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# A global survey of *Puccinia*-rust on Cucurbitaceae

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**Abstract** In this paper, all known autoecious *Puccinia* species (rust fungi, Uredinales) on Cucurbitaceae are described and most of them illustrated. A key and information on their host range and distribution is presented. Four species, *Puccinia antennata*, *P. arbor-miraculensis*, *P. hieroglyphica*, and *P. rhytidoderma* are proposed as new. *P. momordicae* and *P. trochomeriae* are recognised as valid species different from *P. cephalandrae*. *Uredo melothriae* is a new combination for *Uromyces melothriae*. *P. cucumeris* is a new report for Namibia, *P. momordicae* for Zimbabwe and *P. vanderystii* for Kenya. The species appear to be host specific with regard to host tribes, but *P. citrulli* and *P. cucumeris* may pass tribal boundaries. Most species are morphologically very similar and are characterised by a unique set of teliospore characters. They are therefore regarded as a natural group. The distribution of this group in semiarid habitats, mainly from southern Africa to India, is discussed.

## Introduction

Cucurbitaceae are a medium sized, predominantly tropical to subtropical, plant family with many members that are

cultivated for their edible fruits. Prominent genera with several economically important crops are *Citrullus* (melon), *Cucumis* (cucumber), *Cucurbita* (squash and pumpkin) and *Sechium* (chayote). The cucurbits of the Old World are especially diverse, comprising several genera and species that are already cultivated or are potential sources and reservoirs for breeding of new crop and medicinal plants or to improve existing cultivars (Bates et al. 1990).

Among the important fungal pathogens that attack cultivated cucurbits are powdery and downy mildews, *Alternaria*, *Fusarium* and *Verticillium* spp. and *Colletotrichum lagenarium* (Pass.) Ellis and Halst. (Blancard et al. 1994; Robinson and Decker-Walters 1999). Additionally, cucurbits are attacked by rust fungi (Uredinales, basidiomycetes) of the teleomorph genera *Cerotelium*, *Chrysocelis*, *Coleosporium*, *Puccinia* and *Uromyces*. Most of the latter do not seem to cause damage on cultivated cucurbits and they are not mentioned as pests in the manuals of Blancard et al. (1994), Robinson and Decker-Walters (1999) and Zitter et al. (1996). However, the genus *Puccinia* comprises 18 known species that infect wild and cultivated species of many cucurbit genera of the Old World and may therefore be potentially harmful (Rizvi and Hasanain 1960).

Most of these *Puccinia* species are morphologically similar. Where known, they are autoecious, have *Caecoma*- or *Aecidium*-like aecia, the latter often with rudimentary peridia, uredinia of *Uredium* type and, generally, teliospores with a more or less conspicuously bilaminate cell wall. A remarkable, though often overlooked, feature of several species is the presence of two (to three) germ pores per teliospore cell. Several mycologists have noted that the latter teliospore characters are more typical for members of the genus *Uropyxis* (Uropyxidaceae) than for *Puccinia* (Baxter 1959): Ito and Murayama (1943) combined *P. arisanensis* to *Uropyxis arisanensis*, and Ramakrishnan et al. (1952) mentioned that *P. gymnopetali-wightii* was similar to *Uropyxis*

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### Taxonomic novelties

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New species: *Puccinia antennata* R. Berndt and A. Rössel, *P. arbor-miraculensis* R. Berndt, *P. hieroglyphica* R. Berndt, *P. rhytidoderma* R. Berndt

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New combination: *Uredo melothriae* (Henn.) R. Berndt for *Uromyces melothriae* Henn.

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because of the layered cell wall of the teliospores. Ramachar et al. (1985) reported *Uropyxis*-like teliospores with two, rarely three, germ pores per cell in *P. ctenolepidis* from India. The species revealed spermogonia of type 4, however, indicative of Pucciniaceae, not Uropyxidaceae, which have spermogonia of type 5 (Cummins and Hiratsuka 2003). As the morphology of spermogonia has proven to be a reliable marker for higher-level relationships among rust fungi, it is reasonable to accommodate these rust fungi with *Puccinia* according to morphology of spermogonia rather than teliospore traits. Another character that corroborates this affiliation is the presence of *Aecidium*-like aecia in some species—although the aecial peridium is generally vestigial or almost lacking. Members of Uropyxidaceae possess *Uredium*-like aecia (Cummins and Hiratsuka 2003).

