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Gymnographopsis aptrootiana (*Graphidales*), a new addition to a poorly known genus with unique morphological features

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Abstract. The new species *Gymnographopsis aptrootiana* is described from tree bark in rain forests of Costa Rica and Guyana. It is placed in *Gymnographopsis* based on the combination of a partially ecorticate thallus, lirellate ascomata with partly exposed disc, and small, non-amyloid (I–), septate ascospores. Overall, it is most similar to *G. koreaiensis*, but differs in the 1-septate ascospores and the formation of disc-shaped schizidia, as well as its unusual chemistry with three unidentified compounds. We provide a modern overview of the genus *Gymnographopsis*, a key to the five currently accepted species, and a discussion of its position in *Graphidaceae* s.lat. We dedicate this work to our long-standing colleague, friend, and collaborator in the TICOLICHEN project, André Aptroot, for his invaluable contributions to tropical lichenology, on the occasion of his 65th birthday.

Key words: *Heiomasia*, *Redonographa*, *Redonographoideae*, *Stegobolus*, TLC

Introduction

Tropical crustose lichen communities, especially on tree bark, are frequently dominated by members of *Graphidaceae* s.lat. – the second most speciose family of lichen-forming fungi and the most speciose in tropical latitudes – and its allies (Staiger 2002; Frisch et al. 2006; Lücking et al. 2014). *Graphidaceae* s.lat. continues to present novelties for lichenologists almost on a weekly basis. For instance, Lücking et al. (2009) reported 330 accepted species for a worldwide key to *Graphis* Adans., whereas currently well over 400 species are accepted in this genus and its recent segregate, *Allographa* Chevall. (Lücking & Kalb 2018). Aptroot and colleagues described 134 species of *Graphidaceae* s.lat. from Costa Rica and Brazil alone between 2007 and 2024 (Aptroot & Sipman 2007; Lima et al. 2013; Käffer et al. 2014; Cáceres et al. 2014, 2020; Feuerstein et al. 2014, 2022; Aptroot & Feuerstein 2020; Torres et al. 2020; Sipman & Aptroot 2023; Aptroot et al. 2023a, 2024). Lücking et al. (2014) estimated there may be more than 4,300 species of *Graphidaceae* s.lat., globally, with hundreds remaining undiscovered.

Since the turn of the millennium, *Graphidaceae* s.lat. has seen a dramatic taxonomic reorganization and an almost explosive expansion of new genera and species recognized. As a starting point, the modern revision of *Graphidaceae* s.lat. by Staiger (2002) revealed that traditional genus concepts were highly artificial, and a first revised classification was proposed. As shown and predicted by Staiger (2002), Frisch et al. (2006), and Mangold et al. (2008, 2009), many genera in *Graphidaceae* s.lat. are polyphyletic and many other genus-level rearrangements were subsequently proposed (Bungartz et al. 2010; Nelsen et al. 2010; Rivas Plata et al. 2010; Baloch et al. 2013; Barcenas-Peña et al. 2014; Lumbsch et al. 2014a, b; Mercado-Díaz et al. 2014; Lücking et al. 2016; Lücking & Kalb 2018; Jatnika et al. 2019; Aptroot et al. 2023b). In the course of these studies, the taxonomic importance of morphological and chemical characters has been reevaluated in light of frequent parallel and convergent evolution in the family discovered through molecular studies (Rivas Plata & Lumbsch 2011; Lücking 2014; Lumbsch et al. 2014b; Lücking et al. 2015; Lücking & Kalb 2018). Furthermore, the supra-generic classification of this clade was further refined (Lücking & Rivas Plata 2008; Rivas Plata et al. 2013; Kraichak et al. 2014; Lücking et al. 2017; Miranda-Gonzáles et al. 2020). To complicate things further, the family *Thelotremataceae*, previously separated from *Graphidaceae* by the rounded ascomata (Hale 1978,

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1980, 1981; Frisch et al. 2006), was shown to be nested within *Graphidaceae* s.lat. and was synonymized with the latter (Mangold et al. 2008; Lücking et al. 2017; Lücking 2019). The families *Asterothyriaceae*, *Gomphillaceae*, and *Solorinellaceae* (temporarily subsumed within *Graphidaceae* s.lat. in Rivas Plata et al. 2013), were subsequently shown to represent a single sibling clade recognized as family *Gomphillaceae* (Kraichak et al. 2018; Xavier-Leite et al. 2022; Lebreton et al. 2025). The family/subfamily ranks of several clades remaining within *Graphidaceae* s.lat. (including the clade for our new species) are still in flux – see Discussion below.

Within the lirellate *Graphidaceae*, i.e., those that feature elongate to script-like ascomata, one of the rare and poorly known genera resurrected by Staiger (2002) was *Gymnographopsis* C.W. Dodge, originally established by Dodge (1967) for the single species *G. chilena* C.W. Dodge with a very brief description without providing arguments for the recognition of this new genus. Apart from Staiger's treatment, this taxon had not been reported in the literature after its original description. Only one additional species, *G. latispora* Egea & Torrente, described from South Africa (Egea & Torrente 1996), was later added, also only known from the original description so far. Staiger (2002) apparently overlooked that species, redescribing *Gymnographopsis* as a monospecific genus. Her description contained considerably more detail than the protologue, after reexamination and thin-layer chromatography (TLC) of the type. In her description, Staiger highlighted the thallus with an upper layer of woven hyphae (ecorticate), the small, non-amyloid (I–) ascospores, and the unusual thallus chemistry (no known lichen substances, one unknown substance) as its defining features.

Despite the lack of molecular evidence at the time, Lücking et al. (2013) proposed placement of *Gymnographopsis*, together with the newly established genus *Redonographa* Lücking, Tehler & Lumbsch, in subfamily *Redonographoideae* [*Redonographaceae* if this small clade is recognized at the family level (Wijayawardene et al. 2020)]. Molecular evidence later supported this placement (Miranda-González et al. 2020), based on the discovery of an additional new species of the genus, *G. corticicola* R. Miranda, Herrera-Camp. & Lücking. At that time, all three *Gymnographopsis* species were restricted to (semi)-arid habitats: two on acidic rocks in the coastal fog/dew zone (*G. chilena*, *G. latispora*) and one on bark in dry forest (*G. corticicola*). However, given the combination of characters, in particular the ecorticate thallus, poorly developed (thin) labia (the proper exciple in *Graphidales* lirellate ascocarps), non-amyoid (I–) ascospores, and unusual chemistry with several unknown substances, Lücking et al. (2021) also proposed the placement of a bark-dwelling rain forest lichen, *Graphis koreaiensis* Sipman, a taxon described from French Guiana (Sipman 1994), in *Gymnographopsis*, as *G. koraiensis* (Sipman) Lücking & Sipman.

During the NSF-funded Costa Rican lichen biodiversity inventory between 2002 and 2004, also dubbed the TICOLICHEN project (Chaves et al. 2004; Aptroot et al. 2006; Nelsen et al. 2006; Rivas Plata et al. 2006; Lücking et al. 2006, 2007, 2008; Sipman et al. 2012), a strange *Graphidaceae* was found, represented by a single well-developed collection, that displayed many features of *Gymnographopsis*, but with the production of unusual, disc-shaped schizidia and currently unknown substances. Comparison with herbarium material revealed a second, similar set of specimens in material collected from Guyana in 1997. Here, we formally describe this strange *Graphidaceae* as a new taxon and provide a taxonomic update on the genus *Gymnographopsis*.

