothelia papillaria* Dufour, while des Abbayes (1947) kept it as a distinct species. Currently, most authors include it in the genus *Cladonia* (des Abbayes 1966; Boom *et al.* 2011; Sipman 2011). So far, no molecular studies have been undertaken to clarify the phylogenetic relationships of this species.

Another problematic species from this region whose generic affiliation has not been resolved is *Heterodea madagascarea* Nyl. Filson (1978) excluded it from his *Heterodea* monograph, following to Jahns & van der Knapp (1973). Some authors found morphological similarities to *Gymnoderma coccocarpum* (Jahns & van der Knapp 1973; Wei & Ahti 2002; Zhou *et al.* 2006; Boom *et al.* 2011), both have a green-yellowish squamulose thallus. However, it has been considered different from *G. coccocarpum* (Wei & Ahti 2002).

The purpose of the present work is to clarify the taxonomic affiliation of *Cladonia mascarena* and *Heterodea madagascarea*. DNA sequence data are used to elucidate whether *C. mascarena* belongs to the genus *Pycnothelia* or to the genus *Cladonia*.

MATERIAL AND METHODS

Taxon sampling

Specimens of *Cladonia mascarena, Heterodea madagascarea* and *Gymnoderma coccocarpum* from different herbaria (B, H, H-NYL, MACB, O, PC, REN, TUR, Herb. M. Brand) have been studied morphologically in order to characterize these species phenotypically.

The DNA was extracted from one specimen of *C. mascarena* from Réunion (*Brand* 58836a, H) and one fresh specimen of *Gymnoderma coccocarpum* (Vietnam, *Demidova* 389, H). In addition, to assess the phylogenetic relationships of these species we selected sequences from different genera of Cladoniaceae (*Cladia, Heterodea, Carassea* S.Stenroos, *Thysanothecium* Mont. & Berk., *Rexiella* S.Stenroos, Pino-Bodas & Ahti, *Pulchrocladia* S.Stenroos, Pino-Bodas, Lumbsch & Ahti, *Metus* D.J.Galloway & P.James, *Pycnothelia* Dufour, *Notocladonia* S.Hammer and *Pilophorus* Nyl.). *Cladonia* species sampled represent most of the clades recognized in Stenroos *et al.* (2019), the biggest clades (*Cladonia*, *Erythrocarpae* and *Perviae*) are represented by multiple species. Four specimens of *Pycnothelia papillaria* from different geographical regions (Canada, Finland, Spain) were included in order to assess the similarity with *C. mascarena*. Although more sequences of *Pycnothelia papillaria* are deposited in GenBank, we included in the analyses only specimens with sequences for at least two of the three loci used to estimate the phylogeny. Two species of *Stereocaulon* Hoffm., *S. paschale* (L.) Hoffm. and *S. alpinum* (L.) Hoffm. were selected as outgroups. The voucher specimens of the species included in the phylogenetic analyses are listed in Table 1.

Molecular work

The DNA extractions were carried out with E.Z.N.A forensic kit (Omega Biotek) according to the manufacture instructions. The DNA was eluted in 100 µL of the elution buffer provided in the kit. Three loci were selected to estimate the phylogenetic relationships, ITS rDNA, *rpb2* and *ef1α*. The PCRs were carried out using Biotaq polymerase (Bioline). The volume of reaction was 25 µL, with 0.3 µL of *Taq* polymerase, 2.5 µL of 10 × PCR buffer, 1.4 µL of $MgCl_2$ 50 mmol/L, 1.6 µL of dNTPs (2.5 mmol/L), 1 µL of BSA (1 mmol/L), 1 µL of each primer (10 mmol/L), and 1 µL of extracted DNA. The primers used to amplify each region were ITS1F (Gardes & Bruns 1993) and

TABLE 1. — List of specimens included in the analyses with voucher specimens and GenBank accession numbers. New sequences are in **bold**.

