

Xanthonectria, a new genus for the nectrioid fungus *Nectria pseudopeziza*

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Ascomycete.org, 8 (4) : 172-178.
Juillet 2016
Mise en ligne le 08/07/2016



Abstract: A new genus, *Xanthonectria*, is proposed for the enigmatic taxon *Nectria pseudopeziza*. *Xanthonectria* is characterized by nonstromatic, soft-textured, superficial, glabrous, pale yellow to bright orange nectria-like ascomata, not changing colour in 3% KOH or lactic acid, long fusiform, multiseptate ascospores and an acremonium-like asexual morph. Its placement in the *Bionectriaceae* and its relationship to other members of this family are based on morphological, cultural and molecular data.

Keywords: Ascomycota, *Bionectriaceae*, *Hypocreales*, *Nectria*, ribosomal DNA, taxonomy.

Résumé : un nouveau genre, *Xanthonectria*, est proposé pour l'énigmatique taxon *Nectria pseudopeziza*. *Xanthonectria* est caractérisé par des ascomes de type nectria, non stromatiques, de texture souple, jaune pâle à orange vif, glabres, ne changeant pas de couleur dans KOH à 3 % ou dans l'acide lactique, des ascospores longuement fusiformes, multiseptées et un stade asexué de type acremonium. Son placement dans les *Bionectriaceae* et sa position par rapport aux membres de cette famille s'appuient sur des données morphologiques, culturelles et moléculaires.

Mots-clés : ADN ribosomal, Ascomycètes, *Bionectriaceae*, *Hypocreales*, *Nectria*, taxinomie.

Introduction

Historically, the genus *Nectria* (Fr.) Fr. has been the repository for all soft-textured, superficial, uniloculate perithecial ascomycetes with whitish, yellow, orange or red walls, but in the light of recent taxonomic studies on these hypocrealean fungi (ROSSMAN *et al.*, 1999; HIROOKA *et al.*, 2012; LOMBARD *et al.*, 2015), the genus *Nectria* was re-defined in a narrower sense. As a result, many of the taxa formerly placed in *Nectria* have been assigned to different genera in the *Bionectriaceae* and the *Nectriaceae*. *Nectria*-like species having white to orange or brown perithecial walls not changing colour in 3% KOH or lactic acid and an acremonium-like asexual morph belong to the *Bionectriaceae* as defined by ROSSMAN *et al.* (1999). They are accommodated in such genera as *Hydropisphaera* (Tode : Fr.) Dumort., *Ijuhya* Starbäck, *Lasionectria* (Sacc.) Cooke, *Nectriopsis* Maire, *Ochronectria* Rossman & Samuels, *Protocreopsis* Doi and *Verrucosotoma* Hirooka, Tak. Kobay. & P. Chaverri.

A widespread hypocrealean fungus first described as *Sphaeria pseudopeziza* by DESMAZIÈRES (1840) was accommodated during the 19th century in various genera such as *Calonectria* De Not. by SACCARDO (1878), *Dialonectria* (Sacc.) Cooke by COOKE (1884) and *Nectria* (Fr.) Fr. by SACCARDO (1883), before being assigned to *Nectria* by ROSSMAN (1979) in her revision of *Calonectria*, as *N. pseudopeziza* (Desm.) Rossman. ROSSMAN (1983) gave a detailed description of *N. pseudopeziza*, with comments on its unique placement within the genus *Nectria* as it was conceived at this time. Based on its distinctive ascomatal wall structure and its acremonium-like asexual morph obtained in culture, she placed it in "Miscellaneous *Nectria* species with ascocarps which do not change colour in KOH", likely representing "a new group in *Nectria*". This is why *N. pseudopeziza* was regarded as an enigmatic taxon of unclear affinities, a view reinforced by its absence from all comprehensive surveys carried out on *Nectria* and *Nectriaceae* since this time (ROSSMAN *et al.*, 1999; HIROOKA *et al.*, 2012; LOMBARD *et al.*, 2015). The possible affinities of *N. pseudopeziza* with the new family *Bionectriaceae* were not considered in the former study and it was not included either in the two latter studies because it clearly deviates from *Nectria s. str.*, which is characterized by verrucose, brightly coloured ascomata seated on a pseudoparenchymatous stroma, turning dark red in 3% KOH and yellow in lactic acid, with ascospores either 1–4 transversely septate or muriform and a tubercularia-like asexual morph.