Material and methods

Study areas

The studied material was collected by HJMS in Guyana in 1997, in the Upper Mazaruni district near Paruima Mission, and by SWW in Costa Rica in 2004, in Hitoy Cerere Biological Reserve. HJMS has been conducting lichen biodiversity surveys (several thousand collections) since the 1990s under the project *Studies on the Flora of the Guianas* (including the South American countries Guyana, Surinam, and French Guiana), alone or with colleagues, including on several occasions Andre Aptroot (Sipman 1991; Aptroot & Sipman 1993). Paruima is an indigenous village situated in the Cuyuni-Mazaruni Region of Guyana, close to the Venezuelan border. It was originally founded as a mission of the Seventh-day Adventist Church, by converted Pemón Amerindians originating from Venezuela. Paruima is situated in lush Amazon rainforest close to the over 200 m tall Oshi Falls, one of the tallest waterfalls in Guyana. Nearly 750 collections of lichens were gathered from this region in 1997, leading to the discovery of numerous new taxa, including the *Graphidaceae Carbacanthographis inspersomarcescens* Aptroot & M. Cáceres (Sipman & Aptroot 2023) and *Fissurina gigas* Sipman (Sipman 2014), as well as *Enterographa paruimae* Sipman (Van den Boom & Sipman 2016), *Astrothelium corallinum* Aptroot (Aptroot et al. 2016), and *Cladonia persphacelata* Sipman & Ahti (Ahti & Sipman 2013).

The expedition to Hitoy Cerere Biological Reserve in Costa Rica in 2004 was done in the framework of the NSF-funded TICOLICHEN project (2002–2004), a lichen biodiversity inventory of Costa Rica led by RL, in collaboration with LUT, JLCC, HJMS, André Aptroot, SWW, MPN, Marie Trest, William Buck, and other collaborators. The team visited numerous localities representing the diverse ecosystems of the country, assembling more than 21,000 collections with sets in national and international herbaria (Chaves et al. 2004; Lücking et al. 2008). To date, two papers on *Graphidaceae* have been published from this project (Lücking et al. 2008; Sipman et al. 2012). Hitoy Cerere Biological Reserve is tucked away in the Talamanca Mountain Range, southwest of the Estrella Valley and about 67 km from the city of Limón on the Caribbean coast of Costa Rica. Bordered by the Tayni, Telire, and Talamanca Indigenous Reserves, Hitoy Cerere is a vital part of the vast La Amistad Biosphere Reserve. The landscape climbs from 100 to over 1,000 meters

above sea level and is carved by the Hitoy and Cerere rivers. Their names, originating from the Bribri language, mean "woolly" (referring to moss-covered stones) and "clear" – a perfect description of these waters. The vegetation of the reserve represents a rugged, rain-drenched wilderness receiving over 3,500 mm of rain annually, which feeds rocky rivers, rushing rapids, and stunning waterfalls. The forests of the reserve are incredibly dense and stay lush and green year-round. Depending on soil, slope, and wind exposure, one may find different habitats with varying tree species and canopy heights. Most of the trees soar above 30 meters, their branches draped in bryophytes, lichens, and diverse vascular epiphytes. On the forest floor, dominated by palms and palm-like cycads of the genus *Zamia*, thick woody vines hang between the trees, rounding out a rich ecosystem home to around 380 plant species. Lichens of Hitoy Cerere Biological Reserve have been the subject of various studies, including new taxa, such as *Trichothelium argenteum* Lücking & L.I. Ferraro (Lücking & Ferraro 1997) and *Lueckingia polyspora* Aptroot & Umaña (Aptroot et al. 2006), as well as molecular studies in foliicolous *Porina* lichens (Baloch & Grube 2009).

Morphological and chemical studies

The material was examined morphologically, anatomically, and chemically, at the Wisconsin State Herbarium (WIS) of the University of Wisconsin and in the Botanischer Garten und Botanisches Museum Berlin, Freie Universität Berlin (BGBM). For the morphological studies, we used at WIS a LEICA S6D stereomicroscope, and at BGBM a LEICA S6D and a LEICA Zoom 2000 stereomicroscope. Anatomy was assessed using at WIS a ZEISS (2000s-made) compound microscope, with hand sections made in deionized water, and at BGBM a ZEISS Axiostar Plus and a ZEISS Axioskop compound microscope, with hand sections made in tap water. Macrophotography was done using a NIKON Z7 with a NIKKOR MC50/2.8 macro lens, with a RAYNOX Digital Camera Macroscopic Lens 4x attached to it, and a CULLMANN CUlight V 220DL LED light source. Microscopic images were taken under 400× and 1000× magnification with a SAMSUNG Galaxy A71 cell phone attached to the Pl 10×/20 ocular of the ZEISS Axioskop compound microscope. For spot tests, we used commercial bleach (C), 10% potassium hydroxide solution (K), and para-phenylene-diamine crystals dissolved in 96% ethanol (P). Thin-layer chromatography (TLC) at BGBM was performed following Orange et al. (2010), using solvents A (toluene:dioxane = 180:45), B' (hexane:methyl tert-butyl ether:formic acid =140:72:18), and C (toluene:acetic acid = 170:30). Two TLC runs were performed. For one run, which included collections from Guayana and was run in all three solvents, controls were atranorin, norstictic acid, and connorstictic acid (from *Cladonia rangiferina* and *C. symphycarpa*). For the other run, which combined collections from Costa Rica and Guayana together with diverse *Usnea* species and was done in solvent C only, controls were usnic acid, stictic acid, menegazziaic acid, and constictic acid (from *Usnea aranea*). Plates were read in room light and UV 254 nm and 365 nm, before and after charring. Relative R_f values for the observed spots were calculated using the Orange et al. (2010) formula and control standards for that plate, then R_f values for the two plates were averaged. To aid their identification, substances were compared with lichen substance databases (Schumm & Elix 2015, 2016; Elix 2022) as well as Mytabolites (Lafferty et al. 2024).

Results

Gymnographopsis aptrootiana Will-Wolf, Lücking, L. Umaña, Chaves, M.P. Nelsen & Sipman, sp. nov.

MycoBank MB 864726

Diagnosis: Differing from *Gymnographopsis koreaiensis* in the 1-septate ascospores and the formation of disc-shaped schizidia.

Type: Costa Rica, Limón: Hitoy Cerere Biological Reserve, Hitoy Cerere Biological Station, La Amistad Caribe Conservation Area, Talamanca Ridge, 125 km ESE of San José, 40 km S of Limón, near Pandora; trails through forest above station (Sendero Espavel and Sendero Tepesquintle); 83°02′W, 9°40′N, 150–300 m; lowland to lower montane rainforest zone, partly disturbed primary forest on bark (stilt root) of *Arecaceae*; 10 Mar. 2004, S. Will-Wolf 12715f (CR – holotype!; B, F, USJ, WIS – isotypes!).

Description. Thallus crustose, corticolous, epiperidermal, continuous, upper layer of woven hyphae of varying density (ecorticate), light greenish to bluish grey, with a thin, dark brown to blackish prothallus line. Thallus producing disc-shaped schizidia, especially near the margin (Fig. 1A, B); schizidia rounded to somewhat irregular in outline, 0.2–0.6 mm diam., eventually detaching from the surface and leaving holes in the grey thallus surface as if punched out. Thallus in section 50–130 µm thick, with an irregular photobiont layer concentrated above the middle, about 30 µm thick, and a diffuse medulla, nubilous with small, greyish crystals that hardly dissolve in K; photobiont trentepohlioid, rounded to irregular in outline, 8–12 µm diam. Ascocarps abundant, lirelliform, immersed to erumpent, unbranched to more or less radiately branched, but then often interrupted or divided into lines of individual, short ascomata, overall up to 5 mm long and 0.15–0.2 mm broad. Disc partly concealed, partly exposed, beige to brown, non-pruinose; proper margin slightly raised above the disc, visible as thin white line, entire, separated from the greyish/whitish thalline margin by a split (Fig. 1B inset). Excipulum apically entire, 15–25 µm broad, yellowish, but apically darkened (Fig. 1C), I+ reddish brown; no distinct periphysoids observed. Hymenium 50–70 µm high, colorless, not inspersed; paraphyses embedded in a gelatinous matrix, irregular, partly branched and anastomosing (Fig. 1D), I–; epithecium indistinct; hypothecium prosoplectenchymatous, 15–25 µm high, colorless to pale yellowish. Asci clavate, 40–50 × 10–12 µm, with apically thickened tholus and narrow ocular chamber forming a ring-shaped structure projecting down into the lumen (Fig. 1F, G), I– (n = 23, from type and paratype material). Ascospores

8 per ascus, colorless, 1-septate (very rarely with an additional septum near the middle), broadly ellipsoid to ovoid, 7–10(–12) × 3–4(–5) µm (n = 78, from type and paratype material), I–, walls and septum thin to only slightly thickened, lumina rectangular, rounded only at outer ends (Fig. 1E–G). Pycnidia and conidia not observed.