Taxon name	Country	Harvest no. & Herbarium	ITS	*ef1-α*	*rpb2*
Carassea connexa	Brazil, Minas Gerais	*Stenroos 5024* (TUR)	AF453270	–	–
Cladia aggregata	Thailand	*Parnmen 622* (RAMK)	JN115255	MK152535	MK179745
Cladia gorgonea 1	New Caledonia	*Christenhusz 6169* (H)	MK179700	MK152540	MK179749
Cladia gorgonea 2	New Caledonia	*Christenhusz 6165* (H)	MK179702	MK152541	MK179750
Cladonia acuminata	United States, Alaska	*Ahti 63278* (H)	JN621932	JN621996	JN621965
Cladonia amaurocraea	Finland	*Stenroos 5172* (TUR)	AF455245	MK152565	MK179767
Cladonia apodocarpa	United States, North Carolina	*Ahti 60198* (H)	AF455237	MK152571	MK179773
Cladonia bacilliformis	Russia, Dagestan	*Urbanavichus 911170* (H)	MK179529	MK152584	MK179785
Cladonia bahiana	Brazil, Bahia	*Stocker s.n.* (H)	AF456402	MK152586	MK179786
Cladonia bellidiflora	Finland	*Stenroos 5152* (TUR)	AF453700	MK152590	MK179790
Cladonia callosa	Netherlands	*Ahti & Aptroot 72055* (H)	MK179553	MK152609	MK179807
Cladonia cariosa	Spain	*Burgaz s.n.* (MACB 94207)	JN621907	JN621971	JN621939
Cladonia cenotea	Canada, Newfoundland	*Ahti 56950* (H)	AF457900	MK152633	MK179827
Cladonia ciliata var. *ciliata*	United Kingdom, Scotland	*Stenroos 6075* (H)	MK179591	MK152650	MK179839
Cladonia coccifera	Canada, Newfoundland	*Ahti 56952* (H)	AF454437	MK152656	MK179843
Cladonia conista	Spain	*Burgaz s.n.* (MACB)	JF926612	JF926588	JF9265066
Cladonia corniculata	New Zealand	*Stenroos 5911* (H)	MK179664	MK152674	MK179858
Cladonia didyma	United States, North Carolina	*Ahti 56216* (H)	AF453703	MK152711	MK179883
Cladonia divaricata	Brazil, Minas Gerais	*Stenroos 4999* (TUR)	AF457910	MK152718	MK179888
Cladonia firma	Spain	*Burgaz s.n.* (MACB 91619)	FM205909	KC526124	FM207577
Cladonia foliacea	Portugal	*Burgaz s.n.* (MACB 90503)	FM205898	MK152733	FM207566
Cladonia furcata	Spain	*Burgaz s.n.* (MACB 91055)	KR818310	MK152739	KR818488
Cladonia gracilis subsp. *gracilis*	Spain	*Burgaz s.n.* (MACB 94216)	JN811386	MK152747	JN811412
Cladonia kanewskii	Russia, Kamchatka	*Himelbrant 02082011-1* (H)	KR019389	MK152777	MK179931
Cladonia leporina	United States, Georgia	*Ahti 58276* (H)	AF453687	MK152792	MK179944
Cladonia lopezii	Brazil, Minas Gerais	*Stenroos 5029* (TUR)	AF453279	MK152796	MK179950
Cladonia macilenta	Canada, Nova Scotia	*Ahti 57091* (H)	AF453696	MK152801	MK179955
Cladonia mauritiana	France, Réunion	*Shumm & Frahm 15496* (H)	MK179600	MK152816	MK179967
Cladonia mediterranea	Spain, Baleares	*Pino-Bodas s.n.* (MACB 99370)	KP941524	MK152820	KP941569
Cladonia miniata	Brazil, Minas Gerais	*Stenroos 5035* (TUR)	AF453284	MK152836	MK179983
Cladonia mitis	Netherlands	*Aptroot 70573* (H)	MK179624	MK152841	MK179988
Cladonia nipponica	United States, Alaska	*Dillman 19* (H)	KR019397	MK152855	MK179999
Cladonia parasitica	Germany	*Pino-Bodas* (MACB)	MK179731	MK152864	MK180007
Cladonia petrophila	United States, North Carolina	*Perlmutter 2538* (H)	MK179679	MK152868	MK180011
Cladonia portentosa	United Kingdom, Scotland	*Stenroos 6094* (H)	KP941531	MK152896	KP941567
Cladonia rangiferina subsp. *rangiferina*	Finland	*Stenroos 5173* (TUR)	AF458306	MK152926	MK180057
Cladonia rangiformis	Spain, Baleares	*Burgaz s.n.* (MACB 96193)	JF288803	KC525364	JF288838
Cladonia rigida	New Zealand	*Stenroos 5971* (H)	MK179487	MK152941	MK180068
Cladonia signata	Brazil, Minas Gerais	*Stenroos 4955* (TUR)	AF455233	MK152955	MK180082
Cladonia squamosa	Sweden	*Stenroos 5120* (TUR)	AF457886	MK152963	MK180087
Cladonia stellaris	Finland	*Stenroos 5102* (TUR)	AF458301	MK152965	MK180089
Cladonia strepsilis	Canada, Nova Scotia	*Ahti 57244* (H)	AF457879	MK152972	MK180094
Cladonia submitis	United States, New York	*Stenroos 5738* (H)	MK179682	MK152983	MK180105
Cladonia subturgida	Spain	*Burgaz s.n.* (MACB 99488)	JF288793	KC525366	JF288824
Cladonia subulata	Spain	*Burgaz s.n.* (MACB 93151)	FN86566	HM243174	HM243210
Cladonia uncialis subsp. *biuncialis*	Iceland	*Högnabba 1298* (H)	KR019405	MK152594	MK179794
Cladonia ustulata	New Zealand	*Stenroos 5886* (H)	MK179585	MK153025	MK180143
Cladonia verticillata	Netherlands	*Ahti & Aptroot 72002* (H)	KC776935	MK153033	MK180150
Gymnoderma coccocarpum	Vietnam	*Demidova 389* (H)	**MT215516**	**MT215162**	–
Heterodea muelleri	Australia, Westerm Australia	*Christenhusz 6367* (H)	MK179705	MK153043	–
Metus conglomeratus	Australia, Tasmania	*Lumbsch 19982b* (F)	GQ500912	–	MK180161
Notocladonia cochleata	New Caledonia	*Dennetière 53* (TUR)	AF453267	–	–
Pulchrocladia corallaizon	Australia, New South Wales	*Hammer s.n.* (H)	MK179738	MK152536	MK179746
Pycnothelia papillaria 2	Canada, Nova Scotia	*Ahti 74341g, Anderson, Richardson & Porter* (H)	MK179706	MK153050	–
Pycnothelia papillaria 3	Finland	*Pino-Bodas et al. s.n.*(H)	MK179707	MK153051	MK153051
Pycnothelia papillaria 1	Spain	*Burgaz s.n.* (MACB 93242)	JF288804	–	JF288839
Pycnothelia papillaria 4	–	*AFTOL-ID 1377*	HQ650595	–	DQ992473
Pycnothelia mascarena	Réunion	*Brand 58836a* (H)	**MT215515**	–	**MT215163**

