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Herpothallon inopinatum (Arthoniaceae), a new lichen species from Mexico

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Herpothallon inopinatum Frisch & G. Thor *sp. nova* (Arthoniaceae) is described from Chiapas, Mexico. It is the second species of *Herpothallon* known with mature ascospores besides *H. fertile*. It differs from *H. fertile* in smaller asci immersed in the thallus instead of strongly protruding barrel-shaped thallus warts, smaller bean-shaped ascospores and a thallus chemistry of confluentic and chiodectonic acids. *Herpothallon inopinatum* most closely resembles *H. pustulatum*, but differs in the absence of pustules. The closely related *H. rubrocinctum* has distinct bright-red pseudoisidia and a bright-red pigmentation of pro- and hypothallus, while *H. inopinatum* lacks pseudoisidia and has a pro- and hypothallus white mottled pale yellow to orange to purplish brown. A revised key to all 34 currently accepted species in *Herpothallon* is provided.

The genus *Herpothallon* with 29 species was revised by Aptroot *et al*. (2009). That publication renewed the interest in crustose byssoid lichens from tropical forests and eight additional species of *Herpothallon* were described recently, *viz*. *H. flavominutum* and *H. himalayanum* (Jagadeesh Ram & Sinha 2009), *H. granulosum* and *H. isidiatum* (Jagadeesh Ram *et al*. 2009), *H. biacidum* (Frisch *et al*. 2010a), *H. rubroechinatum* (Frisch *et al*. 2010b), *H. sticticum* (Jagadeesh Ram & Sinha 2011), and *H. weii* (Cheng *et al*. 2012). A new genus *Cryptothonia* (Frisch & Thor 2010) was introduced for species combining *Herpothallon*-like thalli with maculate ascomata, ascospores, and asci similar to those found in *Arthonia s. lato*. *Herpothallon albidum* and *H. mycelioides* were transferred to this new genus. Nelsen *et al*. (2010) erected the genus *Heiomasia* for *Herpothallon sipmanii* (= *Heiomasia sipmanii*; Graphidaceae) and Nelsen *et al*. (2012) were able to show by molecular data that *Herpothallon antillarum* belongs in *Diorygma* (= *D. antillarum*; Graphidaceae). *Herpothallon* is still incompletely understood, however, and additional taxonomic changes are expected for this genus. In the present paper we describe a new species of *Herpothallon* from Chiapas, Mexico, which was discovered in the course of recent phylogenetic studies in the Arthoniaceae, and provide an updated key to all currently accepted *Herpothallon* species.

The holotype of the new taxon is located in UPS. Morphology was studied on hand sections in water and lactic cotton blue, and on squash preparations using Olympus BX40 and Leica MZ8 microscopes.

