

Chaconia heliconiae and *C. clusiae* sp. novae from French Guiana with notes on the genus *Chaconia* (Uredinales/Pucciniales) in the neotropics

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Abstract *Chaconia clusiae* on *Clusia* cf. *palmicida* (Clusiaceae) and *C. heliconiae* on *Heliconia psittacorum*, *H. bihai* and *Heliconia* sp. (Heliconiaceae) are described as new from French Guiana in northern South America. Clusiaceae and Heliconiaceae are new host families for members of *Chaconia*, Heliconiaceae is the first one from Monocotyledoneae. *Chaconia clusiae*, *C. heliconiae* and *C. maprouneae* formed tuberous to worm-like D-haustoria originating from haustorial mother cells that were part of the intercellular parasitic mycelium. A key to the recognized *Chaconia* spp. is provided.

Keywords Chaconiaceae · Clusiaceae · D-haustorium · Heliconiaceae · Rust fungi · Teliospore

Introduction

The rust genus *Chaconia* Juel, based on *C. alutacea* Juel, comprises eight recognized species that occur in warm parts of the world on host plants belonging to the families Euphorbiaceae, Fabaceae, Mimosaceae, Oleaceae (Ono and Hennen 1983) and perhaps Bignoniaceae (Ono et al. 1988). Its members are characterised by one-celled, thin-walled, ellipsoid or club-shaped sessile teliospores that are formed by basal meristematic cells and germinate upon maturity by elongation of the apex.

Five of the described species are known from the New World: *C. alutacea* Juel, *C. braziliensis* Y. Ono & J.F. Hennen,

and *C. ingae* (Syd.) Cummins are found on Mimosaceae, *C. hennenii* Berndt on Moraceae, and *C. maprouneae* (Viégas) Y. Ono & J.F. Hennen on Euphorbiaceae. *Chaconia texensis* Arthur on Loranthaceae may not be a rust fungus (Ono and Hennen 1983) and is not considered here.

This paper describes two new species of *Chaconia* from French Guiana and presents a key to the recognized species of the genus.

Materials and methods

The studied rust specimens are listed under the respective species. They are located in Herbarium Turicense (Z+ZT), the holotypes in Paris (PC). ‘FG’ and ‘HeRB’ numbers are collection numbers.

Infected host leaves of *Clusia* were photographed with a Nikon D90 DSLR and picture files processed using Adobe Photoshop CS4. Spores and hand sections obtained from herbarium material were mounted and gently heated in lactophenol or lactic acid on microscopic slides. Hoyer’s Fluid (Cunningham 1972) mixed with a small droplet of cotton blue dissolved in lactic acid was used to clear and stain thicker sections. Preparations were examined with an Olympus BX51 compound microscope equipped with a ColorView IIIu camera. The software package Cell B (Software Imaging System) was used to capture micrographs and to measure spores and details of the spore ornament. The ranges of measurements, followed by the arithmetic means (in parentheses), represent at least 30 measured spores. If fewer spores were studied, this is indicated in the text. Spore states were designated according to the ontogenic terminology (Hiratsuka 1973). The Roman numeral II stands for the presence of uredinia, III for telia.

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Results

Chaconia clusiae Berndt sp. nov. (Figs. 1, 2 and 3).

Etymology: *Clusia*, the host genus.

Mycobank MB 519741

Spermogonia, aecia and uredinia not seen, probably microcyclic. Telia densely aggregated on abaxial side of host leaves covering large, slightly hypertrophied and bright orange patches of leaves; telia develop originally in substomatal cavities, then form tiny, pulvinate and more or less superstomatal sori, later they become larger and tend to coalesce with adjacent sori; teliospores formed by two or three on meristematic hymenial cells, $28\text{--}41 \times 12\text{--}19 \mu\text{m}$ ($35.2 \times 15.6 \mu\text{m}$), clavate, subclavate or ellipsoid, wall smooth, colourless and less than $1 \mu\text{m}$ thick, germinating at maturity with stout, often bent or sickle-shaped phragmobasidia by elongation of the apex. Stalked D-haustoria present.

On leaves of *Clusia* cf. *palmicida* Rich. ex Planch. & Triana (Clusiaceae).

Holotype (PC). French Guiana: Sinnamary canton, road to Barrage de Petit Saut some 100 m after turn-off from route nationale 1, on *Clusia* cf. *palmicida*, leg. R. Berndt & L. Beenken, 17 Jul 2009 (FG09/111. III). Isotype Z+ZT (ZT Myc 3558).