TABLE 1. — Continuation.

Taxon name	Country	Harvest no. & Herbarium	ITS	*ef1-α*	*rpb2*
Rexiella sullivanii	New Zealand	*Stenroos 5958* (H)	MK179741	MK152533	MK179744
Thysanothecium scutellatum	Indonesia, Papua	*Miettinen 11620,4* (H)	MK179740	MK153061	–

ITS4 (White *et al.* 1990) for ITS rDNA, and *rpb2*-dRaq and *rpb2*-revRaq (Pino-Bodas *et al.* 2010) for *rpb2*, CLEF3F and CLEF3R (Yahr *et al.* 2006) for *ef1α*. The PCR programs for each locus are described in Pino-Bodas *et al.* (2013). The PCR products were sequenced in Macrogen Spain (www.macrogen.com) with the same primers used in the PCRs.

PHYLOGENETIC ANALYSES

The sequences were assembled using Sequencher™ (Gene Codes, Ann Arbor, MI, United States). MAFFT was used to align the sequences of each locus with the defect values. After that, each alignment was inspected and improved manually. ITS rDNA alignment contained numerous ambiguous regions and the program Gblock (Talavera & Castresana 2007) was used to delimit and remove them with the less stringent options. The nucleotide substitution model was chosen using jModeltest (Posadas 2008), according to AIC criterion. The best-fitting models were: GTR+I+G for ITS rDNA, TIM2ef+I+G for *ef1α* and TrNef+I+G for *rpb2*. Maximum likelihood analyses were implemented in RAxML 7.04 (Stamatakis *et al.* 2008), assuming the GTRGAMMA model for each locus separately with 1000 of fast bootstrap replicates. The best ML trees were searched using every fifth bootstrap tree as a starting tree. The congruences among the different topologies were done according to the method of Kauff & Lutzoni (2002). Clades with bootstrap values ≥75% were inspected in order to search any conflict among loci. No incongruence was detected among the loci, and the different datasets were concatenated. The concatenated dataset was analyzed by ML and Bayesian approach. ML analysis was run with the same conditions that the single locus ML analyses considering seven partitions (ITS rDNA and each codon position of *rpb2* and *ef1α*). Bayesian analysis was run in MrBayes 3.2 (Ronquist *et al.* 2012) in CIPRES portal (Miller *et al.* 2010) with seven partitions and the substitution models selected by jmodeltest. Two simultaneous runs with 20 000 000 generations, each starting with a random tree and employing four simultaneous chains, were executed. Every 1000th tree was saved into a file. The first 1 000 000 generations (i.e. the first 1000 trees) were deleted as the "burn-in" of the chain. The convergence of the chains was assessed with average standard deviation of split frequencies <0.005 and plotting the likelihood versus generation number in Tracer v. 1.7 (Rambaut *et al.* 2018).