Remarkably, DESMAZIÈRES (1840) suggested that this fungus was close to *Nectria peziza* (Tode) Fr. [= *Hydropisphaera peziza* (Tode: Fr.) Dumort.] which indeed macroscopically resembles *X. pseudopeziza* and shares with it an acremonium-like asexual morph, but primarily differs by its ascomatal wall composed of large thin-walled cells in-

volving a collapse upon drying and having striate ascospores. Even though the placement of *N. pseudopeziza* in the *Bionectriaceae* appeared plausible because of its pale ascomata not changing colour in KOH or acid lactic and its acremonium-like asexual morph, the question of its affinities with the other genera of the *Bionectriaceae* was still pending. This situation was taxonomically problematic since it concerned a fairly common, widespread and frequently reported species for which the placement in the genus *Nectria* as currently circumscribed was untenable.

In order to elucidate the familial status of this fungus and its affinities with morphologically similar genera, an ITS-LSU-based phylogenetic analysis was carried out on a dataset including *N. pseudopeziza*, representatives of 14 nectriaceous genera, and 11 morphologically related bionectriaceous genera. The phylogenetic analysis clearly shows that *N. pseudopeziza* belongs to the *Bionectriaceae*, which is in agreement with the morphology of its sexual and asexual morphs, and is unrelated with the most similar bionectriaceous genera. We therefore propose the new genus *Xanthonectria* for *N. pseudopeziza*. *Xanthonectria pseudopeziza* (Desm.) Lechat, J. Fourn. & P.-A. Moreau comb. nov. is given herein a morphological description and illustrations of its sexual and asexual morphs. Its affinities with other bionectriaceous genera are discussed.

Materials and Methods

Specimens of *N. pseudopeziza* were examined using the method described by ROSSMAN *et al.* (1999). Microscopic observations and measurements were made in water and the ascospore ornamentation was observed in unheated lactic cotton blue. The specimens are deposited in LIP herbarium (Lille), cultures at CBS and sequences at GenBank. Cultures of both specimens were made by removing a mass of ascospores and asci from a single perithecialium of each collection with a fine needle, and placed in a drop of sterile water that was stirred with a needle to distribute the elements on the slide; a part of the drop containing ascospores was placed on PDA using a sterile micropipette; then the Petri dish was incubated at 25°C. DNA extraction, amplification, and sequencing were performed by ALVALAB (Santander, Spain). Total DNA was extracted from dry specimens blending a portion of them using a micropestle in 600 µl CTAB buffer (CTAB 2%, NaCl 1.4 M, EDTA pH 8.0 20 mM, Tris-HCl pH 8.0 100 mM). The resulting mixture was incubated for 15 min at 65°C. A similar volume of chloroform: isoamylalcohol (24:1) was added and carefully mixed with the samples until their emulsion. It was then centrifugated for 10 min at 13.000 g, and the DNA in the supernatant was precipitated with a volume of isopropanol. After a new centrifugation of 15 min at the same speed, the pellet was washed in

cold 70% ethanol, centrifugated again for 2 min and dried, and finally resuspended in 200 µl ddH₂O. PCR amplification was performed with the primers ITS1F and ITS4 (WHITE *et al.*, 1990; GARDES & BRUNS, 1993) for ITS, while LR0R and LR5 (VILGALYS & HESTER, 1990) were used to amplify the 28S rDNA region. PCR reactions were performed under a program consisting of a hot start at 95°C for 5 min, followed by 35 cycles at 94°C, 54°C and 72°C (45, 30 and 45 s respectively) and a final 72°C step 10 min. PCR products were checked in 1% agarose gels, and positive reactions were sequenced with primer ITS4 (for ITS) and LR5 (for LSU). Chromatograms were checked searching for putative reading errors, and these were corrected. The phylogenetic affinities of *N. pseudopeziza* and allied taxa were inferred using a combined ITS and LSU dataset of sequences generated in this study, together with sequences downloaded from GenBank (Table 1) representing 14 genera of *Nectriaceae*, 11 genera of *Bionectriaceae*, and 1 genus of *Hypocreaceae* (*Hypomyces aurantius*) which was selected as an outgroup.

Phylogenetic analyses (Fig. 4) were performed online at www.phylogeny.lirmm.fr (DEREEPER *et al.*, 2008). Maximum likelihood phylogenetic analyses were performed with PhyML 3.0 aLRT (ZWICKL, 2006), using the GTR + I + Γ model of evolution. Branch support was assessed using the non-parametric version of the approximate likelihood-ratio test, implemented in PhyML (SH-aLRT; ANISIMOVA & GASCUÉL, 2006).

Taxonomy

Xanthonectria Lechat, J. Fourn. & P.-A. Moreau., *gen. nov.* – MB 816960

Holotype: *Sphaeria pseudopeziza* Desm.