The attempt to determine a *Puccinia* on Cucurbitaceae may confront the investigator with unexpected problems: some species are deceptively similar with regard to certain spore stages and have not always been adequately characterised by the original descriptions. Additionally, quite often the descriptions do not comprise the holomorph but only single spore stages. Taken together, the morphological similarity of the fungi and the incompleteness of the descriptions may lead—and has led—to misidentifications and erroneous synonymy that hamper our understanding of the biology of this group of fungi.

The present study intends to portray all known autoecious *Puccinia* spp. on Cucurbitaceae and to facilitate their identification. It gives an account of the known fungus–host relationships and summarises present knowledge of the geographic distribution of the species.

## Materials and methods

All descriptions are based on dried herbarium specimens. Spore scrapes were mounted in lactophenol and gently heated to boiling. The preparations were examined with a Carl Zeiss “Axiophot” light microscope using DIC optics, and photographs were taken with a Zeiss MC-80 camera on Kodak Ektachrome 64 Professional slide film. Freehand line drawings were prepared combining the observed characters. Details of the spore surface and layering of the spore wall are shown only in some of the depicted spores. At least 30 spores were measured for each spore stage; exceptions are mentioned in the text. Measurements comprise the usual range and the arithmetic means; extremes are given in brackets. The names of herbaria are abbreviated by their acronyms according to *Index Herbariorum* (Stafleu et al. 1981). The Roman numerals 0, I, II, III are used in “Material studied” to designate the spore stages spermogonia, aecia, uredinia or telia, respectively.

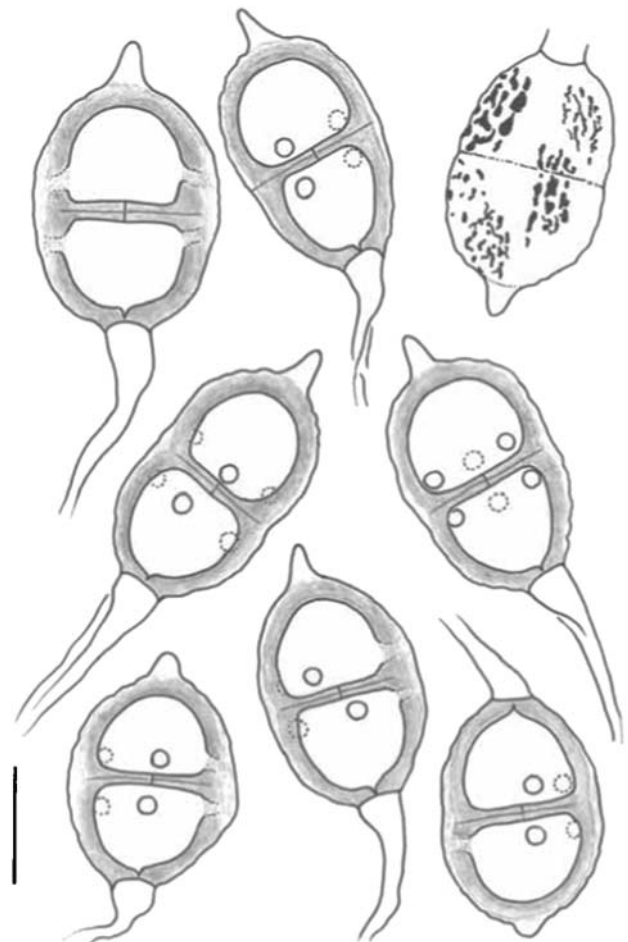
## Results

All species are listed in alphabetical order and described in detail. Their validity and status are discussed briefly following the descriptions. The study resulted in the recognition of the new species *P. antennata*, *P. arbor-miraculensis*, *P. hieroglyphica*, and *P. rhytidoderma*.

*Puccinia antennata* R. Berndt and A. Rössel, sp. nov.