Shimodaira-Hasegawa test (SH; Shimodaira & Hasegawa 1999) and expected likelihood weight test (ELW; Strimmer & Rambaut 2002) were conducted in order to dismiss the possibility that the placement of *C. mascarena* into *Pycnothelia* is an artefact of the phylogenetic estimation. RAxML 7.04 was used to estimate the maximum likelihood tree consistent with the alternative hypothesis (*C. mascarena* belongs to *Cladonia*). The SH and ELW tests were run in TREE-PUZZLE 5.2 (Schmidt *et al.* 2002), using the GTR + I + G model and with four-category approximation to the gamma distribution for substitution rate among sites and 1000 replicates under the RELL method.

RESULTS

The new sequences were deposited in GenBank (Table 1). The final ITS rDNA alignment, after Gblock removed ambiguous positions, kept the 67% of the all original positions. The concatenated dataset included 68 taxa and 1993 positions, 744 of which were parsimony informative. ML analysis yielded a tree with –Lnl = 19376.63 and Bayesian analysis generated a tree with an arithmetic mean –Lnl = 19760.61. The topology of both trees was the same and only the 50% consensus majority tree from the Bayesian analysis is shown in Fig. 1. The relationships among the genera were the same found in Stenroos *et al.* (2019). *Pycnothelia*, *Carassea*, *Gymnoderma* and *Metus* formed a well-supported clade sister to *Cladonia*. *Thysanothecium* and *Notocladonia* are closely related and they are related to *Heterodea*. *Cladonia mascarena* formed a well-supported clade with *Pycnothelia papillaria*.

The SH and ELW (–Lnl = 21186.03, *P-value* of SH = 0.000, *P-value* of EL = 0.000) rejected the hypothesis that *C. mascarena* belongs to *Cladonia*.

TAXONOMY

Family CLADONIACEAE Zenker
Genus *Pycnothelia* Dufour

Pycnothelia mascarena (Nyl.) Nyl.
(Fig. 2A)

In Leighton, *Annals and Magazine of Natural History*, ser. 3, 18: 405 (1866).

Cladonia mascarena Nyl., *Annales des Sciences Naturelles*; *Botanique* 4 (11): 250 (1859). — *Cladonia papillaria* var. *mascarena* Nyl., *Mémoires de la Société Imperiale des Sciences Naturelles de Cherbourg* 5: 95 (1858 [1857]) *nom. nud.* — *Cladonia papillaria* subsp. *mascarena* (Nyl.) Nyl., *Synopsis Methodica Lichenum* 1 (2): 189 (1860).

MYCOBANK. — MB477440.

LECTOTYPE. — **Réunion** (Île Bourbon), Salazie, 1840, *P. Lepervanche-Mezières 116* (H-NYL no. 38692 = H9504381; isolecto-, G[G00047551]; PC-Hue; PC-Thuret [Ahti 1993]).
Primary thallus poorly known (absent from most specimens),