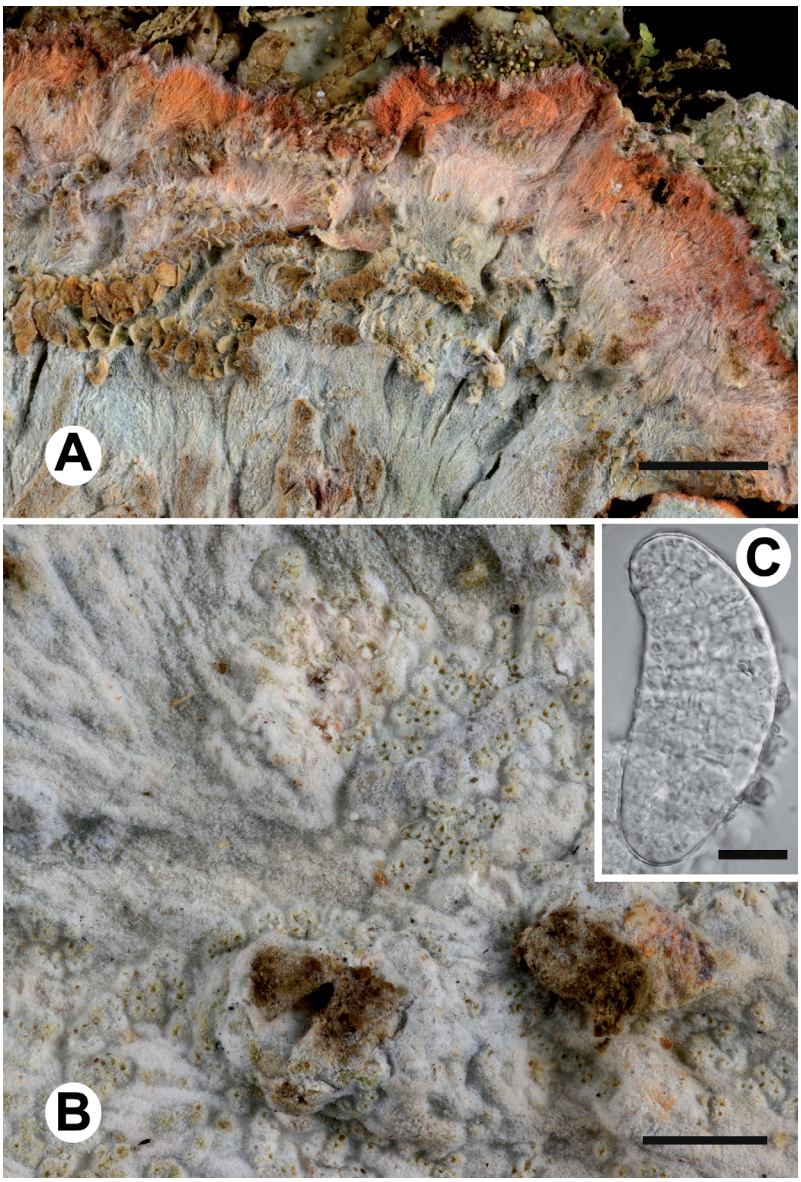

Fig. 1. *Herpothallon inopinatum* (from the holotype). — **A**: Marginal thallus with prothallus. — **B**: Central thallus with ascus cavities. — **C**: Ascospore. Sale bars: **A** = 1 mm, **B** = 2 mm, **C** = 20 *µ*m.

Secondary lichen compounds were identified by TLC (Orange *et al*. 2010) using solvents B´ and C. The amyloidity of thallus hyphae and asci was examined using 0.2% (I_{dil}) aqueous iodine solution, and 1% aqueous iodine solution without and with pretreatment with 10% aqueous potassium hydroxide (I and KI, respectively). The colour reaction of the thallus was tested using 10% aqueous potassium hydroxide (K), common household bleach (C), 10% aqueous potassium hydroxide followed by common household bleach (KC), 1,4-phenylendiamine in 96% ethanol (PD) and short wave UV_{254} light. Calcium oxalate crystals were identified using 10% sulphuric acid.

Herpothallon inopinatum Frisch & G. Thor, *sp. nova* (Fig. 1)

MycoBank [MB 807535]

Type: Mexico. Chiapas: Soconusco region, Tapachula municipality, Finca Irlanda, 15°11´N, 92°20´W, 1000 m a.s.l., on unidentified tree in coffee plantation, July 2011, *Rudolphi 12* (holotype UPS).

Etymology. From the Latin *inopinatus* (= unexpected) referring to the presence of ascospores in the new species.