**Etymology:** denominating the long apiculi of the teliospores (Figs. 1, 2, 3 and 4).

**Aecia** in gregibus parvis, dense constipatis, foliicola, amphigena sed praecipue abaxialia, bullata, irregulariter cupulato-aperta, sine peridio, copia sporarum pallide cinnamomea; **aeciosporae** ellipsoideae, late ellipsoideae, subglobosae, saepe subangulariter obovoideae, nonnunquam apicaliter paulum elongatae et subapiculatae, 21–28(32)×(16)18–23 μm (medium 24.5×19.9 μm), pariete ca. 1–1.5 μm crasso, apicaliter leniter incrassato usque ad 3 μm (usque ad 6 μm in sporis subapiculatis), subhyalino ad ochraceo, delicate denseque



**Fig. 1** *Puccinia antennata* (type), teliospores. The surface ornament illustrated on a single spore represents types of warts found on different spores. Bar 20 μm

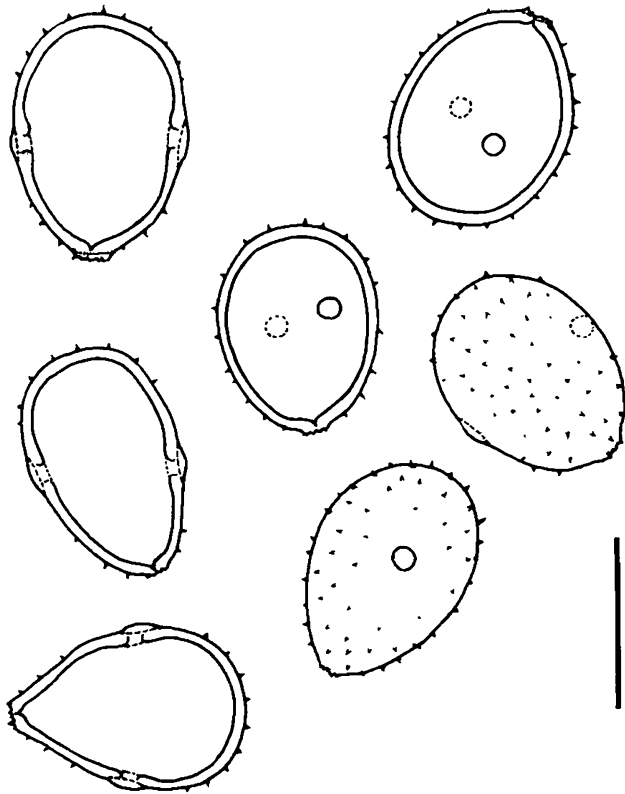


Fig. 2 *P. antennata* (type), urediniospores. Bar 20  $\mu\text{m}$

verruculoso verrucis delicate cylindricis, ca. 0.5  $\mu\text{m}$  longis, poris germinationis obscuris, verosimiliter sparsis. **Uredinia** amphigena in foliis, sed praecipue abaxialia, 0.3–1 mm diam., sate ferruginea, pulverulenta; **urediniosporae** (late) ellipsoideae, obovoideae (ad subglobosae), 23–29 $\times$ 19–23  $\mu\text{m}$  (medium 26.6 $\times$ 20.8  $\mu\text{m}$ ), pariete 1.5–2  $\mu\text{m}$  crasso, ferrugineo, delicate echinulato praeter duas tonsuras indistinctas circum poros germinationis, ca. (1.5)2–3  $\mu\text{m}$  inter spinas, poris germinationis 2(3) aequatorialibus, plusminusve oppositis, papilla parva et inconspicua praeditis. **Telia** foliicola, amphigena, 0.3–1 mm diam. vel majora ob coalescentiam, atra, pulverulenta; **teliosporae** praecipue late ellipsoideae, rariter ellipsoideae vel subglobosae, utrinque rotundatae, non vel aegre constrictae ad septum, etiam leniter inflatae, 34–44(48) $\times$ 26–32  $\mu\text{m}$  (medium 37.9 $\times$ 28.6  $\mu\text{m}$ ), pariete indistincte bistrato, ca. 4  $\mu\text{m}$  crasso, usque ad 8  $\mu\text{m}$  in poris germinationis, strato inferiori exteriori crassiore, castaneo, strato exteriori fulvo vel non distinguibili, praecipue apicaliter vel subapicaliter apiculum (rariter duo) tenuem usque ad late conicem, 3–9(10)  $\mu\text{m}$  longum, facienti, irregulariter ruguloso ad rugoso, verrucis irregularibus, delicatis usque ad grossis dense vel laxe obsito, poris germinationis binis vel ternis (rariter quaternis) septum juxta; pedicello subhyalini, persistenti, usque ad 60  $\mu\text{m}$  longo praeditae. Mesosporae rae.