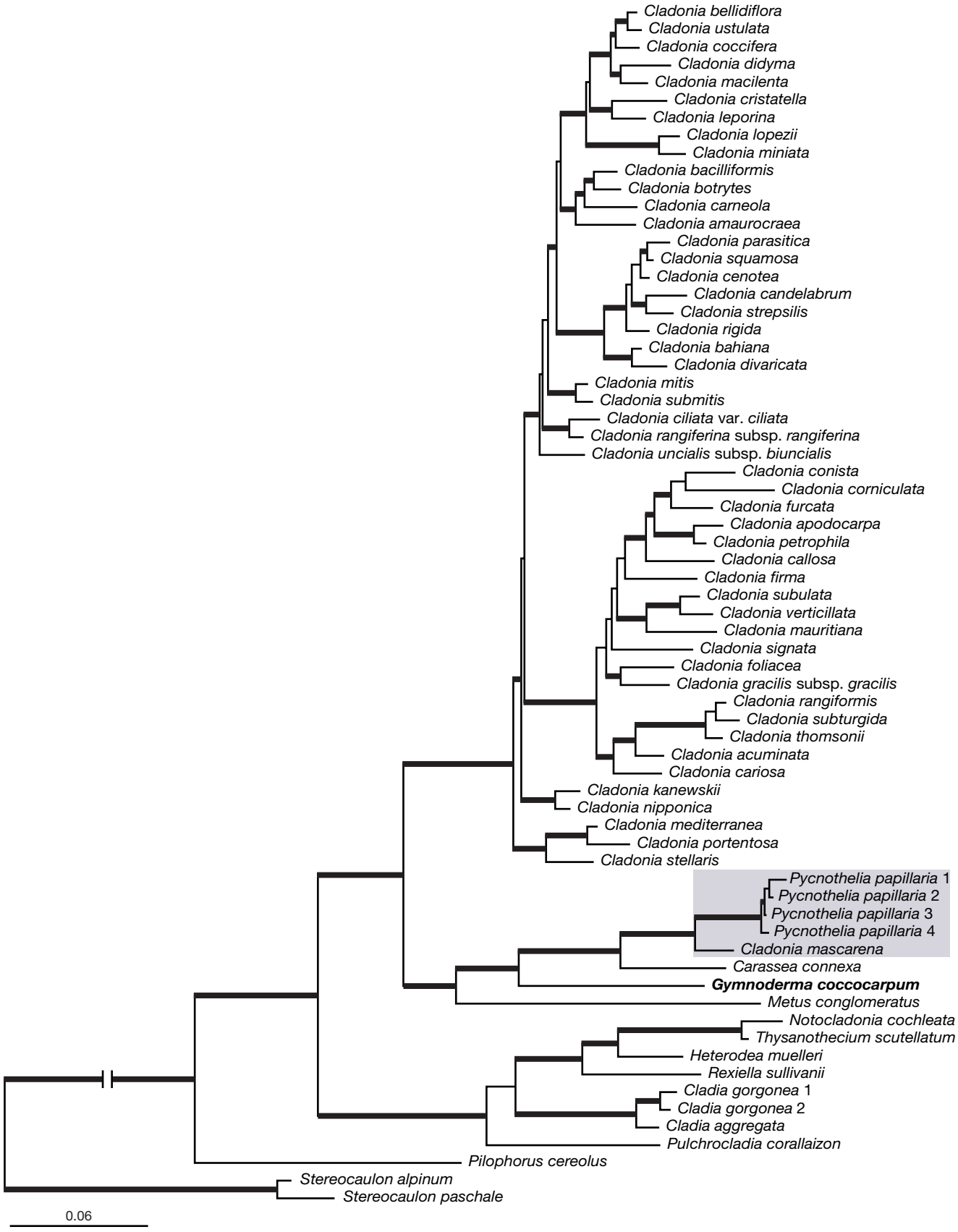

Fig. 1. — Phylogeny of Cladoniaceae based on ITS rDNA, *ef1α* and *rpb2*. 50% consensus majority tree from the Bayesian analyses. Branches supported with p.p. ≥0.95 and bootstrap values ≥75% are in **bold**.

perhaps slightly granulose. Podetia 20-40 mm tall, 0.5-1 mm thick, dark to pale brown, fragile (wall very thin) densely packed together, slender, not or somewhat swollen, hollow, usually characterized by short, bulbous, lateral branchlets towards the tips, which are acute. Ascomata and conidiomata unknown.

CHEMISTRY. — Atranorin and fatty acids of apparently the lichesterinic acid group (TLC).

DISTRIBUTION. — Only known from Réunion.

ADDITIONAL MATERIAL EXAMINED. — **Réunion**, type locality, 1840, *P. Lepervanche-Mezières 115* (H-NYL 38692 p.p. = H9504381 p.p., PC-Thuret); "Secus semitam inter locos dictos Côteau-Maigre et Entre-Deux, ad terram humosam et truncos putridos, inter *Philippias*", 2200 m, 1956, *H. des Abbayes* in des Abbayes, Lich. Madag. Borb. Sel. Exs. No. 21 (REN, TUR, UPS); Forêt de Bébour, 2008, *A. M. Brand* 58836 (H, Herb. Brand), 58836a (H); St. Paul, 2008, *A. M. Brand* 59533 (Herb. Brand).