Diagnosis: Ascomata superficial, non-stromatic, soft-textured, pale yellow to orange, not changing colour in 3% KOH or in lactic acid, globose, not collapsing upon drying, glabrous, ascomatal wall up to 80 µm thick, of three regions composed of thick-walled cells; ascospores long fusiform, attenuated and rounded at ends, spinulose, multiseptate; asexual morph: acromonium-like.

Etymology: from Greek *ξανθός* = yellow, fawn, golden red, for the colour of the ascomata varying from pale yellow to orange.

Xanthonectria pseudopeziza (Desm.) Lechat, J. Fourn. & P.-A. Moreau, *comb. nov.* – MB 816961 – Fig. 1

Basionym: *Sphaeria pseudopeziza* Desm., *Ann. Sci. Nat., Bot., sér. 2*, 13: 186 (1840).

≡ *Calonectria pseudopeziza* (Desm.) Sacc., *Michelia*, 1: 307. (1878); *Dialonectria pseudopeziza* (Desm.) Cooke, *Grevillea*, 12 (64): 111 (1884); *Nectria pseudopeziza* (Desm.) Rossman, *Mycotaxon*, 8 (2): 536 (1979).

= *Sphaeria mellina* Durieu & Mont., *Expl. Sci. Algérie, Bot.*, 1: 497 (1849); *Calonectria mellina* (Durieu & Mont.) Höhn., in Höhnel & Weese, *Ann. Mycol. Berl.*, 8: 467 (1910).

= *Sphaeria ochraceopallida* Berk. & Broome, *Ann. Mag. nat. Hist., Ser. 2*, 7: 187 (1851); *Calonectria ochraceopallida* (Berk. & Broome) Sacc., *Atti Soc. Veneto-Trent. Sci. Nat., Ser. 4*, 4: 23 (1875); *Nectria ochraceopallida* (Berk. & Broome) Sacc., *Syll. fung.*, 2: 551 (1883); *Dialonectria ochraceopallida* (Berk. & Broome) Cooke, *Grevillea*, 12 (64): 111 (1884).

= *Nectria ochraceopallida* var. *corallina* Berk. & Broome, *Ann. Mag. nat. Hist., Ser. 2*, 13: 467 (1854).

= *Calonectria plowrightiana* Sacc., *Michelia*, 1 (3): 307 (1878); *Dialonectria plowrightiana* (Sacc.) Cooke, *Grevillea*, 12 (64): 111 (1884).

Ascomata solitary or in small groups of 2–6, sometimes coalescent, superficial, non-stromatic, firmly attached to host, soft-textured, variously coloured, whitish to pale yellow when immature, then varying from yellow to pale orange, pale brownish orange, bright yellow or bright orange, not changing colour in 3% KOH or lactic acid, globose (240–)260–350(–380) µm diam., smooth, glabrous, not collapsing when dry but frequently apically flattened; ostiole minu-

tely papillate at centre of a slightly darker discoid area. **Cells** at surface of ascomatal wall forming a *textura epidermoidea* in surface view. **Ascomatal wall** in vertical section (35–)40–65(–80) µm thick, composed of three regions; outer region 20–35 µm thick, composed of subglobose to globose, thick-walled cells 3–5(–7) µm diam. with wall 1.5–2 µm thick; middle region 15–28 µm thick, composed of globose to ellipsoidal thick-walled cells 5–8(–10) × 3–4(–5) µm with wall 1.5–2.5 µm thick, becoming more flattened inwardly and containing scattered orange oily droplets; inner region 10–15 µm thick, composed of elongated, hyaline, thin-walled cells obscured by abundant orange oily droplets. **Ostiole canal** periphysate. **Asci** unitunicate, fusiform to clavate, short-stipitate, with eight irregularly multiseriate ascospores, (75–)85–100(–110) × 10–13(–15) µm, apically rounded, lacking an apical apparatus, interspersed with filamentous paraphyses up to 6 µm diam filled with numerous bright orange oily droplets. **Ascospores** (28–)35–50(–60) × (4.5–)5–6(–6.5) µm (Me = 45.5 × 5.5 µm, n = 30), narrowly fusiform with rounded ends, hyaline, spinulose, (3–)5–7(–9) septate.