Secondary chemistry. The thallus surface is K+ pale yellow (all other spot tests negative) and UV– to faintly UV+ bluish. Three unidentified substances were detected with TLC. They were most clearly differentiated in solvent C (Fig. 2); they were not or barely visible before charring (no quenching under UV 254 nm and partial reaction under UV 365 nm) and were barely visible after charring under natural light. These substances are clearly apparent under UV light, particularly UV 365 nm (long-wave), with a broad spot with bright turquois fluorescence (unknown 1, major), a narrow spot with light blue fluorescence (unknown 2; minor), and a narrow spot with pinkish fluorescence (unknown 3, minor) at the height of usnic acid. The three unknown substances from the type CR specimen and the three

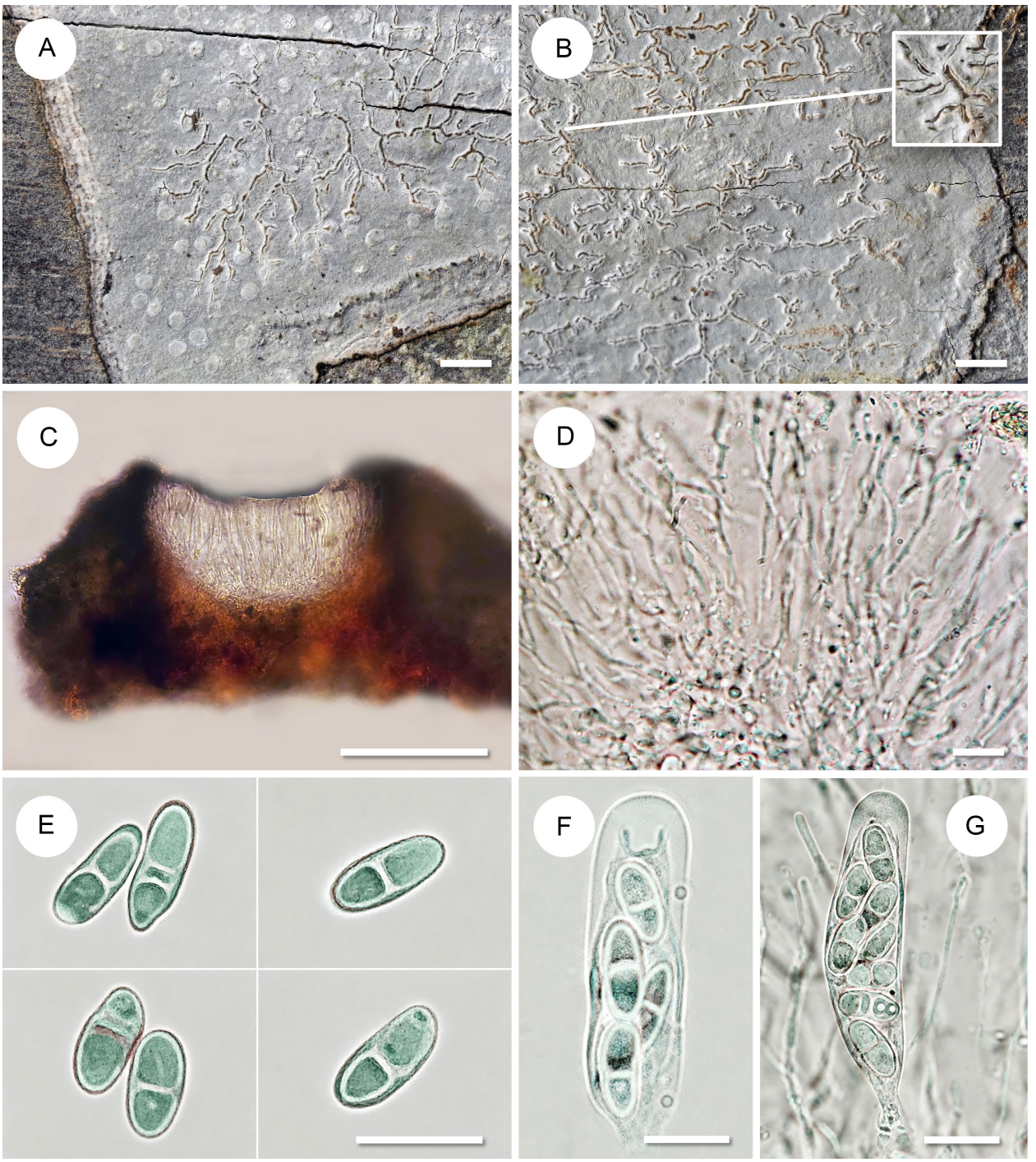

Figure 1. Morphology and anatomy of *Gymnographopsis aptrootiana* (isotype in B). A, B – thallus with lirellae and schizidia; C – section through lirella; D – portion of the lateral hamathecium showing partly branched and anastomosing paraphyses; E – ascospores; F – ascospores in loose collapsing ascus; G – intact ascus with ascospores, showing the apical plug/ring-structure projecting down into the lumen, typical of *Graphidaceae*. Scales: A, B = 1 mm; C = 100 µm; D–G = 10 µm. C–G – sections in water; D–G – 1000× oil immersion.

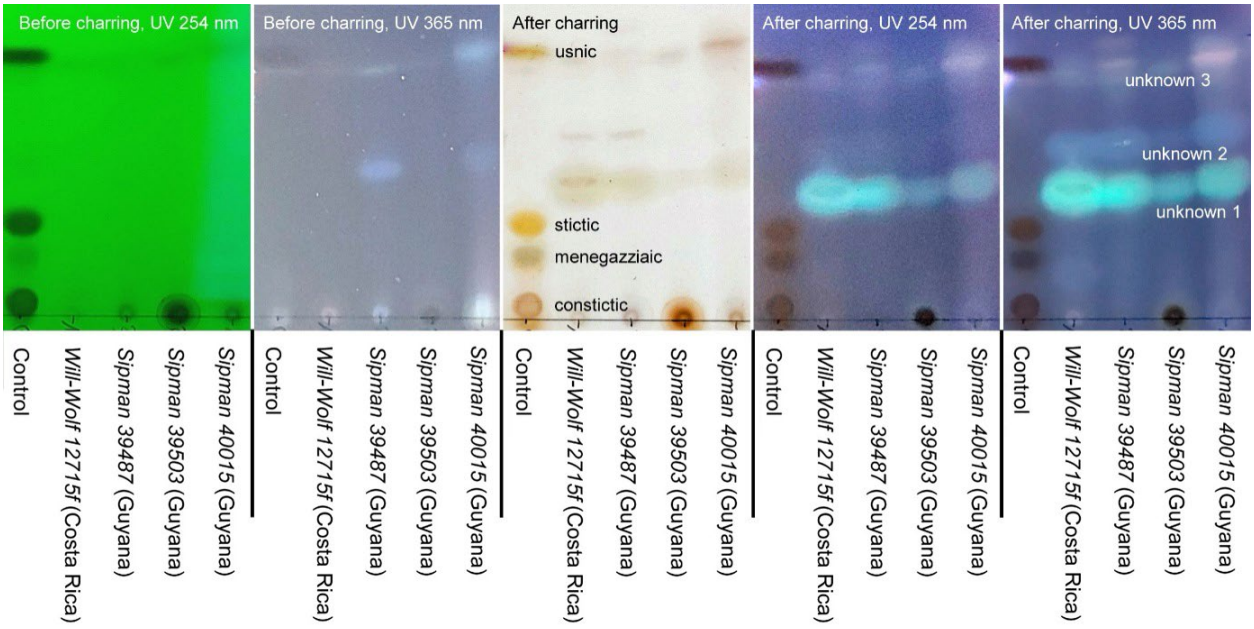

Figure 2. Results of the TLC analysis of four specimens of *Gymnographopsis aptrootiana* in solvent C. From left to right, before charring with UV short then long, charred plate in room light, after charring with UV short then long.