In foliis *Dactyliandrae welwitschii* Hook.

**Aecia** amphigenous, predominantly abaxial on leaves, in compact small groups, bullate, opening by an irregular pore,

ordinary peridium lacking, spore mass pallid cinnamon; **aeciospores** ellipsoidal, broadly ellipsoidal, subglobose, often slightly angular obovate, sometimes apically slightly elongated and subapiculate, 21–28(32) $\times$ (16)18–23  $\mu\text{m}$  (mean 24.5 $\times$ 19.9  $\mu\text{m}$ ), spore wall ca. 1–1.5  $\mu\text{m}$  thick, apically generally slightly thickened to 3  $\mu\text{m}$ , or—in subapiculate spores—up to 6  $\mu\text{m}$ , subhyaline to ochraceous, densely verruculose by delicate, slenderly cylindrical warts to ca. 0.5  $\mu\text{m}$  long, germ pores obscure, most probably scattered. **Uredinia** amphigenous, predominantly abaxial, 0.3–1 mm diam., deeply ferrugineous, pulverulent; **urediniospores** (broadly) ellipsoidal, obovoidal (to subglobose), 23–29 $\times$ 19–23  $\mu\text{m}$  (mean 26.6 $\times$ 20.8  $\mu\text{m}$ ), spore wall 1.5–2  $\mu\text{m}$  thick, ferrugineous, finely and evenly echinulate except for two indistinct smooth patches around the germ pores, ca. (1.5)2–3  $\mu\text{m}$  between spines, with 2(3) equatorial, more or less opposite germ pores provided with small, inconspicuous papillae. **Telia** amphigenous, 0.3–1 mm diam. or larger by confluence, black, pulverulent; **teliospores** mostly broadly ellipsoidal, rarely ellipsoidal or subglobose, rounded at both ends, not or hardly constricted at the septum or even slightly inflated, 34–44(48) $\times$ 26–32  $\mu\text{m}$  (mean 37.9 $\times$ 28.6  $\mu\text{m}$ ), spore wall indistinctly bilaminar, ca. 4  $\mu\text{m}$  thick, up to 8  $\mu\text{m}$  over germ pores by swollen outer wall layer, inner wall layer