Cultural characteristics (Fig. 2)

Colony after two weeks on PDA reaching 25–30 mm diam, aerial mycelium white in centre, cream to pale yellow with some pinkish tinges in median area, sporulating at white margin, reverse pale yellowish brown in centre, pale yellow at margin. Primary conidiophores macronematous, mononematous, unbranched, flexuous, hyaline, smooth, arising from smooth, hyaline hyphae 2–2.5 µm diam. Conidiogenous cells monophialidic, 18–35(–45) µm long, 1.5–2 µm wide at apex with unflared collarette, 2–2.5 µm wide at base. Conidia in small slimy head at tip of phialide, aseptate, narrowly ellipsoidal to subcylindrical with rounded apex, attenuated at base with a small abscission scar, smooth, hyaline, 5–7(–8) × 1.8–2.2 µm (Me = 6 × 2 µm, n = 50). After four weeks, white sporodochia 150–180 µm diam. appearing at margin of colony, composed of fasciculate conidiophores 2–2.5 µm diam, arising from smooth, hyaline hyphae, 2–2.5 µm wide; conidiogenous cells, 18–30 µm long, 1.5–2.2 µm wide at base, 1 µm wide at apex without collarette, produced in large slimy heads similar conidia to those observed after two weeks.

Specimens examined

BELGIUM: Bruxelles, Forêt de Soignes, on *Heracleum sphondylium*, 31 Jan. 2014, *leg.* R. Vandiest, CLL14003. FRANCE: Ariège: Alzen, banks of Alzen brook downstream from the waterfall, ca. 580 m, on bark of *Alnus glutinosa*, 25 Mar. 2000, *leg.* J. Fournier, JF 00032; Lescure, Bois du Pas du Baup, banks of Volp brook, ca. 515 m, on partly submerged decorticated wood of *Fraxinus excelsior*, 26 Oct. 2006, *leg.* J. Fournier, JF 06279; Rimont, Palétès, banks of Peyrau brook, ca. 400 m, corticated branchlet of *Cydonia oblonga*, 21 Dec. 1996, *leg.* J. Fournier, JF 96197. Calvados: vicinity of Caen, 1829, decorticated wood, *leg.* M. Roberge, PC 723563, lectotype designated by ROSSMAN (1983); Charente-Maritime: île de Ré, Ars-en-Ré, on *Suaeda vera*, 9 Apr. 2015, *leg.* M. Hairaud, CLL15075 (LIP), culture CBS140160, GenBank KU593584 ITS and KU593583 LSU; *ibid.*, on *Smyrniolus olusatrum*, 2 Feb. 2016, *leg.* M. Hairaud, CLL16005 (LIP), culture CBS141245, GenBank KU946963 ITS and KU946964 LSU. Côte-d'Or: Gevrey-Chambertin, Combe Lavaux, on *Buxus sempervirens*, 24 Dec. 2009, *leg.* A. Gardiennet, AG09329; *ibid.*, on twig of *Tilia*, 12 Mar. 2016, *leg.* A. Gardiennet AG16050; Loire Atlantique: Pors er Ster, on *Ulex europaeus*, 6 Nov. 2011, *leg.* C. Lechat, CLL07015; Deux-Sèvres: Availles-sur-Chizé, on bark of *Ulmus*, 18 Apr. 2013, *leg.* C. Lechat, CLL13014 (LIP); Villiers-en-Bois, Virollet, on *Spartium junceum*, 28 Dec. 2009, *leg.* C. Lechat, CLL9242; Vendée: Le Mazeau, on *Populus* sp., 1 Aug. 2008, *leg.* C. Lechat, CLL08329; Moutiers-le-Mauxfaits, roadside to La-Roche-sur-Yon 3 km from the town, corticated branch of *Ulex europaeus* in a pile of dead branches, 6 Jun. 2003, *leg.* J. Fournier & C. Lechat, JF 03092. SPAIN: Asturias: Saliencas, Parque natural de Somiedo, on *Rhamnus alpina*, 5 Jun. 2013, *leg.* C. Lechat, CLL13017.