Guyanas specimens performed quite similarly across two TLC runs. Average relative R_f values (from both the B isotype and the Guyanas specimens) from solvents A/B'/C are 41-42/8-10/24-25 for unknown 1, 52-53/10-12/31-32 for unknown 2, and 68-71/58-62/66-68 for unknown 3. Their characteristics did not match known compounds (Schumm & Elix 2015, 2016; Elix 2022; Lafferty et al. 2024), and Jack Elix confirmed from images of the TLC plates (personal correspondence with HJMS) that our three unknown substances remain unidentified. These substances are not fatty acids and, given their rounded shape and spot colors, not terpenoids either; more work is needed to identify their nature.

Ecology and distribution. *Gymnographopsis aptrootiana* is presently known from only two countries. The type locality is in Costa Rica, where it was found along a forest trail through partly disturbed primary lowland rain forest at about 250 m altitude, growing on the stilt roots of an unidentified palm (possibly *Iriartea deltoidea* Ruiz & Pav.). It was accompanied by *Arthonia rubiginella* Nyl., *Porina curtula* Malme, and unidentified species of *Pertusaria* and *Vezdaea*, as well as an unknown sorediate crust. Other specimens are from three localities in Guyana, in sites representing primary rain forest and selectively logged forest at 400–600 m altitudes. Two were near Paruima village, growing on the rough bark of different, unidentified phorophyte trees.

Remarks. This new species is characterized by a unique combination of features: (i) a crustose, ecorticate thallus similar in appearance to thalli of *Diorygma* or *Thalloloma*, but forming disc-shaped schizidia, combined with branched, pale gray-white, *Diorygma*-like lirellae, and (ii) producing very small, 1-septate, I-negative, colorless ascospores. Currently the only genus combining (in at least some of the species placed in that genus) a similar thallus morphology with I-negative, colorless ascospores is *Gymnographopsis* (Staiger 2002; Lücking & Rivas Plata 2008; Miranda-González et al. 2020; Lücking et al. 2021). Therefore, the new species is placed into that genus. It is similar to *G. koreaiensis* (Sipman 1994; Lücking et al. 2021), which agrees in thallus and, to some extent, lirellae morphology, but that species lacks vegetative propagules and its ascospores are 3-septate.

The new species should not be confused with representatives of the genus *Heiomasia* (Nelsen et al. 2010; Jagadeesh Ram 2014; Kalb 2020). These also produce whitish, ecorticate thalli and, with one exception, are furnished with disc-shaped propagules. In contrast to *Gymnographopsis aptrootiana*, the disc-shaped or isidioid outgrowths are attached to the thallus by one side and usually oriented obliquely upright, so they cannot be compared to genuine schizidia in which the upper layers of the proper thallus detach (Poelt 1965). *Heiomasia* species also produce lirellate ascomata, but have well-developed, internally carbonized labia, so are easily set apart from *Gymnographopsis*. *Heiomasia* is not closely related to *Gymnographopsis* (subfamily *Redonographoideae*), but falls in a small clade in tribe *Wirthiotremateae* within subfamily *Graphidoideae*, close to the genus *Carbacanthographis* (Nelsen et al. 2010; Medeiros et al. 2017). Sterile thalli of the genus *Stegobolus* (tribe *Ocellularieae* in subfamily *Graphidoideae*) with disc-shaped schizidia can be easily set apart by the olive-green, densely corticate thallus and schizidia (Frisch et al. 2006).

Additional specimens examined. GUYANA. Upper Mazaruni District: Raruima Mission, Rain Mountain SE of the village; 61°04′W, 05°48′N, 500 m; primary forest relic on W-foot, on bark; 30 Apr. 1997, H. Sipman 39487 (B 60 0165585); ibid., 600 m; tall primary forest on top plateau, on bark; 30 Apr. 1997, H. Sipman 39503 (B 60 0165601). Kamarang, 0–1 km along the trail to Waramadan; 60°37′W, 05°52′N, 400 m; selectively logged Mora forest, on bark; 12 May 1997, H. Sipman 40015 (B 60 0167410). Upper Takutu District: ~50 km S of Aishalton,

~6 km S of Kuyuwini Landing, along trail to Kassikaityu river; 59°15′W, 02°01′N, 230 m; seasonally dry, ~25 m tall primary forest, 0–5 m high on bark of 22 m tall *Licania densiflora* (*Chrysobalanaceae*) tree; 19–21 Oct. 1992, H. Sipman 65863a (B 60 0208447).

Discussion

Circumscription and delimitation of the genus *Gymnographopsis*

As outlined above, *Gymnographopsis* was originally established by Dodge (1967) for a single species, *G. chilena* C.W. Dodge, a rock-dwelling lichen from Chile. Two subsequently established names, "G. follmannii Dodge" and *G. cerei* Follmann (Follmann 1967), do not belong to this genus. "Gymnographopsis follmannii Dodge" is a clerical error introduced in the compilation of fungal names in the *Index of Fungi* (Hawksworth 1972), as the name to be listed was *Graphis follmanii* C.W. Dodge. According to the *Code*, the listed name, even if representing an unintentional error, is to be interpreted as an inadvertent yet valid combination, to be cited as *Gymnographopsis follmannii* (C.W. Dodge) D. Hawksw. The underlying material actually belongs in *Opegrapha* s.lat. (Lücking et al. 2013). In contrast, *Gymnographopsis cerei* appears to represent a species of *Fissurina* (Lücking et al. 2013).

As a result, the originally monospecific genus *Gymnographopsis* now contains five species: *G. chilena*, *G. latispora*, *G. corticicola*, *G. koreaiensis* (Egea & Torrente 1996; Staiger 2002; Miranda-Gonzáles et al. 2020; Lücking et al. 2021), and the new species introduced here. With each added species, the circumscription of the genus has widened, from initially saxicolous species in (semi-) arid climates (*chilena*, *saxicola*), to corticolous species in dry forest (*corticicola*) and then rain forest (*koreaiensis*, *aptrootiana*), to species with vegetative propagules (*aptrootiana*). In parallel with other *Graphidaceae* s.lat. genera, *Gymnographis* species vary in chemistry, either lacking secondary substances, or one species with stictic acid complex compounds, or with different unknown substances in the three remaining species. As a diagnostic feature of the genus, the ascospores are I-negative and small, ranging from 1-septate to submuriform according to the species.

Morphologically, *Gymnographopsis* is similar to species of *Diorygma* Eschw. and *Thalloloma* Trevis. in the ecorticate thallus, but differs in the small, non-amyloid (I–) ascospores and the short periphysoids emerging from the upper excipulum. Its anatomical characteristics point to a possible relationship with *Anomalographis* Kalb, which differs in the well-developed, prominent lirellae and the absence of excipular periphysoids (Staiger 2002; Lücking & Rivas Plata 2008; Lücking et al. 2013). The latter genus has not yet been sequenced and so its systematic position in the family is unknown. A close relationship of *Gymnographopsis* with the genus *Redonographa*, a genus with distinctly carbonized labia, has been shown for the only sequenced species, *G. corticicola* (Miranda-González et al. 2020). However, no sequence data are yet available for the type species, *G. chilena*. Many species of *Fissurina* s.lat., situated in the neighboring clade (*Fissurinaceae*/*Fissurinoideae*) agree in the non-amyloid ascospores, but differ in the either densely corticate or ecorticate and then endoperidermal thallus (Staiger 2002; Archer 2009).

Systematic placement of *Gymnographopsis*

As noted in the Introduction, delimitation of families in the order *Graphidales* has varied over the past two decades. While most workers have accepted a single family, *Graphidaceae*, with a structured division into subfamilies and tribes (Mangold et al. 2008; Rivas Plata et al. 2012, 2013; Lücking et al. 2013, 2015; Lumbsch et al. 2014a; Cáceres et al. 2020), others recognized several clades at family level, including *Diploschistaceae*, *Fissurinaceae*, *Redonographaceae*, and *Thelotremataceae* (Hodkinson 2012; Kraichak et al. 2018; Wijayawardene et al. 2020).