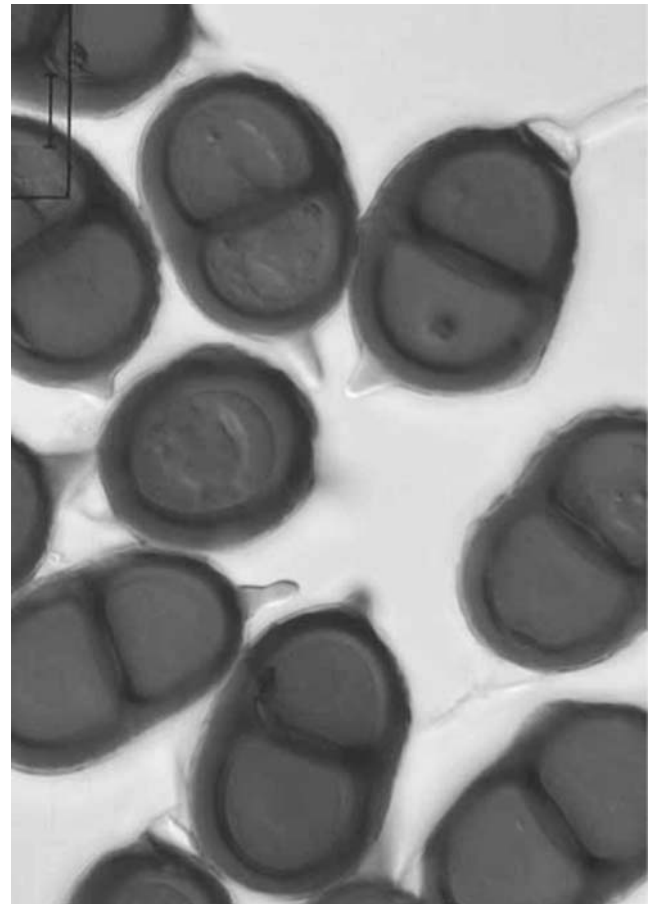
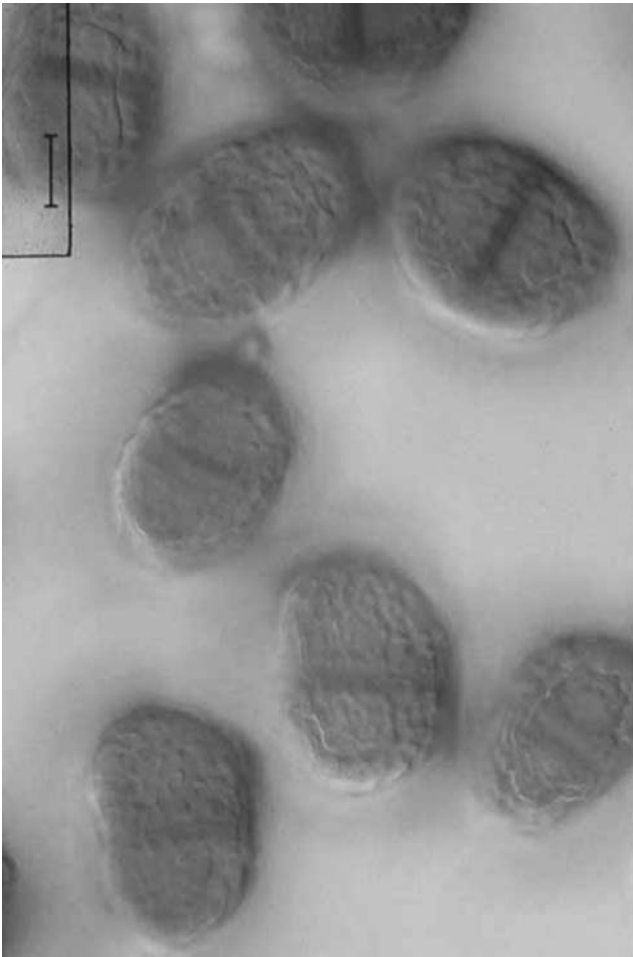


Fig. 3 *P. antennata* (type), teliospores. Bar 10  $\mu\text{m}$



**Fig. 4** *P. antennata* (type), teliospores. Focus on surface ornament. Bar 10  $\mu\text{m}$

thicker than outer one, chestnut brown, outer layer brownish yellow or not distinguishable, generally forming a slender, 3–9(10)  $\mu\text{m}$  long apiculus, that is located apically or subapically (more rarely without or with two apiculi), surface irregularly rugulose to rugose, densely to sparsely covered with rather fine to coarse and very irregularly shaped warts, 2–3(4) germ pores per teliospore cell close to septum or shortly distant; pedicels subhyaline, persistent, up to 60  $\mu\text{m}$  long but often breaking shorter, inserted basally or somewhat shifted to the side. Mesospores rare.

On leaves of *Dactyliandra welwitschii* Hook.

Holotype (PREM): Africa, Namibia, Caprivi Strip, Katima Mulilo, at the camp site of “Zambezi Lodge”, on *Dactyliandra welwitschii*, leg. A. Rössel, det. R. Berndt, 10 May 2004 (isotype in Z+ZT). Paratype (HerB 5171, in Z+ZT): Africa, Zimbabwe, Botanical Garden of Harare, on unidentified Cucurbitaceae, possibly *Cucumis* sp., leg. C. and K. Vánky, det. R. Berndt, 19 Feb 1999.