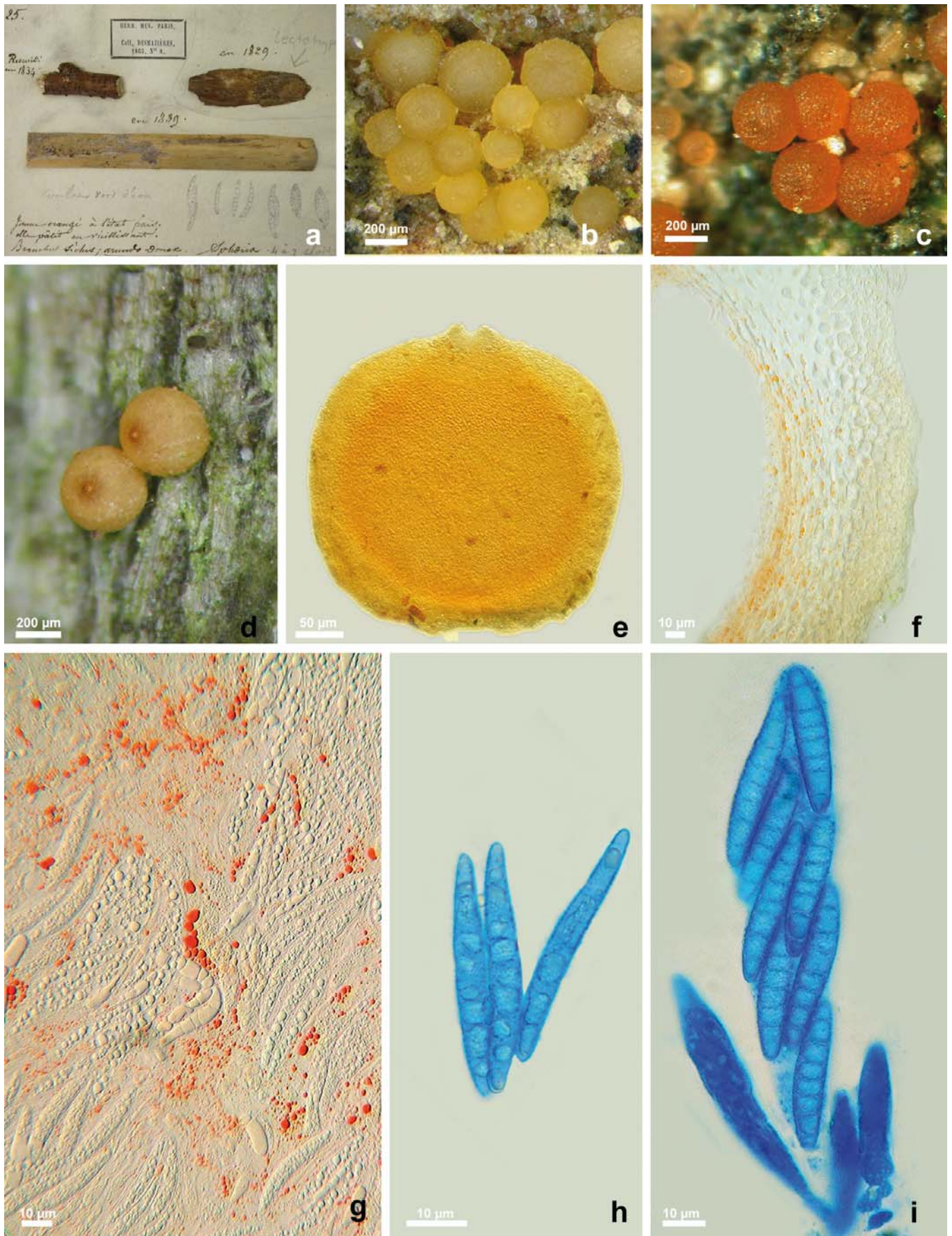


Fig. 1 – a-k: *Xanthonectria pseudopeziza*; a: Lectotype from PC. b-c: Fresh ascomata in natural environment showing various colours. d: Dry ascomata on the substratum. e: Perithecium observed in water. f: Section through the ascomatal wall with orange oily droplets. g: Hymenium and paraphyses containing numerous orange oily droplets. h: Ascospores. i: Asci and ascospores. (b: CLL13014, c: CLL13017, d-i: CLL15075)

Discussion

The above morphological definition of *Xanthonectria pseudopeziza* is based on the material examined during this study, including the lectotype of *Sphaeria pseudopeziza*, and is consistent with the detailed description made by ROSSMAN (1983). Minor differences ap-

pear in ascotal wall colour and thickness and in conspicuousness of orange oily droplets in the ascotal wall and in the hymenium, which are regarded as reflecting intraspecific variations. The ascospore wall reported as smooth or rarely spinulose by Rossman was observed as spinulose in all the material studied, including the lectotype, but we did not study subtropical material as Rossman did.