Thallus overgrowing corticolous bryophytes and lichens, byssoid, 4.5 cm diam., loosely attached to substrate, ecorticate, minutely felty, pale grey-olive to almost whitish in thallus centre, heteromerous, 0.2–0.3 mm thick. *Photobiont layer* 35–60 µm thick; photobiont trentepohlioid, in short chains or single-celled, cells irregularly globose to ovoid, 5–16 × 4–9 µm; hyphae 1.5–2.0 µm wide, densely branched and anastomosing, with numerous brownish granules attached to outer walls; appressorial hyphae short, often branched, slightly wavy, about 1 µm wide. *Medulla* up to 200 µm thick, formed of mainly periclinal, loosely woven hyphae 2–4 µm wide; granules numerous, brownish, attached to walls of hyphae. *Calcium oxalate crystals* numerous, 2–10 µm diam. *Hypothallus* present throughout otherwise white lower surface but thin and discontinuous, mottled pale yellow to orange. *Prothallus* up to 2 mm wide, byssoid, of loosely interwoven radiating hyphae, orange to purplish brown; hyphae 1.5–2.5 µm wide, hyaline to pale orange to pale purplish, with orange granules attached. *Pseudoisidia* absent. *Asci* aggregated in small groups of 2–10 in thallus centre, each group 0.2–0.4 mm diam., slightly protruding; most asci evanescent and empty cavities recognisable as tiny pores in thallus surface; only young or disrupted asci seen in microscopical preparations, ± globular, stalked, ca. 130–150 × ca. 100 µm, *Cryptothecia*-type. *Paraphysoids* enclosing asci loosely attached, 1–1.5 µm wide, I– and KI–. *Ascospores* (?6–)8/ascus, hyaline, muriform with wavy septa, ± bean-shaped, 90–110 × 38–45 µm (n = 6). *Pycnidia* not seen.

Chemistry. Confluentic acid (major) and chiodectonic acid (trace) detected with TLC (solvents B', C); thallus K–, C–, KC–, PD–, UV–, I+ and KI+ pale blue in patches; orange pigment K+ purple.

Habitat and distribution. *Herpothallon inopinatum* was collected from smooth bark of an unidentified tree in the 280 ha organically certified coffee farm Finca Irlanda (15°11´N, 92°20´W, WGS84), growing over a thin layer of bryophytes and lichens. The farm has maintained a high density and diversity of shade trees (approximately 25 species/ha), totalling at least 100 tree species with between 60%–90% canopy cover over the coffee plants. The original forest type is montane tropical rainforest but there is virtually no remaining unmodified forest nearby. The surrounding land largely consists of farms managed in a similar way (Perfecto *et al*. 2003). The area is located between 950–1150 m a.s.l. and receives approximately 4500 mm rain per year (Richter 1992). *Herpothallon inopinatum* is only known from its type locality.

Taxonomy. *Herpothallon* species are usually sterile and reproduce by means of byssoid isidia-like structures often referred to as *pseudisidia* (Aptroot *et al*. 2009) or *pseudoisidia* (Frisch *et al*. 2010a, 2010b). The only noticeable exception reported in the literature is *H. fertile* (Aptroot *et al*. 2009). This species is easily distinguished from *H. inopinatum* by the much larger asci (ca. 250 µm × ca. 150 µm) formed singly in strongly protruding barrel-shaped thallus warts, the larger and narrower, often moustache-shaped ascospores (75–250 × 30–40 µm), and gyrophoric and lecanoric acids as thallus compounds. We observed asci with immature ascospores of the *Cryptothecia*-type in few specimens of *Herpothallon philippinum*, *H. rubromaculatum* and *H. pustulatum*. Among these, the new species most closely resembles *H. pustulatum* (reported from Venezuela, Costa Rica and Brazil) from which it can be distinguished mainly by the absence of pustules on the thallus surface.

In the absence of fertile structures, *Herpothallon* is here circumscribed by its byssoid thallus with trentepohlioid photobiont, often pseudoisidia or other vegetative structures as granules, granular soredia or warts on the thallus surface, and the presence of yellow to red pigments in a large proportion of its species. Byssoid thallus organisation, however, is affected by environmental factors such as high humidity and large amount of precipitation in the natural habitat of the species, and similar organisation is also found in unrelated groups of lichens such as, e.g., the Arthoniales (Henssen *et al*. 1979, 1982, Rogers & Hafellner 1987, Thor 1990, Egea *et al*. 1995, Aptroot *et al*. 2009, Frisch & Thor 2010, etc.), Lecanorales (Hafellner & Vězda 1992), and Ostropales (Rivas-Plata *et al*. 2006, Nelsen

et al. 2010, 2012). Without fruit bodies such species are often difficult to place. *Herpothallon*, as outlined in the key below, shows considerable morphological and chemical diversity and is certainly heterogeneous. However, the exact delimitation of the genus, in particular the distinction from *Cryptothecia* and related groups in Arthoniaceae, is not finally established and needs further study including molecular data.