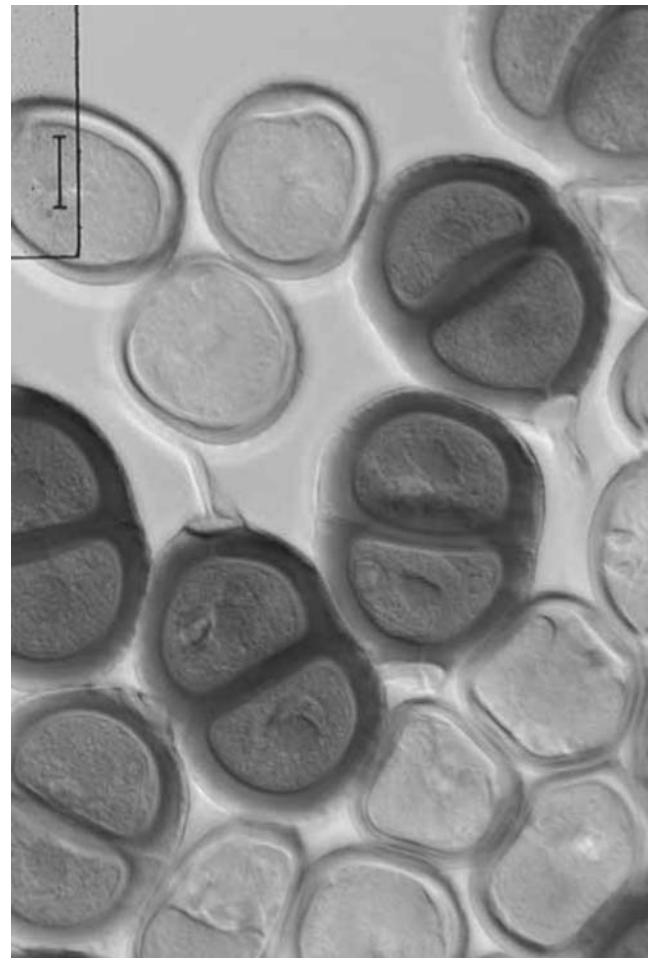
This rust is similar to *P. ctenolepidis* and *P. windhoekensis* but differs by conspicuously apiculate teliospores. The specimen from Zimbabwe consists of a small, infected part of the host with a single shrivelled flower. The host could not be

determined reliably but is not *Dactyliandra* and may represent *Cucumis* sp. If this is correct it belongs to the same tribe as *Dactyliandra*, i.e. to Melothrieae. The specimen was assigned to *P. antennata* despite slight differences: the teliospores have two germ pores per teliospore cell (a spore with three pores per cell was found only once), the outer teliospore wall layer is more sharply delimited from the inner layer and thicker, and the teliospores are slightly longer on average (43.2  $\mu\text{m}$ ). To my knowledge, no rust fungus has been reported hitherto from the genus *Dactyliandra*.

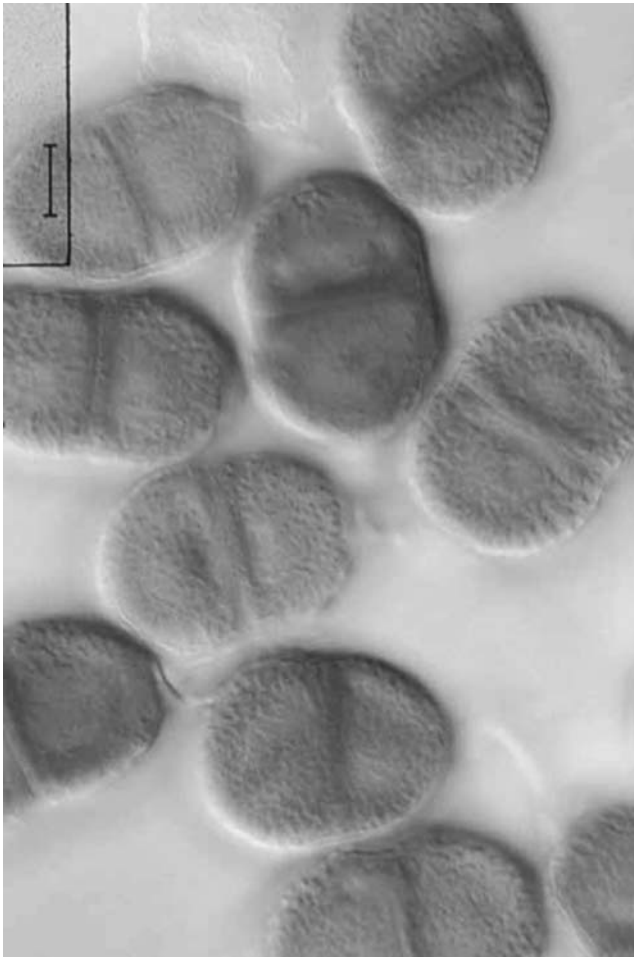
*Puccinia arbor-miraculensis* R. Berndt, sp. nov.