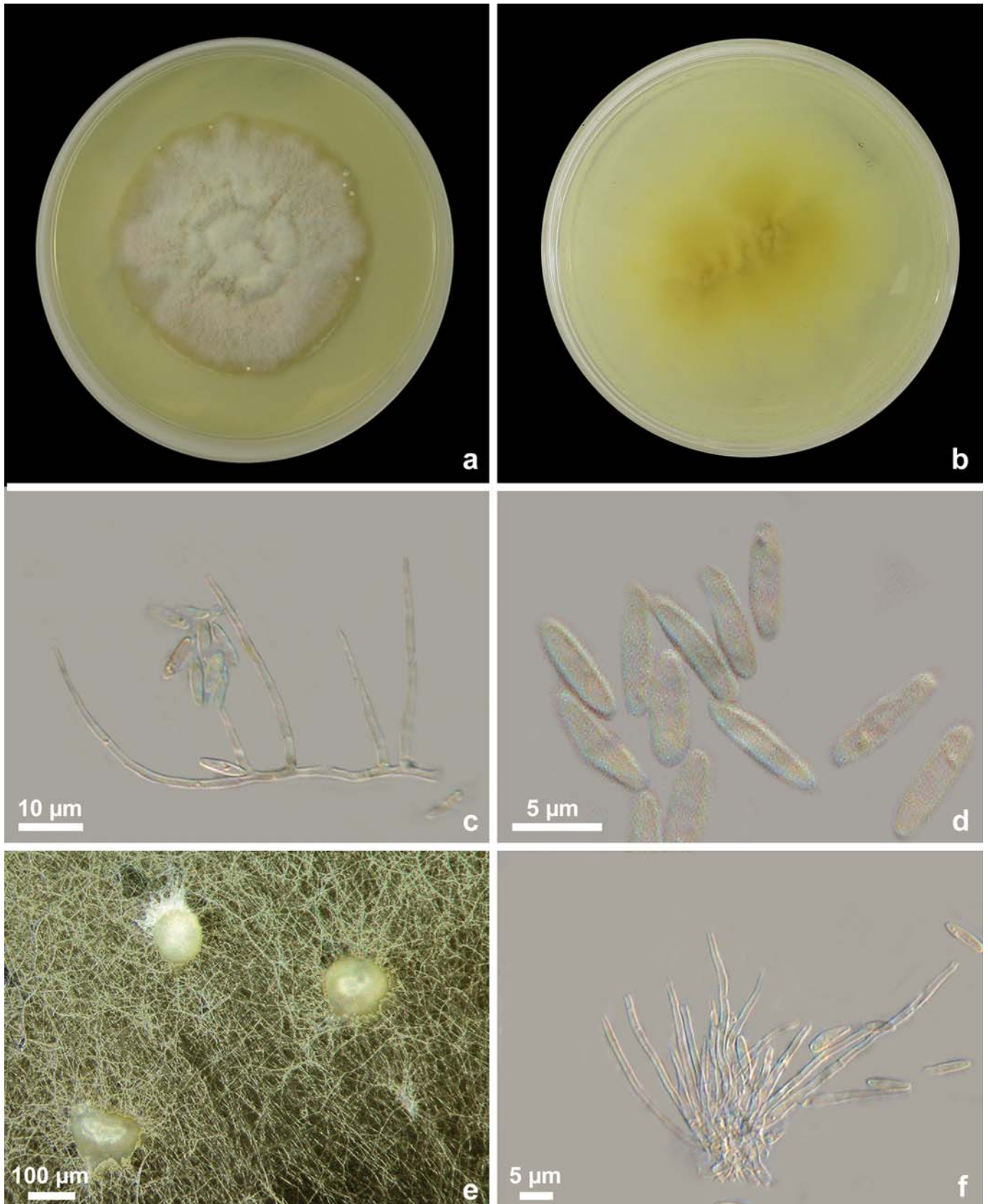


Fig. 2 – a-f: *Xanthonectria pseudopeziza* (CLL15075); a: Culture at four weeks. b: Reverse of culture. c: Primary conidiophores and conidia. d: Conidia. e: Sporodochia at margin of the colony. f: Conidiophores and conidia from sporodochium.

Our phylogenetic results based on the comparison of ITS + LSU sequences of two collections of *Xanthonectria pseudopeziza* with those of 14 nectriaceous genera and 10 bionectriaceous genera with acremonium-like asexual morph as well as one species of *Clonostachys* (= *Bionectria* Speg., the type genus of the *Bionectriaceae*) (Fig. 3) clearly demonstrate its affinities with the *Bionectriaceae*, which is in agreement with its morphological traits.

The lack of clear affinities of *X. pseudopeziza* with other genera was already suspected, which accounted for the uncertainty about its taxonomic placement (ROSSMAN, 1983). Our molecular results confirm its morphological distinctiveness: the clade formed by the two sequences of *X. pseudopeziza* is distant from the other bionectriaceous genera included in the phylogenetic analysis, and seems to represent, with the genus *Ijuhya* (STARBÄCK, 1899), a basal lineage in the *Bionectriaceae*. *Ijuhya* differs from *Xanthonectria* in having smaller ascospores with a wall 15–45 µm thick, composed of one region of small thick-walled cells. Likewise *Ijuhya* typically features a discoid ascospore apex bearing fasciculate hairs forming a stellate crown. While most lignicolous bionectriaceous genera compared with *Xanthonectria* in our cladogram feature somewhat hairy or verrucose ascospores, the monotypic genus *Ochronectria* represented by *O. calami* Rossman & Samuels resembles *Xanthonectria* in having glabrous pale yellow to yellow-orange ascospores (ROSSMAN *et al.*, 1999). Moreover, the ascospore wall of *Ochronectria* is thick (45–60 µm), composed of three regions and contains orange oily droplets resembling that of *Xanthonectria*, and its ascospores are