Infected host leaves generally bore one conspicuous, large telial patch of several centimetres diameter (Fig. 1). The slightly hypertrophied patches were bright orange, later dark orange or ferruginous and bordered by a pale green front. *Chaconia clusiae* differs from other described *Chaconia* spp. in the host family and the apparently microcyclic life cycle. Only two other rust fungi are known on Clusiaceae, the anamorphic *Uredo clusiae* Arthur and *U. zarumae*



Fig. 1 Leaves of *Clusia* cf. *palmicida* infected with *Chaconia clusiae* (type). Telia cover the abaxial side of large, slightly hypertrophied patches of leaves and induce bright orange decolouration (dark in B&W reproduction) bordered by a bleached rim. Bar 2 cm

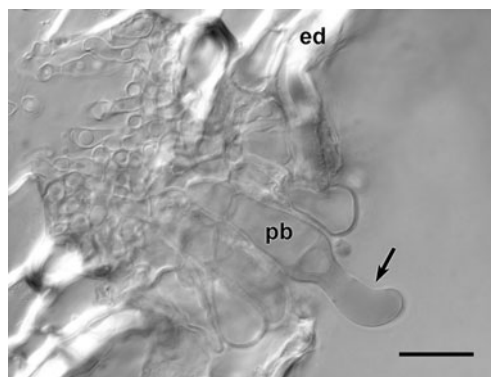


Fig. 2 *Chaconia clusiae* (type). Section through telium showing sub-epidermal position of sorus (*ed* epidermis) and a probasidium (*pb*) germinating by apical elongation (*arrow*). Bar $20 \mu\text{m}$

H.S. Jacks. & Holw. Because *C. clusiae* has the aspect of a microcyclic rust, it is unlikely to comprise one of these anamorphs in its life cycle.

We compared the present rust fungus also with species from genera similar to *Chaconia*, namely *Aplopsora* Mains, *Chrysocelis* Lagerh. & Dietel, *Olvea* Arthur, *Ceraceopsis* Kakish., T. Sato & S. Sato and *Maravalia* Arthur, but did not find coincidences.

The basidia, produced by apical elongation of the probasidia, appeared to collapse rapidly after formation and basidiospore discharge. Only remnants of four-celled basidia were observed or a few with single cells still turgescient. Delicately stalked D-haustoria with an elongated haustorial body tapering into a worm-like distal part were found in infected host cells under the telia (Fig. 3).

Chaconia heliconiae Berndt, sp. nov. (Figs. 4, 5, 6 and 7).

Etymology: *Heliconia*, the host genus.

Mycobank MB 519742

Spermogonia and aecia unknown. Uredinia mainly scattered on abaxial side of leaves, tiny, subepidermal, *Uredo*-type, lacking sterile bounding structures; urediniospores short-ly and inconspicuously stalked, broadly ellipsoid, obovoid or

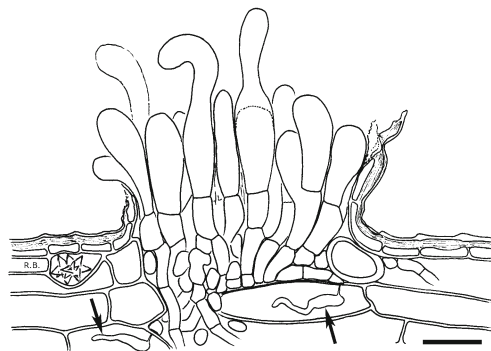


Fig. 3 *Chaconia clusiae* (type). Section through telium showing young and germinating probasidia and developing basidia. D-haustoria are indicated by *arrows*. The section is shown upside down for easier orientation. Bar $20 \mu\text{m}$

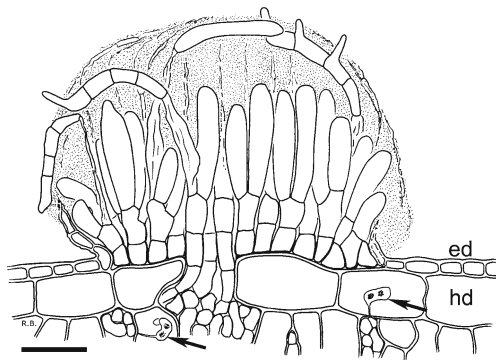


Fig. 4 *Chaconia heliconiae* (FG09/96). Section through telium showing young and germinated probasidia and basidia embedded in a gelatinous matrix (indicated by *dotting*). Basidia are generally bent and their remnants often border the outside of the sorus. Development of telium originates between the epidermis (*ed*) and the hypodermis (*hd*). D-haustoria are indicated by *arrows*. The section is oriented upside down for easier orientation. *Bar* 20 μ m