Etymology: denominating the collection site: Wonderboom—literally, miracle tree (Figs. 5, 6 and 7).

**Spermogonia** et **aecia** absentia. **Uredinia** amphigena, praecipue abaxialia, ferruginea, pulverulenta, ca. 0.4–1 mm diam.; **urediniosporae** obovoideae, late ellipsoideae (ad subgloboseae), 23.5–30 $\times$ 20–24  $\mu\text{m}$  (medium 26.8 $\times$ 22.0  $\mu\text{m}$ ), pariete ochraceo–brunneo, ca. 1–1.5  $\mu\text{m}$  crasso, apicaliter et



**Fig. 5** *Puccinia arbor-miraculensis* (type), teliospores among one-celled urediniospores. Bar 10  $\mu\text{m}$



**Fig. 6** *P. arbor-miraculensis* (type), teliospores. Focus on surface ornament. Bar 10  $\mu\text{m}$

hilum versus paulum crassiore, poris germinationis 2(3), plus minusve aequatorialibus oppositisque, papillis parvis, hyalinis praeditis et tonsura copertis qui regionem aequatoris fere cingit, praeterea moderate delicate echinulato, ca. 2–3  $\mu\text{m}$  inter spinas. **Telia** urediniis similia, atro-brunnea; **teliosporae** late ellipsoideae, raro ellipsoideae vel subgloboseae, utrinque rotundatae, non vel aegre constrictae ad septum, (34.5)36–44  $\times$  26–32  $\mu\text{m}$  (medium 38.8  $\times$  29.7  $\mu\text{m}$ ), pariete ca. 3.5–4.5  $\mu\text{m}$  crasso, in poris germinationis usque ad 6  $\mu\text{m}$ , indistincte bilaminato, strato inferiori exteriori crassiore, ferrugineo vel dilute castaneo, strato exteriori ochraceo, verrucis irregularissimis, parvis vel grossis crebre obsito, sine apiculo, poris germinationis ternis (binis), septum juxta vel apicem versus 1/3–1/2 (2/3) positus, pedicello tenue tunicato, hyalino, basaliter (ad lateraliter) inserto, usque ad 80  $\mu\text{m}$  longo praeditae.

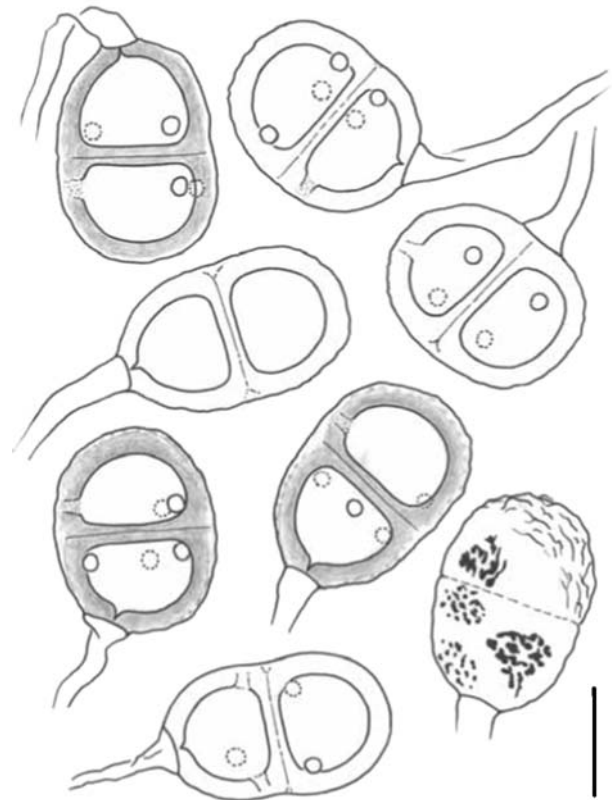
In foliis *Kedrostidis africanae* (L.) Cogn. vel *Momordicae balsamineae* L.