likewise narrowly fusiform and multiseptate. Beside these similarities, *O. calami* differs from *Xanthonectria* by smaller ascospores which are seated on a thin subiculum and collapse upon drying, and a tropical distribution with a strong preference for monocotyledonous hosts. The disparity between the two genera is supported by their distant position in our dendrogram.

Morphologically, *Xanthonectria* resembles some species of *Hydropisphaera* in having glabrous, yellow to orange ascospores and multiseptate ascospores, but differs from them in having an ascospore wall of three regions, composed of thick-walled cells and not collapsing upon drying. On the contrary, the ascospore wall of *Hydropisphaera* is composed of two regions of thin-walled cells, which accounts for the collapse upon drying (ROSSMAN, pers. comm.). Multiseptate ascospores are reported from other genera belonging to the *Bionectriaceae* such as *Hydropisphaera*, *Ijuhya*, *Pronectria* and *Protocreopsis*, thus this character cannot be discriminant at the generic level.

The presence of orange oily droplets in the ascospore wall might be seen as an interesting discriminating character that can be easily observed. However, this character is not always consistent within a given species and is not considered taxonomically relevant at the generic level because this feature is encountered in several bionectriaceous genera such as *Clonostachys* Corda (= *Bionectria* Speg.), *Hydropisphaera* Dumort., *Lasionectriella* Lechat & J. Fourn., *Ochronectria*, *Paranectria* Sacc., *Peethambaria* Subram. & D.J. Bhat and *Pronectria* Clem.

Table 1 – Genera, species and GenBank accession numbers of sequences used in the phylogenetic analyses. In bold: sequences generated for this study.

Species	Asexual morph	GenBank accession numbers	
		ITS	LSU
<i>Albonectria rigidiuscula</i>	fusarium-like	HM054158	HM042403
<i>Clonostachys byssicola</i>	clonostachys-like	KC806270	GQ506011
<i>Calonectria lauri</i>	cylindrocladium-like	GQ280584	GQ280706
<i>Cosmospora viridescens</i>	acremonium-like	KC291731	KC291765
<i>Hydropisphaera erubescens</i>	acremonium-like	KF813068	AY545726
<i>Hypomyces aurantius</i>	cladobotryum-like	KM509060	KC009213
<i>Ijuhya paraparilis</i>	acremonium-like	FJ969801	HM050303
<i>Lanatonectria flocculenta</i>	actinostilbe-like	JF832657	JF832714
<i>Lasionectria mantuana</i>	acremonium-like	HM484858	GQ505994
<i>Microcera coccophila</i>	fusarium-like	KC338994	KC338993
<i>Nalanthamala psidii</i>	nalanthamala-like	AY554208	AY554259
<i>Nectria cinnabarina</i>	tubercularia-like	HM484712	HM484756
<i>Nectriopsis exigua</i>	acremonium-like	HM484865	GQ505986
<i>Neocosmospora vasinfecta</i>	fusarium-like	AY381155	AY381155
<i>Neonectria ditissima</i>	cylindrocarpon-like	HM364298	HM364311
<i>Ochronectria calami</i>	acremonium-like	–	AF193244
<i>Pseudocosmospora rogersonii</i>	acremonium-like	KC291729	KC291780
<i>Pseudonectria pachysandricola</i>	volutella-like	JF832658	JF832715
<i>Roumegueriella rufula</i>	gliocladium-like	–	GQ505999
<i>Selinia pulchra</i>	acremonium-like	HM484859	GQ505992
<i>Stylonectria wegeliniana</i>	fusarium-like	KM231817	KM231690
<i>Varicosporella aquatica</i>	fusarium-like	KP192668	KP192670
<i>Verrucostoma freycinetiae</i>	acremonium-like	HM484866	GQ506013
<i>Viridisporea diparietispora</i>	penicillifer-like	HM484859	AY489735
<i>Xanthonectria pseudopeziza</i>	acremonium-like	KU593584	KU593583
<i>Xanthonectria pseudopeziza</i>	acremonium-like	KU946963	KU946964

Acknowledgements

The authors gratefully acknowledge Dr Amy Rossman (Oregon State University, Corvallis, U.S.A.) for her advices and scientific support and for her presubmission review. Special thanks go to Christian Feuillet (Smithsonian and Oregon State) for his judicious suggestion of the name *Xanthonectria*. Alain Gardiennet, Michel Hairaud and Ralph Vandiest are warmly thanked for the material they collected, which was very useful for this work. We are also grateful to Lionel Kervran (Muséum national d'Histoire naturelle, herbarium PC, Paris) for the loan of the original material of Desmazières for the

purpose of this study, and for having facilitated the visits of P.-A. Moreau at PC.