In two cases (*Diploschistaceae*, *Thelotremataceae*), the thus defined families are polyphyletic or paraphyletic assemblies (Lücking 2019), whereas the other two are monophyletic and well-supported and could be recognized as either subfamilies (*Fissurinoideae*, *Redonographoideae*) or families (*Fissurinaceae*, *Redonographaceae*). Thus, *Gymnographopsis* could be placed in either *Graphidaceae* subfam. *Redonographoideae* or in the separate family *Redonographaceae*. However, there appears to be no new morpho-anatomical-chemical information gain in doing so if the only underlying reasoning is clade age (reconstructed from temporal banding) and not topology or diagnostic characters. For instance, there are no discernable morphological, anatomical and chemical differences between *Fissurinaceae* and the residual *Graphidaceae*. Both agree in virtually all features, displaying the same variation of ascoma types (lirellate, rounded, pseudostromatic, variously carbonized, without or with columella), ascospore types (size range, septation, variation in amyloidity/spore reaction in I), and secondary chemistry (stictic and psoromic acid, as well as pigments as common substances). We therefore lean towards recognizing *Graphidaceae* in the sense of Lumbsch et al. (2014a), Lücking et al. (2017) and Lücking (2019), as a single family, with major clades distinguished at the subfamily and tribe level, thus placing the genus *Gymnographopsis* in *Graphidaceae* subfamily *Redonographoideae*.

Key to the species of *Gymnographopsis*

The following key distinguishes the species currently placed in *Gymnographopsis*, i.e., *Graphidaceae* with thallus upper layer of woven hyphae (ecorticate), lirellate ascomata with thin labia, thin excipulum, and I-negative ascospores. Potentially similar species of *Diorygma* and *Thalloloma* can be distinguished by their amyloid (I+ violet-blue) ascospores, whereas *Heiomasia* features lirellae with distinct, prominent labia and/or vegetative propagules that grow out from the thallus surface and do not represent genuine schizidia. Other schizidiate genera, such as *Stegobolus*, feature densely corticate *schizidia*.

1 Ascospores submuriform; growing on acidic rocks in coastal fog/dew areas 2

Ascospores transversely 1–3-septate; growing on bark 3

2(1) Lirellae elongate, up to 3 mm long; ascospores 20–26 × 8–12 µm; conidia 6–8 × 1–1.5 µm; thallus with unknown substance that reacts P+ orange (Egea & Torrente 1996); southern South America (Chile) . . . . . ***G. chilena***

Lirellae short, crowded, up to 1.5 mm long; ascospores 20–35 × 12–18 µm; conidia 10–15 × 1–1.5 µm; thallus lacking secondary compounds, P–; South Africa . . . . . ***G. latispora***

3(1) Ascospores 1-septate; disc-shaped schizidia present; thallus containing three unknown substances; in rain forest; known from Costa Rica and Guyana . . . ***G. aptrootiana***

Ascospores 3-septate; vegetative propagules absent; chemistry and ecology variable 4

4(3) Lirellae irregularly to almost radiately branched; excipulum colourless; ascospores 8–12 × 3–5 µm; thallus with unknown lichen substance, K–, P–; in rain forest; known from Colombia, Guyana, French Guiana . . . . . ***G. koraiensis***

Lirellae short, unbranched; excipulum apically dark brown; ascospores 12–18 × 3–5 µm; norstictic (major) and connorstictic (minor) acids, K+ yellow then red, P+ orange; in dry forest; known from Mexico . . . . . ***G. corticicola***

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References

Ahti, T. & Sipman, H. J. M. 2013. Ten new species of *Cladonia* (*Cladoniaceae*, Lichenized Fungi) from the Guianas and Venezuela, South America. *Phytotaxa* 93: 25–39. https://doi.org/10.11646/phytotaxa.93.1.2

Aptroot, A. & Feuerstein, S. 2020. New *Graphidaceae* from south and central Brazil. *Archive for Lichenology* 16: 1–11.

Aptroot, A. & Sipman, H. J. M. 1993. *Trichotheliaceae (Lichens). Flora of the Guianas*. Series E: Fungi and Lichens, Fascicle 2, Koeltz Scientific Books, Königstein, Germany.

Aptroot, A. & Sipman, H. J. M. 2007. A new *Schistophoron* (*Graphidaceae*) from Costa Rica. *Bibliotheca Lichenologica* 96: 21–24.

Aptroot, A., Umaña-Tenorio, L., Chaves, J. L. & Trest, M. T. 2006. A first assessment of the TICOLICHEN biodiversity inventory in Costa Rica: three new squamulose genera (*Lecanorales*: *Ramalinaceae* and *Pilocarpaceae*). *The Journal of the Hattori Botanical Laboratory* 100: 617–623. https://doi.org/10.18968/jhbl.100.0_617

Aptroot, A., Ertz, D., Etayo, J. A., Gueidan, C., Mercado-Díaz, J. A., Schumm, F. & Weerakoon, G. 2016. Forty-six new species of *Trypetheliaceae* from the tropics. *The Lichenologist* 48: 609–638. https://doi.org/10.1017/S002428291600013X

Aptroot, A., Lücking, R. & Cáceres, M. E. S. 2023a. New species and records of *Graphidaceae* and *Gomphillaceae* (Lichenized Fungi) from Brazil. *Plant and Fungal Systematics* 68: 249–261. https://doi.org/10.35535/pfsyst-2023-0010

Aptroot, A., Weerakoon, G., Cannon, P., Coppins, B., Sanderson, N. & Simkin, J. 2023b. *Ostropales*: *Graphidaceae*, including the genera *Allographa*, *Clandestinotrema*, *Crutarndina*, *Diploschistes*, *Fissurina*, *Graphis*, *Leucodecton*, *Phaeographis*, *Schizotrema*, *Thelotrema* and *Topeliopsis*. *Revisions of British and Irish Lichens* 36: 1–23. https://britishlichensociety.org.uk/sites/default/files/Graphidaceae.pdf

Aptroot, A., Lücking, R. & Cáceres, M. E. S. 2024. New species, records and combinations of *Graphidaceae* (Lichenized Fungi) from Brazil. *The Bryologist* 127: 22–55. https://doi.org/10.1639/0007-2745-127.1.022

Archer, A. W. 2009. *Graphidaceae*. In: McCarthy, P. M. (ed.), *Flora of Australia*, Volume 57. *Lichens* 5. ABRS and CSIRO Publishing, Canberra and Melbourne, pp. 84–194.

Baloch, E. & Grube, M. 2009. Pronounced genetic diversity in tropical epiphyllous lichen fungi. *Molecular Ecology* 18: 2185–2197. https://doi.org/10.1111/j.1365-294X.2009.04183.x

Baloch, E., Lumbsch, H. T., Lücking, R. & Wedin, M. 2013. New combinations and names in *Gyalecta* for former *Belonia* and *Pachyphiale* (*Ascomycota*: *Ostropales*) species. *The Lichenologist* 45: 723–727. https://doi.org/10.1017/S0024282913000492

Barcenas Peña, A., Lücking, R., Miranda-González, R. & Herrera-Campos, M. A. 2014. Three new species of *Graphis* (*Ascomycota*: *Ostropales*: *Graphidaceae*) from Mexico, with updates to taxonomic key entries for 41 species described between 2009 and 2013. *The Lichenologist* 46: 69–82. https://doi.org/10.1017/S0024282913000637

Bungartz, F., Lücking, R. & Aptroot, A. 2010. The family *Graphidaceae* (*Ostropales*: *Lecanoromycetes*) in the Galapagos Islands. *Nova Hedwigia* 90: 1–44. https://doi.org/10.1127/0029-5035/2010/0090-0001

Cáceres, M. E. S., Aptroot, A., Parnmen, S. & Lücking, R. 2014. Remarkable diversity of the lichen family *Graphidaceae* in the Amazon rain forest of Rondônia, Brazil. *Phytotaxa* 189: 87–136. https://doi.org/10.11646/phytotaxa.189.1.8

Cáceres, M. E. S., Lücking, R., Schumm, F. & Aptroot, A. 2020. A lichenized family yields another renegade lineage: *Papilionovela albothallina* is the first non-lichenized, saprobic member of *Graphidaceae* subfam. *Graphidoideae*. *The Bryologist* 123: 144–154. https://doi.org/10.1639/0007-2745-123.2.144

Chaves, J. L., Lücking, R., Sipman, H. J., Umaña, L. & Navarro, E. 2004. A first assessment of the Ticolichen biodiversity inventory in Costa Rica: the genus *Dictyonema* (*Polyporales*: *Atheliaceae*). *The Bryologist* 107: 242–249. https://doi.org/10.1639/0007-2745(2004)107[0242:AFAOTT]2.0.CO;2

Dodge, C. W. 1967 ("1966"). New lichens from Chile. *Nova Hedwigia* 12: 307–352.