With respect to thallus morphology, *Herpothallon* is closest to *Crypthonia*. In both genera there are several species with a loosely attached byssoid thallus. Some *Crypthonia* are only known in sterile condition, which complicates the distinction of the two genera and the correct placement of the species. In general, the thallus of *Crypthonia* is more loosely organized than that of *Herpothallon*, but there is a broad overlap between the genera with regard to this character. In the three pseudoisidiate *Crypthonia* species (*C. albida*, *C. mycelioides*, and *C. palaeotropica*), the pseudoisidia are formed by loosely byssoid hyphae, bearing some structural resemblance to the hypothallus, whereas they are firmly byssoid in *Herpothallon* with the exception of *H. aurantiacoflavum*. In microscopical view, the wavy appressorial hyphae enclosing the photobiont cells are quite characteristic of *Crypthonia* (Frisch & Thor 2010), although some variability with respect to the development of the appressorial hyphae is extant in the genus. No similarly close contact between the myco- and the photobiont has so far been observed in *Herpothallon* and *Cryptothecia*, but only a limited number of species of these genera were investigated in this respect. Confluentic acid, perlatolic acid and related compounds are not known from *Crypthonia*.

Based on morphological and chemical considerations, the central group of *Herpothallon* may include all species with distinct pseudoisidia and a chemistry related to confluentic and perlatolic acids, and chiodectonic acid as pigment in pro- and hypothallus. Within this group of species, *H. inopinatum* was found closely related to *H. rubrocinctum*, the type species of the genus *Herpothallon* by molecular data (authors' unpubl. data). The always sterile *H. rubrocinctum* differs from the new species mainly by its distinct bright red pseudoisidia and the bright red pigmentation of pro- and hypothallus. Only few disrupted asci were observed in the type specimen of *H. inopinatum*. From the observations, however, it can be deduced, that the asci are similar to the *Cryptothecia*-type as depicted in Grube (1998). The ascospores and interascal filaments clearly resemble those of *Cryptothecia*, supporting the hypotheses on the close phylogenetic relationship of both genera.

Key to the species of *Herpothallon*

Species of *Herpothallon* have a complex chemistry of secondary lichen compounds, most of which do not react to spot tests. Therefore, species identification usually requires co-chromatography (TLC or HPTLC) with reliable control samples. We have not seen material of *H. flavominutum*, *H. granulosum*, *H. himalayanum*, *H. isidiatum*, *H. sticticum* and *H. weii*, and the characters included in the key are derived from the protologues.

1. Asci abundant; pseudoisidia, warts, granules or granular soredia absent 2
1. Asci absent or extremely rare; pseudoisidia, warts, granules or granular soredia present 3
2. Asci ca. 250 × ca. 150 μm, formed singly in strongly protruding barrel shaped thallus warts; spores 75–250 × 30–40 μm; gyrophoric and lecanoric acids (C+ pink-red) ..... *H. fertile*
2. Asci ca. 130–150 × ca. 100 μm, aggregated in small groups of 2–10 in thallus centre; spores 90–110 × 38–45 μm; confluentic acid (major) and chiodectonic acid (trace) (C–) ..... *H. inopinatum*
3. Pigments present, colouring at least parts of thallus yellow, orange, red, or pink, K+ red to purple (sometimes weak) 4
3. Pigments absent in thallus but pseudoisidia rarely with pinkish discolouration (*H. weii*) 21
4. Thallus with yellow to yellow-orange, K+ red pigments (occasionally mottled with red, K+ purple pigment) ... 5
4. Thallus with red to orange, K+ purple pigments, or with pink pigment 6
5. Thallus, pseudoisidia, and prothallus yellow-orange (rugulosin), sometimes mottled with patches of red, K+ purple pigment (chiodectonic acid); hypothallus at least in parts blackish ..... *H. aurantiacoflavum*
5. Thallus, pseudoisidia, and prothallus pale yellow mineral grey to grey-green, with scattered red granules; hypothallus whitish to mostly lemon yellow (unknown pigment) ..... *H. himalayanum*
6. Prothallus pink, hypothallus pink-brown; confluentic acid and three substances in brialmontin chemosyn-