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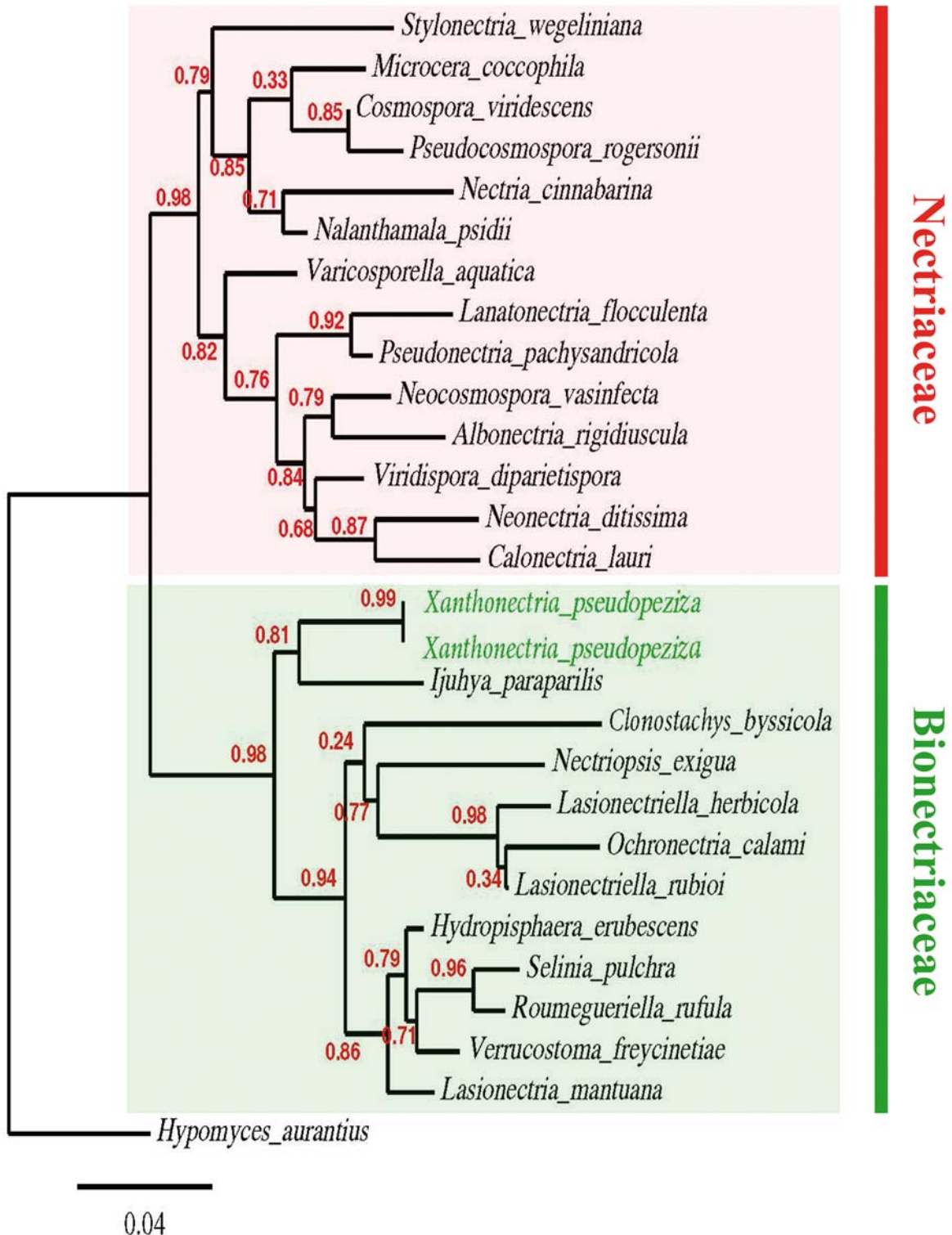


Fig. 3 – Phylogenetic reconstruction of Nectriaceae and Bionectriaceae based on ML analysis of combined ITS and LSU sequences

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