ellipsoid, more rarely subglobose to pyriform, 25–31(35) \times 19–25.5 μ m (27.2 \times 24.0 μ m), wall 1–1.5 μ m thick, golden brown, evenly covered with moderately coarse spines ca. 2.5–3.5(4) μ m apart, germ pores obscure. Telia among uredinia on abaxial side of leaves, tiny, ferruginous, bullate or forming small crusts, with waxy consistency; teliospores ellipsoid, formed on 2–3 loci on slightly thick- and pale golden-walled meristematic hymenial cells, 27–36 \times 8–11 μ m (20 spores measured), wall colourless, smooth, ca. 0.5 μ m thick; phragmobasidia narrowly cylindrical, produced upon maturity by elongation of apex of probasidia. Delicately stalked bulbous D-haustoria present.

On leaves of *Heliconia* spp. (Heliconiaceae).

Holotype (PC). French Guiana: Kourou canton, hiking trail on golf course adjacent to Kourou Space Center, on *Heliconia* cf. *psittacorum* L. f., leg. R. Berndt & L. Beenken, 16 Jul 2009 (FG09/106. II, III). Isotype Z+ZT (ZT Myc 3559).

Additional material studied. French Guiana: Kourou canton, hiking trail on golf course next to Kourou Space Center, on *Heliconia* sp., leg. R. Berndt & L. Beenken, 16 Jul 2009

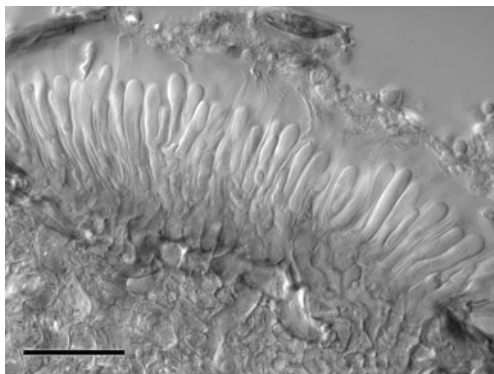


Fig. 5 *Chaconia heliconiae* (type). Section through subepidermal telium. The outside of the gelatinous matrix is covered by basidial remnants, basidiospores and undefined debris. *Bar* 50 μ m

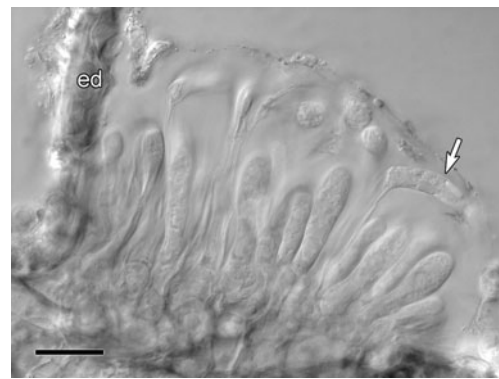


Fig. 6 *Chaconia heliconiae* (FG09/96). Section through lateral part of telium showing the torn epidermis (*ed*) and young and germinated probasidia. Germinated probasidia are collapsed; the bent basidia more or less line the gelatinous matrix of the sorus (*arrow*). *Bar* 20 μ m

(FG09/97. II). Sinnamary canton, Piste de St. Elie, degraded savannah and swampy area shortly after turn-off from route nationale 1, on *H. psittacorum*, leg. R. Berndt & L. Beenken, 24 Jul 2009 (FG09/68. II). Roura canton, Montagne de Kaw, “sentier botanique”, on *H. bihai* L. f., leg. R. Berndt & L. Beenken, 25 Jul 2009 (FG09/69. II). Matoury canton, Massif de Mirande, “sentier de Mirande”, on *Heliconia* sp., leg. R. Berndt & L. Beenken, 15 Jul 2009 (FG09/96. [II], III).

Chaconia maprouneae (Viégas) Y. Ono & J.F. Hennen. French Guiana: Matoury canton, savannah at route nationale 2 shortly W of the Roura crossing, On *Maprounea guianensis* Aubl., leg. R. Berndt & L. Beenken, 26 Jul 2009 (FG09/29. II).