drome; thallus with minute warts to 0.1 mm diam. .... *H. brialmonticum*
6. Prothallus red, hypothallus red or mottled white-red or white-brown; brialmontin chemosyndrome absent; thallus with distinct pseudoisidia, granular soredia or broadly attached pustules, rarely with small granules and then with neodiffractaic acid 7
7. Gyrophoric and ovoic acid (C+ pink-red); red pigment *O*-methylvioxanthin; pseudoisidia long and slender (up to 1.0 × 0.1 mm) ..... *H. rubrocinctoides*
7. Other substances (C–); red pigment chiodectonic or rhodocladonic acid; pseudoisidia mostly shorter 8
8. Psoromic acid chemosyndrome (PD+ yellow) 9
8. Other substances (PD– or PD+ orange-red) 11
9. Scattered red pigment crystals attached to projecting hyphae of pseudoisidia and patches of thallus; red pigment chiodectonic acid ..... *H. rubroechinatum*
9. Without scattered red pigment crystals attached to projecting hyphae of pseudoisidia and thallus (pseudoisidia may be intensive red) 10
10. Pseudoisidia and prothallus intensive red, K+ purple; red pigment chiodectonic acid; calcium oxalate crystals absent ..... *H. globosum*
10. Pseudoisidia green-grey to white, K–; prothallus white-grey mottled with red; pigment an unknown quinone; calcium oxalate crystals present ..... *H. australasicum*
11. Constictic, stictic, and salazinic acids, lichexanthone (K+ yellow then red, UV+ yellow); hypothallus red-black; red pigment ?chiodectonic acid ..... *H. elegans*
11. Different substances (K–, UV–) 12
12. Hypoprotocetraric and convirensic acids (PD+ orange-red); calcium oxalate crystals absent; red pigment chiodectonic acid ..... *H. hypoprotocetraricum*
12. Other substances (PD–); calcium oxalate crystals mostly present 13
13. Neodiffractaic acid major, confluentic acid minor 14
13. Confluentic acid major, 2´-*O*-methylmicrophyllinic and 2´-*O*-methylperlatolic acids (or rarely evernic and 2´-*O*-methylevernic acids) minor 15
14. Hypothallus black; pseudoisidia rather robust (to 0.4 × 0.3 mm), with orange-red pigment; red pigment chiodectonic acid; calcium oxalate crystals absent .... *H. nigroisidiatum*
14. Hypothallus red; pigment chiodectonic acid; pseudoisidia granuliform (0.05 × 0.05 mm), of thallus colour; calcium oxalate crystals present ..... *H. rubromaculatum*
15. Thallus with broadly attached pustules (to 0.5 mm diam.) of thallus colour; red pigments chiodectonic and rhodocladonic acids ..... *H. pustulatum*
15. Thallus with narrow pseudoisidia or soredia-like granules (0.05–0.3(–0.4) mm diam.) that are usually at least in part pigmented (rarely entirely of thallus colour); red pigment chiodectonic acid or unknown substance, if rhodocladonic acid present then thallus with soredia-like granules 16
16. Pseudoisidia robust (to 0.5 × 0.4 mm) 17
16. Pseudoisidia or granules delicate (to 0.15 × 0.15 mm) but sometimes in moniliform chains 18
17. Pseudoisidia rather compact and regular, entirely red; prothallus deep red; pigment chiodectonic acid .... *H. rubrocinctum*