Egea, J. M. & Torrente, P. 1996. Tres nuevas especies de hongos liquenizados de la Provincia del Cabo (Sudáfrica). *Cryptogamie, Bryologie-Lichénologie* 17: 295–312.

Elix, J. A. 2022. *Catalogue of Standardized Chromatographic Data and Biosynthetic Relationships for Lichen Substances*. Sixth Edition. Published by the author, Canberra.

Feuerstein, S. C., Cunha-Dias, I. P. R. Aptroot, A., Eliasaro, S. & Cáceres, M. E. S. 2014. Three new *Diorygma* (*Graphidaceae*) species from Brazil, with a revised world key. *The Lichenologist* 46: 753–761. https://doi.org/10.1017/S002428291400036X

Feuerstein, S. C., Aptroot, A., da Silveira, R. M. B., Lücking, R. & Cáceres, M. E. S. 2022. An updated world key to the species of *Acanthothecis* s.lat. (*Ascomycota*: *Graphidaceae*), with ten

new species from Brazil. *The Lichenologist* 54: 87–99. https://doi.org/10.1017/S0024282922000019

Follmann, G 1967. Die Flechtenflora der nordchilenischen Nebeloase Cerro Moreno. *Nova Hedwigia* 14: 215–281.

Frisch, A., Kalb, K. & Grube, M. (eds). 2006. Contributions towards a new systematics of the lichen family *Thelotremataceae*. *Bibliotheca Lichenologica* 92: 1–556.

Hale, M. E. 1978. A revision of the lichen family *Thelotremataceae* in Panama. *Smithsonian Contributions to Botany* 38: 1–60.

Hale, M. E. 1980. Generic delimitation in the lichen family *Thelotremataceae*. *Mycotaxon* 11: 130–138. https://doi.org/10.5962/p.417244

Hale, M. E. 1981. A revision of the lichen family *Thelotremataceae* in Sri Lanka. *Bulletin of the British Museum (Natural History), Botany Series* 8: 227–332.

Hawksworth, D. L. 1972. *Index of Fungi Supplement. Lichens 1961–1969*. Commonwealth Mycological Institute, Kew.

Hodkinson, B. P. 2012. An evolving phylogenetically based taxonomy of lichens and allied fungi. *Opuscula Philolichenum* 11: 4–10.

Jagadeesh Ram, T. A. M. 2014. The genus *Herpothallon* (*Arthoniaceae*) in the Andaman Islands, India. *The Lichenologist* 46: 39–49. https://doi.org/10.1017/S0024282913000571

Jatnika, M. F., Weerakoon, G, Arachchige, O., Noer, I. S., Voytsekhovich, A. & Lücking, R. 2019. Discoveries through social media and in your own backyard: two new species of *Allographa* (*Graphidaceae*) with pigmented lirellae from the Palaeotropics, with a world key to species of this group. *The Lichenologist* 51: 227–233. https://doi.org/10.1017/S0024282919000094

Käffer, M. I., De Azevedo Martins, S. M., Cáceres, M. E. S. & Aptroot, A. 2014. A new, locally common *Graphis* (*Graphidaceae*) species from Southern Brazil. *Cryptogamie, Mycologie* 35: 233–237. https://doi.org/10.7872/crym.v35.iss3.2014.233

Kalb, K. 2020. New or otherwise interesting lichens. VII, including a world key to the lichen genus *Heiomasia*. *Archive for Lichenology* 15: 1–18.

Kraichak, E., Parnmen, S., Lücking, R., Rivas Plata, E., Aptroot, A., Cáceres, M. E. S., Ertz, D., Mangold, A., Mercado-Diaz, J. A. Papong, K., van den Broeck, D., Weerakoon, G. & Lumbsch, H. T. 2014. Revisiting the phylogeny of *Ocellularieae*, the second largest tribe within *Graphidaceae* (lichenized *Ascomycota*: *Ostropales*). *Phytotaxa* 189: 52–81. https://doi.org//10.11646/phytotaxa.189.1.6

Kraichak, E., Huang, J. P., Nelsen, M., Leavitt, S. D. & Lumbsch, H. T. 2018. A revised classification of orders and families in the two major subclasses of *Lecanoromycetes* (*Ascomycota*) based on a temporal approach. *Botanical Journal of the Linnean Society* 188: 233–249. https://doi.org/10.1093/botlinnean/boy060

Lafferty, D., Bungartz, F., Elix, J. A. & Schumm, F. 2024. Mytabolites – a program developed at Arizona State University for the interpretation thin-layer chromatography plates, for the analysis of secondary metabolites from lichens, based on an original concept published by E. Mietzsch, H. T. Lumbsch & J. A. Elix. Help & Resources for the Consortium of Lichen Herbaria, available at https://help.lichenportal.org/index.php/en/resources/metabolites/

Lebreton, E., Ertz, D., Lücking, R., Aptroot, A., Carriconde, F., Ah-Peng, C., Huang, J. P., Chen, K. H., Stenger, P. L., Cáceres, M. E. S. & van den Boom, P. 2025. Global phylogeny of the family *Gomphillaceae* (*Ascomycota*, *Graphidales*) sheds light on the origin, diversification and endemism in foliicolous lineages. *IMA Fungus* 16: e144194. https://doi.org/10.3897/imafungus.16.144194

Lima, E. L., Maia, L. C., Aptroot, A. & Cáceres, M. E. S. 2013. New lichen species from Vale do Catimbau, Pernambuco, Brazil. *The Bryologist* 116: 327–329. https://doi.org/10.1639/0007-2745-116.4.327

Lücking, R. 2014. A key to species of the *Ocellularia papillata*, *perforata* and *terebrata* morphodemes (*Ascomycota*: *Graphidaceae*). *Glalia* 6(3): 1–34.

Lücking, R. 2019. Stop the abuse of time! Strict temporal banding is not the future of rank-based classifications in fungi (including lichens) and other organisms. *Critical Reviews in Plant Sciences* 38: 199–253. https://doi.org/10.1080/07352689.2019.1650517

Lücking, R. & Ferraro, L. I. 1997. New species or interesting records of foliicolous lichens. I. *Trichothelium argenteum* (Lichenized *Ascomycetes*: *Trichotheliaceae*). *The Lichenologist* 29: 217–220. https://doi.org/10.1006/lich.1996.0078

Lücking, R. & Kalb, K. 2018. Formal instatement of *Allographa* (*Graphidaceae*): How to deal with a hyperdiverse genus complex with cryptic differentiation and paucity of molecular data. *Herzogia* 31: 535–561. https://doi.org/10.13158/heia.31.1.2018.535

Lücking, R. & Rivas Plata, E. 2008. Clave y guía ilustrada para géneros de *Graphidaceae*. *Glalia* 1(1): 1–41.

Lücking, R., Aptroot, A., Umaña, L., Chaves, J. L., Sipman, H. J. & Nelsen, M. P. 2006. A first assessment of the Ticolichen biodiversity inventory in Costa Rica: the genus *Gyalideopsis* and its segregates (*Ostropales*: *Gomphillaceae*), with a world-wide key and name status checklist. *The Lichenologist* 38: 131–160. https://doi.org/10.1017/S0024282905005657

Lücking, R., Aptroot, A., Chaves, J. L., Sipman, H. J. M. & Umana, L. 2007. A first assessment of the TICOLICHEN biodiversity inventory in Costa Rica: the genus *Coccocarpia* (*Peltigerales*: *Coccocarpiaceae*). *Bibliotheca Lichenologica* 95: 429–457.