Puccinia heliconiae Arthur. Costa Rica: Province Alajuela, San Ramón, Reserva Forestal “Alberto Brenes” at Río San Lorencito, on *Heliconia* sp., leg. R. Berndt 14 Mar 1991 (HeRB 2501. II, III). Province Puntarenas, Osa Peninsula, entrance to Corcovado National Park at “Los Patos”, on *H. cf. latispatha* Benth., leg. R. Berndt, 24 Mar 1992 (HeRB 3087. II).

Chaconia heliconiae differs from the known members of *Chaconia* in its monocot host *Heliconia*. Waxy telia were also

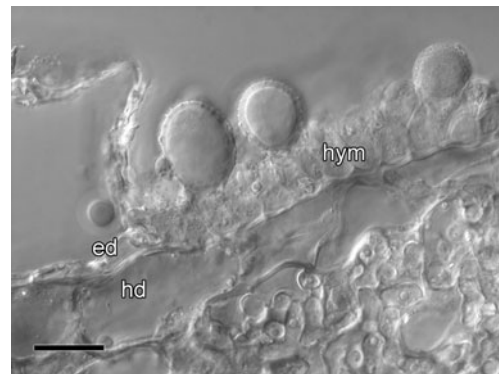


Fig. 7 *Chaconia heliconiae* (FG09/69). Section through uredinium showing the hymenial sporogenous cells (*hym*) initially formed between hypo- and epidermis (*hd*, *ed*). *Bar* 20 μ m

described in *C. butleri* (Syd.) Mains on *Jasminum* from India (Sydow et al. 1912) and in *C. braziliensis*. Both differ from *C. heliconiae* in other morphological characters (Ono and Hennen 1983). Species of *Goplana* Racib. have very similar gelatinous telia but none occur on Heliconiaceae (Ono and Hennen 1983).

The rust fungi described from *Heliconia*, *Cerotelium rectangularata* Buriticá & J.F. Hennen and *Puccinia heliconiae* are entirely different from the present species in the telial state. Farr and Rossman (2011) list *Maravalia* sp. on *H. caribaea* Lam. from Venezuela, but apparently this species has not been described. *Puccinia heliconiae* could be confused with *C. heliconiae* in the uredinial state but it has urediniospores with slightly thicker and paler spore wall and two inconspicuous germ pores according to Arthur (1922) and Dietel (1897). Germ pores could not be seen in the urediniospores of two specimens of *P. heliconiae* from Costa Rica, indicating that the thicker, pale spore wall is the main feature to tell its urediniospores apart from *C. heliconiae*.

Uredinia and telia of *C. heliconiae* developed between the epi- and hypodermis of the host leaves (Fig. 7). The urediniospores had short, evanescent and easily overlooked stalks. The bases of the stalks were surrounded by membranous sheaths, probably remnants of pedicels of discharged spores, that indicate that the spores are successively produced on sporogenous loci of meristematic cells. Uredinia of *C. maprouneae* were similar but sometimes showed a few peripheral sterile cells that did not form a well-defined bordering layer.

Delicately stalked bulbous D-haustoria (Fig. 4) similar to the ones observed in *C. clusiae* (Fig. 3) were found in infected host cells. Similar D-haustoria were also encountered in *C. maprouneae*.

Key to the species of *Chaconia*

This key is based on morphological characters and host taxa (data taken from Berndt 2008; Hernández and Hennen 2003; Ono and Hennen 1983; Ono et al. 1988; Sydow 1937, and unpublished results).

- 1 Telia tiny, densely aggregated on large, bright orange and slightly hypertrophied leaf areas (Fig. 1); probably microcyclic; on *Clusia* (Clusiaceae) *C. clusiae*
 - With other characters, not on *Clusia* 2
- 2 Aecia and/or uredinia paraphysate (*Physopella*-type) .. 3
 - Aecia and/or uredinia paraphysate (a few peripheral sterile cells may occur in *C. maprouneae* but do not form a well defined border) 5