17. Pseudoisidia rather loose-byssoid and irregular, green-grey to white or partly mottled with red; prothallus pale red to orange-red; pigment chiodectonic acid .... *H. roseocinctum*
18. 2´-*O*-methylevernic and evernic acids minor; pseudoisidia sparse, of thallus colour; red pigment chiodectonic acid ..... *H. confusum*
18. 2´-*O*-methylmicrophyllinic (and partly 2´-*O*-methylperlatolic) acids minor; pseudoisidia abundant, at least in part pigmented 19
19. Thallus with soredia-like granules; red pigment rhodocladonic acid ..... *H. furfuraceum*
19. Thallus with moniliform pseudoisidia or isidia-like granules; rhodocladonic acid absent 20
20. Pseudoisidia in part proliferating to form coralloid, moniliform structures; hypothallus red; calcium oxalate crystals present; pigments chiodectonic acid and ± rugulosin ..... *H. corallinum*
20. Pseudoisidia not proliferating; hypothallus white; calcium oxalate crystals absent; red pigment chiodectonic acid, rugulosin absent ..... *H. adnatum*
21. Stictic acid (K+ yellow) 22
21. Different combination of substances (K–) 23
22. Pseudoisidia granular to globose, or irregular wart-like, 0.05–0.1(–0.25) × 0.05–0.1(–0.2) mm ..... *H. sticticum*
22. Pseudoisidia cylindrical, 0.5–1.5 × 0.08–0.15 mm .... *H. isidiatum*
23. Gyrophoric and sometimes additional lecanoric acid major to minor (C+ pink-red) 24
23. Gyrophoric and lecanoric acids absent (C–) 27
24. Confluentic acid major, gyrophoric acid minor; thallus firmly attached ..... *H. queenslandicum*
24. Gyrophoric acid (and in part ovoic acid) major; norstictic, confluentic and/or lecanoric acids minor; thallus loosely attached 25
25. Norstictic acid (minor) present; hypothallus blackish brown; pseudoisidia short (to 0.3 mm long) .... *H. biacidum*
25. Norstictic acid absent; hypothallus whitish; pseudoisidia long (to 1 mm long) 26
26. Ovoic acid present; pseudoisidia rather robust (0.2 mm diam.); calcium oxalate crystals absent ... *H. japonicum*
26. Ovoic acid absent; pseudoisidia slender (0.1 mm diam.); calcium oxalate crystals present ..... *H. philippinum*
27. Thallus UV+ yellow (lichexanthone) .. *H. flavominutum*
27. Thallus UV– 28
28. Psoromic acid chemosyndrome (PD± yellow) 29
28. Other substances (PD–) 30
29. Thallus often almost farinose due to loose soredioid fragments on the surface; pseudoisidia pale mineral green; psoromic acid ..... *H. echinatum*
29. Thallus not farinose; pseudoisidia pinkish; additional unknown substances ..... *H. weii*
30. Thallus with soredia-like granules to 0.05 × 0.05 mm; barbatic or perlatolic acid 31
30. Thallus with pseudoisidia 0.5–1 mm long; other substances 32
31. Perlatolic acid ..... *H. granulare*
31. Barbatic acid ..... *H. granulosum*

32. 2´-*O*-methylperlatolic acid major; prothallus and hypothallus white to grey-green ..... *H. minimum*
32. Confluentic acid major; prothallus and/or hypothallus mottled with brown 33
33. Calcium oxalate crystals present; 2´-*O*-methylmicrophyllinic and 2´-*O*-methylperlatolic acids minor .... *H. cinereum*
33. Calcium oxalate crystals absent; confluentic acid only .. .. *H. confluenticum*

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