Lücking, R., Chaves, J. L., Sipman, H. J. M., Umaña, L. & Aptroot, A. 2008. A first assessment of the Ticolichen biodiversity inventory in Costa Rica: The genus *Graphis*, with notes on the genus *Hemithecium* (*Ascomycota*: *Ostropales*: *Graphidaceae*). *Fieldiana Botany, New Series* 46: 1–126. https://doi.org/10.3158/0015-0746(2008)46[1:AFAOTT]2.0.CO;2

Lücking, R., Archer, A. W. & Aptroot, A. 2009. A word-wide key to the genus *Graphis* (*Ostropales*: *Graphidaceae*). *The Lichenologist* 41: 363–452. https://doi.org/10.1017/S0024282909008305

Lücking, R., Tehler, A., Bungartz, F., Rivas Plata, E. & Lumbsch, H. T. 2013. Journey from the West: did tropical *Graphidaceae* (lichenized *Ascomycota*: *Ostropales*) evolve from a saxicolous ancestor along the American Pacific coast? *American Journal of Botany* 100: 844–856. https://doi.org/10.3732/ajb.1200548

Lücking, R., Johnston, M. K., Aptroot, A., Kraichak, E., Lendemer, J. C., Boonpragob, K., Cáceres, M. E. S., Ertz, D., Ferraro, L. I., Jia, Z.-F., Kalb, K., Mangold, A., Manoch, L., Mercado-Díaz, J. A., Moncada, B., Mongkolsuk, P., Papong, K., Parnmen, S.. Peláez, R., Poengsungnoen, V., Rivas Plata, E., Saipunkaew, W., Sipman, H. J. M., Suttjaritturakan, J., van den Broeck, D., von Konrat, M., Weerakoon, G., Lumbsch, H. T. 2014. One hundred and seventy-five new species of *Graphidaceae*: closing the gap or a drop in the bucket? *Phytotaxa* 189: 7–38. https://doi.org/10.11646/phytotaxa.189.1.4

Lücking, R., Mangold, A., Rivas Plata, E., Parnmen, S., Kraichak, E., & Lumbsch, H. T. 2015. Morphology-based phylogenetic binning to assess a taxonomic challenge: A case study in *Graphidaceae* (*Ascomycota*) requires a new generic name for the widespread *Leptotrema wightii*. *Botanical Journal of the Linnean Society* 179: 436–443. https://doi.org/10.1111/boj.12327

Lücking, R., Mangold, A. & Lumbsch, H. T. 2016. A worldwide key to species of the genera *Myriotrema* and *Glaucotrema* (lichenized *Ascomycota*: *Graphidaceae*), with a nomenclatural checklist of species published in *Myriotrema*. *Herzogia* 29: 493–513. https://doi.org/10.13158/heia.29.2.2016.493

Lücking, R., Hodkinson, B. P. & Leavitt, S. D. 2017. The 2016 classification of lichenized fungi in the *Ascomycota* and *Basidiomycota* – Approaching one thousand genera. *The Bryologist* 119: 361–416. https://doi.org/10.1639/0007-2745-119.4.361

Lücking, R., Moncada, B., Soto-Medina, E., Simijaca, D. & Sipman, H. J. M. 2021. Actualización nomenclatural y taxonómica del Catálogo de Líquenes de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 45: 147–189. https://doi.org/10.18257/raccefyn.1266

Lumbsch, H. T., Kraichak, E., Parnmen, S., Rivas Plata, E., Aptroot, A., Cáceres, M. E. S., Ertz, D., Feuerstein, S. C., Mercado-Díaz, J. A.,

Staiger, B., van den Broeck, D. & Lücking, R. 2014a. New higher taxa in the lichen family *Graphidaceae* (lichenized *Ascomycota*: *Ostropales*) based on a three-gene skeleton phylogeny. *Phytotaxa* 189: 89–51. https://doi.org/10.11646/phytotaxa.189.1.5

Lumbsch, H. T., Parnmen, S., Kraichak, E., Papong, K. B. & Lücking, R. 2014b. High frequency of character transformations is phylogenetically structured within the lichenized fungal family *Graphidaceae* (*Ascomycota*: *Ostropales*). *Systematics and Biodiversity* 12: 271–291. https://doi.org/10.1080/14772000.2014.905506

Mangold, A., Martín, M. P., Lücking, R. & Lumbsch, H. T. 2008. Molecular phylogeny suggests synonymy of *Thelotremataceae* within *Graphidaceae* (*Ascomycota*: *Ostropales*). *Taxon* 57: 476–486. https://doi.org/10.2307/25066016

Mangold, A., Elix, J. A. & Lumbsch, H. T. 2009. *Thelotremataceae*. In: McCarthy, P. M. (ed.), *Flora of Australia*, Volume 57. *Lichens* 5. ABRS and CSIRO Publishing, Canberra and Melbourne, pp. 195–420.

Medeiros, I. D., Kraichak, E., Lücking, R., Mangold, A. & Lumbsch, H. T. 2017. Assembling a taxonomic monograph of tribe *Wirthiotremateae* (lichenized *Ascomycota*: *Ostropales: Graphidaceae*). *Fieldiana Life and Earth Sciences* 9: 1–31. https://doi.org/10.3158/2158-5520-16.9.1

Mercado-Díaz, J. A., Lücking, R. & Parnmen, S. 2014. Two new genera and twelve new species of *Graphidaceae* from Puerto Rico: a case for higher endemism of lichenized fungi in islands of the Caribbean? *Phytotaxa* 189: 186–203. https://doi.org/10.11646/phytotaxa.189.1.14

Miranda-González, R., Lücking, R., Barcenas-Peña, A. & Herrera-Campos, M. A. 2020. The new genus *Jocatoa* (*Lecanoromycetes*: *Graphidaceae*) and new insights into subfamily *Redonographoideae*. *The Bryologist* 123: 127–143. https://doi.org/10.1639/0007-2745-123.2.127

Nelsen, M. P., Lücking, R., Chaves, J. L., Sipman, H. J., Umaña, L. & Navarro, E. 2006. A first assessment of the Ticolichen biodiversity inventory in Costa Rica: the genus *Haematomma* (*Lecanorales*: *Lecanoraceae*). *The Lichenologist* 38: 251–262. https://doi.org/10.1017/S0024282906005573

Nelsen, M., Lücking, R., Plata, E. R. & Mbatchou, J. S. 2010. *Heiomasia*, a new genus in the lichen-forming family *Graphidaceae* (*Ascomycota*: *Lecanoromycetes*: *Ostropales*) with disjunct distribution in Southeastern North America and Southeast Asia. *The Bryologist* 113: 742–751. https://doi.org/10.1639/0007-2745-113.4.742

Orange, A., James, P. W. & White, F. J. 2010. *Microchemical Methods for the Identification of Lichens*. 2nd. Edition. British Lichen Society. London.

Poelt, J. 1965. Uber einige Artengruppen der Flechtengattungen *Caloplaca* und *Fulgensia*. *Mitteilungen der Botanischen Staatssammlung München* 5: 571–607.

Rivas Plata, E. & Lumbsch, H. T. 2011. Parallel evolution and phenotypic disparity in lichenized fungi: a case study in the lichen-forming fungal family *Graphidaceae* (*Ascomycota*: *Lecanoromycetes*: *Ostropales*). *Molecular Phylogenetics and Evolution* 61: 45–63. https://doi.org/10.1016/j.ympev.2011.04.025

Rivas Plata, E., Lücking, R., Aptroot, A., Sipman, H. J. M., Chaves, J. L., Umaña, L. & Lizano, D. 2006. A first assessment of the Ticolichen biodiversity inventory in Costa Rica: the genus *Coenogonium* (*Ostropales*: *Coenogoniaceae*), with a world-wide key and checklist and a phenotype-based cladistic analysis. *Fungal Diversity* 23: 255–321.