- 3 Teliospores apically thickened, germinating from a sub-apical pore; urediniospores with 4(–6), often bipolar germ pores; on *Maclura* (Moraceae) *C. hennenii*
 - Teliospores apically not thickened, germinating by apical elongation 4
- 4 Aecio- and urediniospores cinnamon-brown, with 3 equatorial germ pores positioned on projecting lobes; spore wall 1.5–2.5 μm thick, slightly thicker at the apex; on *Milletia* (Fabaceae).....*C. coetanea*
 - Urediniospores (sub)hyaline; spore wall ca. 1 μm thick, germ pores obscure; on cf. Bignoniaceae sp.....*C. thailandica*
- 5 (2) Aecio- and/or urediniospores longitudinally striate or almost reticulate, or with longitudinal lines of warts, not echinate 6
 - Aecio- and/or urediniospores echinate 7
- 6 Aecio- and urediniospores with longitudinal ridges usually connected by cross ridges, hence almost reticulate; spore wall 2–4 μm thick, slightly thicker at the apex and base, germ pores 3–4 equatorial; on *Inga* (Mimosaceae) *C. ingae*
 - Urediniospores with delicate longitudinal ridges composed of rod-like tiny warts, not connected by cross ridges; spore wall evenly ca. 1.5 μm thick (without ridges), germ pores obscure; on *Jasminum* (Oleaceae) *C. butleri*
- 7 (5) On monocots (*Heliconia*, Heliconiaceae); telia waxy, crustose; urediniospores broadly ellipsoid, obovoid or ellipsoid *C. heliconiae*
 - On dicots.....8
- 8 (7) On *Maprounea* (Euphorbiaceae); urediniospores pyriform to subreniform *C. maprouneae*
 - On *Pithecellobium* or *Stryphnodendron* (Mimosaceae)....9
- 9 On *Pithecellobium*; demicyclic; aecia Uredo-like, aecio-spores symmetric, 20–26 \times 16–20 μm *C. alutacea*
 - On *Stryphnodendron*; uredinia and telia known; urediniospores asymmetric, 23–38 \times 18–25 μm ... *C. braziliensis*

Discussion

Family Chaconiaceae was proposed by Cummins and Hiratsuka (1983) to accommodate genera of rust fungi with usually thin-walled, stalked or sessile teliospores (probasidia) that germinate by elongation of the apex. Ono and Hennen (1983) pointed out that Chaconiaceae as circumscribed by Cummins and Hiratsuka (1983) may not be a natural group. As a first step towards a more natural classification, they excluded all genera with pedicellate teliospores. Cummins and Hiratsuka (2003) did not follow this treatment, but excluded *Chrysocelis* from Chaconiaceae which differs from the other genera in the spermogonial type and *Petersonia*-like aecia. Ono and Harada (1994) emphasized that genera assigned to Chaconiaceae were not clearly circumscribed because of incomplete knowledge of life cycles and morphological characters of the sori.

The type genus *Chaconia* is also vaguely defined and can only be characterized by a combination of traits of which each is widespread in rust fungi: the teliospore morphology and germination as described above, spermogonia of type 5 or 7, and uredinia assignable to the anamorph genera *Uredo* Pers. or *Physopella* Arthur. In addition, all known *Chaconia* spp. are autoecious. As a consequence, a rust fungus cannot be assigned to *Chaconia* with certainty based on telial or even telial plus uredinial characters. Both *C. heliconiae*, collected with uredinia and telia, and *C. clusiae*, only with telia, could have been assigned to *Chrysocelis* with equal justification. *Chaconia heliconiae* might have been placed alternatively in *Goplana* due to the consistency of the telia. To affiliate both species with *Chaconia* was essentially a gut decision that may in future turn out to be wrong. Evidence from DNA sequences is still unavailable as the type species of the genera in question have not so far been sequenced (e.g. Aime 2006).

With the species described in this paper, *Chaconia* comprises ten recognized species of which seven occur in the New World, and three in India, Thailand or West Africa. They inhabit a broad range of mostly unrelated host families encompassing members of the dicotyledonous Clusiaceae, Euphorbiaceae, Fabaceae, Mimosaceae, Moraceae, Oleaceae and possibly Bignoniaceae, as well as the monocotyledonous Heliconiaceae. Given the possibility that *Chaconia* is heterogeneous, it seems idle to try to interpret this host diversity.

This paper describes the D-haustoria of *C. clusiae*, *C. heliconiae* and, for the first time, of *C. maprouneae*. They had ‘ordinary’ D-haustoria (cf. Littlefield and Heath 1979, pp. 128–158) formed by haustorial mother cells that were

part of the intercellular mycelium. This is in contrast to *C. ingae*, in which the entire parasitic mycelium grew within the host cells and formed intracellular hyphae and D-haustoria (Berndt 2012). Different haustorial types and colonization strategies were also found in the well-circumscribed genus *Ravenelia* (Berndt 1997). This indicates that these haustorial characters are not fixed within a genus and cannot be used as taxonomic markers.

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