NOTES

The later combinations of the name *Cladonia mascarena* have been overlooked by nomenclatural sources such as the Index Fungorum and MycoBank.

Gymnoderma Nyl.
(Fig. 2E, F)

Flora 43: 546 (1860), *nom. cons.* — Type species: *Gymnoderma coccocarpum* Nyl.

Baeoderma Vain., *Acta Societatis pro Fauna et Flora Fennica* 53 (1): 3 (1922). — Type species: *Baeoderma madagascareum* (Nyl.) Vain. — Basionym: *Heterodea madagascarea* Nyl., *Lichenes Novae Zelandiae* (1888).

LECTOTYPE. — Designated by Jahns (1969): Madagascar, Rev. R. Baron s.n. (H-NYL 37528).

NEW SPECIMENS OF G. COCCOCARPUM EXAMINED. — Vietnam, prov. Lam Dong: Bi Doup Massif, E of Giang Ly, on bark of *Pinus dalatensis* and other trees, 2012 *A. N. Demidova 334*, *335 346*, *358* (H), *389* (H, MACB). Mauritius, Savanne, Mt. Cocotte, SE of peak, on road to Bassin Blanc, 620 m, 1991 *H. Krog & E. Timdal* MAU29 (O). Réunion, NW of Plaine-des-Palmistes, NW side of Forêt de Bébour, 3.5 km on trail Gîte de Bélouve to Caverne Mussard, 1980 m, 2008 *P. v.d. Boom 40494*, *B. v.d. Boom*, *D. Brand, M. Brand & E. Sérusiaux* (H).

NOTES

Confused with *Sphaerophorus madagascareus* Nyl., now recognized as *Bunodophoron madagascareum* (Nyl.) Wedin (Wedin 1993), in Zahlbruckner's (1922) Catalogus. The latter error was noticed by Lamb (1963), but he suggested that *Baeoderma* belongs to *Baeomyces*. Jahns (1970) and Jahns & van der Knapp (1973) already included *Heterodea madagascarea* in *Gymnoderma coccocarpum,* but we hesitated (Zhou *et al.* 2006: 878) to synonymize them. After seeing the material collected by H. Krog and E. Timdal in Mauritius (see below) we are ready to accept the synonymy (Fig. 2). Unfortunately, we could not confirm it also with DNA data.

Gymnoderma coccocarpum has a squamulose thallus with green-yellowish upper surface and white lower surface, margin crenate. Podetia absent or very short and solid, born marginally, apothecia common, pale brown, sessile, globose. For more details see the description on Sato (1940) and Wei & Ahti (2002).

DISCUSSION

This study settles the taxonomic confusion around *Cladonia mascarena* and *Heterodea madagascarea*. Our results, based on the analyses of three genic regions, clearly show that *Cladonia mascarena* should be included in the genus *Pycnothelia*. Although Nylander included this species in the genus *Pycnothelia*, most of the authors (des Abbayes 1966; Boom *et al.* 2011; Sipman 2011) have considered it as belonging to the genus *Cladonia*. Vainio (1887) treated *P. mascarena* as a synonym of *P. papillaria*, but both morphological or phylogenetic results indicate that they are different species (though some morphotypes of *P. papillaria* with long podetia similar to *P. mascarena,* e.g. the peculiar morph called *Cladonia trapezuntica* from Turkey, with podetia up to 50 mm long; see Senkardesler *et al.* 2016). With the inclusion of *Pycnothelia mascarena* in *Pycnothelia,* the genus currently comprises three species, *P. papillaria, P. caliginosa* and *P. mascarena*. Laundon (1986) published a thorough study of the nomenclature and typification of the synonymy of *Pycnothelia papillaria.* It is unusually complicated, but turned out to be essentially correct in a re-examination, although not followed by many recent authors. *Pycnothelia,* correctly used at generic level first by Dufour (1821), is characterized by a persistent, granulose primary thallus, with hollow podetial that are simple to branched near apices and with completely or partially corticated surface (Ahti 2000). This genus has a disjunct distribution. *Pycnothelia papillaria*