Rivas Plata, E., Lücking, R., Sipman, H. J. M., Mangold, A., Kalb, K. & Lumbsch, H. T. 2010. A world-wide key to the thelotremoid *Graphidaceae*, excluding the *Ocellularia-Myriotrema-Stegobolus* clade. *The Lichenologist* 42: 139–185. https://doi.org/10.1017/S0024282909990491

Rivas Plata, E., Lücking, R. & Lumbsch, H. T. 2012. A new classification for the family *Graphidaceae* (*Ascomycota*: *Lecanoromycetes*: *Ostropales*). *Fungal Diversity* 52: 107–121. https://doi.org/10.1007/s13225-011-0135-8

Rivas Plata, E., Parnmen, S., Staiger, B., Mangold, A., Frisch, A., Weerakoon, G., Hernández, J., Cáceres, M. E. S., Kalb, K., Sipman, H. & Common, R. S. 2013. A molecular phylogeny of *Graphidaceae* (*Ascomycota*, *Lecanoromycetes*, *Ostropales*) including 428 species. *MycoKeys* 6: 55–94. https://doi.org/10.3897/mycokeys.6.3482

Schumm, F. & Elix, J. A. 2015. *Atlas of Images of Thin Layer Chromatograms of Lichen Substances*. Books on Demand, Norderstedt, Germany. http://www.bod.de

Schumm, F. & Elix, J. A. 2016. *Atlas of Images of Thin Layer Chromatograms of Lichen Substances.* Supplement. Books on Demand, Norderstedt, Germany. http://www.bod.de

Sipman, H. J. M. 1991. Notes on the lichen flora of the Guianas, a neotropical lowland area. In: Galloway, D. J. (ed.), *Tropical Lichens: Their Systematics, Conservation, and Ecology*. Systematics Association Special Volume, Clarendon Press, Oxford, pp. 135–150.

Sipman, H. J. M. 1994. New *Graphidales* (lichenized *Ascomycotina*) from the Guianas and nearby areas [Studies on the Flora of the Guianas no. 79]. *Acta Botanica Fennica* 150: 165–172.

Sipman, H. J. M. 2014. New species of *Graphidaceae* from the Neotropics and Southeast Asia. *Phytotaxa* 189: 289–311. https://doi.org/10.11646/phytotaxa.189.1.21

Sipman, H. J. M. & Aptroot, A. 2023. Fourteen new *Carbacanthographis* species from the Neotropics, with ecological observation. *Plant and Fungal Systematics* 68: 320–334. https://doi.org/10.35535/pfsyst-2023-0016

Sipman, H. J. M., Lücking, R., Aptroot, A., Chaves, J. L., Kalb, K. & Umaña-Tenorio, L. 2012. A first assessment of the Ticolichen biodiversity inventory in Costa Rica and adjacent areas: the thelotremoid *Graphidaceae* (*Ascomycota*: *Ostropales*). *Phytotaxa* 55: 1–214. https://doi.org/10.11646/phytotaxa.55.1.1

Staiger, B. 2002. Die Flechtenfamilie *Graphidaceae*. Studien in Richtung einer natürlicheren Gliederung. *Bibliotheca Lichenologica* 85: 1–526.

Torres, J. M., Spielmann, A. A., Aptroot, A., Cardoso, K. F. & Honda, N. K. 2020. The lichen genus *Schistophoron* Stirt. (*Ascomycetes*, *Graphidaceae*) in Brazil, with a world key to the species. *Cryptogamie, Mycologie* 41: 211–217. https://doi.org/10.5252/cryptogamie-mycologie2020v41a13

Van den Boom, P. P. & Sipman, H. J. M. 2016. Foliicolous lichens from Suriname and Guyana: new records and three new species. *Folia Cryptogamica Estonica* 53: 101–110. https://doi.org/10.12697/fce.2016.53.12

Wijayawardene, N. N., Hyde, K. D., Al-Ani, L. K. T., Tedersoo, L., Haelewaters, D., Rajeshkumar, K. C., Zhao, R. L., Aptroot, A., Leontyev, D. V., Saxena, R. K., Tokarev, Y. S., Dai, D. Q., Letcher, P. M., Stephenson, S. L., Ertz, D., Lumbsch, H. T., Kukwa, M., Issi, I. V., Madrid, H., Phillips, A. J. L., Selbmann, L., Pfliegler, W. P., Horváth, E., Bensch, K., Kirk, P. M., Kolaříková, K., Raja, H. A., Radek, R., Papp, V., Dima, B., Ma, J., Malosso, E., Takamatsu, S., Rambold, G., Gannibal, P. B., Triebel, D., Gautam, A. K., Avasthi, S., Suetrong, S., Timdal, E., Fryar, S. C., Delgado, G., Réblová, M., Doilom, M., Dolatabadi, S., Pawłowska, J. Z., Humber, R. A., Kodsueb, R., Sánchez-Castro, I., Goto, B. T., Silva, D. K. A., de Souza, F. A., Oehl, F., da Silva, G. A., Silva, I. R., Błaszkowski, J., Jobim, K., Maia, L. C., Barbosa, F. R., Fiuza, P. O., Divakar, P. K., Shenoy, B. D., Castañeda-Ruiz, R. F., Somrithipol, S., Lateef, A. A., Karunarathna, S. C., Tibpromma, S., Mortimer, P. E., Wanasinghe, D. N., Phookamsak, R., Xu, J., Wang, Y., Tian, F., Alvarado, P., Li, D. W., Kušan, I., Matočec, N., Mešić, A., Tkalčec, Z., Maharachchikumbura, S. S. N., Papizadeh, M., Heredia, G., Wartchow, F., Bakhshi, M., Boehm, E., Youssef, N., Hustad, V. P., Lawrey, J. D., Santiago, A. L. C. M. A., Bezerra, J. D. P., Souza-Motta, C. M., Firmino, A. L., Tian, Q., Houbraken, J., Hongsanan, S., Tanaka, K., Dissanayake, A. J., Monteiro, J. S., Grossart, H. P., Suija, A., Weerakoon, G., Etayo, J., Tsurykau, A., Vázquez, V., Mungai, P., Damm, U., Li, Q. R., Zhang, H., Boonmee, S., Lu, Y. Z., Becerra, A. G., Kendrick, B., Brearley, F. Q., Motiejūnaitė, J., Sharma, B., Khare, R., Gaikwad, S., Wijesundara, D. S. A., Tang, L. Z., He, M. Q., Flakus, A., Rodriguez-Flakus, P., Zhurbenko, M. P., McKenzie, E. H. C., Stadler, M., Bhat, D. J., Liu,

J. K., Raza, M., Jeewon, R., Nassonova, E. S., Prieto, M., Jayalal, R. G. U., Erdoğdu, M., Yurkov, A., Schnittler, M., Shchepin, O. N., Novozhilov, YK., Silva-Filho, A. G. S., Gentekaki, E., Liu, P., Cavender, J. C., Kang, Y., Mohammad, S., Zhang, L. F., Xu, R. F., Li, Y. M., Dayarathne, M. C., Ekanayaka, A. H., Wen, T. C., Deng, C. Y., Pereira, O. L., Navathe, S., Hawksworth, D. L., Fan, X. L., Dissanayake, L. S., Kuhnert, E., Grossart, H. P. & Thines, M. 2020. Outline of fungi and fungus-like taxa. *Mycosphere* 11: 1060–1456. https://doi.org/10.5943/mycosphere/11/1/8

Xavier-Leite, A. B., Cáceres, M. E. S, Aptroot, A., Moncada, B., Lücking, R. & Goto, B. T. 2022. Phylogenetic revision of the lichenized family *Gomphillaceae* (*Ascomycota*: *Graphidales*) suggests post-K–Pg boundary diversification and phylogenetic signal in asexual reproductive structures. *Molecular Phylogenetics and Evolution* 168: 107380. https://doi.org/10.1016/j.ympev.2021.107380