KEY OF PYCNOTHELIA DUFOUR

1. Podetia 20-40 mm tall, thin, corticate, densely packed, with short lateral branchlets towards the tip .... *Pycnothelia mascarena* (Nyl.) Nyl.
— Podetia up to 20 mm tall, corticate or decorticate, branched at tips with age, but without short lateral branchlets 2

2. Podetia tooth-like, partly swollen, smoothly corticate, with apothecia becoming branched, medulla white .... *Pycnothelia papillaria* Dufour
— Podetia subterete, with cracked cortex or surface granulate, partially decorticate, with apothecia single or forming clusters, medulla black ..... *Pycnothelia caliginosa* D.J.Galloway & P.James

Fig. 2. — **A**, *Pycnothelia mascarena* (Nyl.) Nyl., Réunion, *Lepervanche-Méziéres 116* (PC-Thuret); **B**, *Pycnothelia caliginosa* D.J.Galloway & P.James, New Zealand, *Galloway s.n.* (isotype, H). Photo: Sanna Laine; **C**, *Pycnothelia papillaria* Dufour, Canada, New Brunswick, *Ahti* 74425 & *Clayden* (H). Photo: Sanna Laine; **D**; *Pycnothelia papillaria*, Canada, Ontario, *Burgaz s.n.* (MACB); **E**, *Gymnoderma coccocarpum* Nyl., Taiwan, *Stenroos 3462* (H); **F**, *Gymnoderma coccocarpum* (Synonym of *Heterodea madagascarea*), Réunion, *v.d. Boom 40494* (H). Scale bars: 1 cm.

is the species most broadly distributed, occurring in Europe (for numerous local maps, see Scholz 2007), North America (East and Alaska), Asia (only Turkey, Azerbaijan, Russian Far East), Dominican Republic, Brazil (Ahti 2000) and Uruguay. Although *P. papillaria* is fairly common in areas such as much of Scandinavia and coastal eastern Canada, it has recently clearly decreased in some countries such as Poland, Netherlands or Turkey (Cieśliński 1991; Haveman & Ronde 2013; Şenkardeşler *et al.* 2016). *Pycnothelia caliginosa* is restricted to New Zealand and Tasmania (Galloway & James 1987), and *P. mascarena* is limited to Réunion. Other Cladoniaceae genera, such as *Pilophorus* and *Gymnoderma,* also present disjunct distributions, but their patterns are different from those of *Pycnothelia.*

The phylogenetic placement of *Gymnoderma* in our analyses agrees with the results previously found by other authors using different gene regions (Zhou *et al.* 2006; Stenroos *et al.* 2019). *Gymnoderma* is phylogenetically rather closely related to *Carassea* and *Pycnothelia*. Stenroos *et al.* (2019) discussed the phenotypical similarities among these genera. The main feature that distinguishes *Gymnoderma* from the remaining genera of Cladoniaceae is the entirely amyloid ascus (Verdon & Elix 1986; Döring *et al.* 1999; Peršoh *et al.* 2004: fig. 1B). We have recently examined several good specimens of *G. coccocarpum* (H) collected by Anna Demidova on Bi Doup mountain massif, Lam Dong Province in southern Vietnam. One of them (Demidova 389; H, MACB) was subjected to a DNA analysis. On the basis of morphological examinations, we considered that the specimens from Réunion correspond to the same species present in East of Asia, and accepted the synonymy of Jahns (1970), who studied the ontogeny. Therefore, *G. coccocarpum* is distributed in temperate and tropical areas of East Asia (Borneo, China, Japan, Malaysia, Philippines, Sikkim, Taiwan, Vietnam) and tropical Africa (Mauritius Island, Réunion). In the meantime, we detected *Baeoderma* as a new synonymy of *Gymnoderma* which has been overlooked or confused in recent sources.

Our results contribute to clarify the taxonomy and nomenclature of two species of Cladoniaceae from Madagascan Region, including *C. mascarena* in the genus *Pycnothelia,* on the base of morphological and DNA sequence data and synonymizing *Heterodea masgagascarea* with *Gymnoderma coccocarpum*. The long-standing taxonomic confusion around these species has been largely due to the shortage of specimens for study. New collections are however necessary to resolve the taxonomy of other species in the region. For example, in the recently published phylogeny of Cladoniaceae, the common Madagascan species *Cladonia gigantea* (Bory) H.Olivier turned out to be polyphyletic (Stenroos *et al.* 2019) and the identity of the specimens of *C. centrophora* Müll. Arg. from Réunion, is uncertain.

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