**Spermogonia** and **aecia** absent. **Uredinia** amphigenous on leaves, predominantly abaxial, ca. 0.4–1 mm diam., ferrugineous, pulverulent; **urediniospores** obovoidal, broadly ellipsoidal (to subglobose), 23.5–30  $\times$  20–24  $\mu\text{m}$  (mean

26.8  $\times$  22.0  $\mu\text{m}$ ), spore wall ochraceous-brown, ca. 1–1.5  $\mu\text{m}$  thick, at apex and hilum slightly thicker, germ pores 2(3), more or less opposite and equatorial, with small, flat, hyaline papillae and a smooth patch covering almost the entire equatorial region, the remaining wall moderately fine echinulate with spines about 2–3  $\mu\text{m}$  apart. **Telia** like the uredinia but blackish-brown; **teliospores** broadly ellipsoidal, more rarely ellipsoidal, rarely to subglobose, rounded at both ends, not or very slightly constricted at septum, (34.5)36–44  $\times$  26–32  $\mu\text{m}$  (mean 38.8  $\times$  29.7  $\mu\text{m}$ ), spore wall ca. 3.5–4.5  $\mu\text{m}$  thick, at germ pores swollen to 6  $\mu\text{m}$ , indistinctly bilaminated with a thick inner, ferrugineous or light chestnut brown layer and an outer, ochraceous and much thinner layer that is densely verrucose by very irregular rather fine to rather coarse warts and does not form an apiculus, germ pores 3(2) per teliospore cell, often pairwise in adjacent cells, close to the septum but sometimes offset 1/3–1/2 (2/3) towards the apex, pedicel inserted basally or slightly offset, rarely laterally, thin-walled, hyaline, up to 80  $\mu\text{m}$  long but most often breaking shorter.

On leaves of *Kedrostis africana* (L.) Cogn. or *Momordica balsaminea* L.

Holotype [Z+ZT, on a sheet of *Kedrostis africana* (L.) Cogn. from the phanerogam collection]: South Africa, Transvaal Prov., Pretoria District, Wonderboom siding, on



**Fig. 7** *P. arbor-miraculensis* (type), teliospores. The surface ornament illustrated on a single spore represents various types of warts and the rugose surface found on different spores. Bar 20  $\mu\text{m}$

*Kedrostis africana*, 27 Feb 1932, leg. A.O.D. Mogg (no. 16479). Isotype in PREM (PREM 26400). Paratype: South Africa, Free State Prov., Bloemfontein, on *K. punctulata* Cogn., leg. G. Potts, 13 Apr 1917 (PREM 11301, sub *P. cephalandrae*).

A rust fungus discovered on a specimen of *Kedrostis africana* kept in the phanerogam collection of Z+ZT proved to be different from the similar *P. ctenolepidis* and *P. windhoekensis* by irregularly verrucose to rugulose teliospores lacking apiculi. The rust-infected leaves contained in PREM 26400 (sub *P. cephalandrae*) stem from the same collection according to the data on the label. On the latter specimen, however, the original host name, *Kedrostis*, was crossed out and replaced by *Momordica balsaminea* L. The specimen is listed under this host name in Doidge (1950). In spite of comparing numerous specimens of both possible host plants in Z+ZT, I could not decide which host determination is correct.

PREM 11301 (sub *P. cephalandrae*) on *K. punctulata* is indistinguishable from the type specimens and certainly belongs to the same species.

*Puccinia arisanensis* Hirats. f. and Hashioka 1941

Bot. Mag. Tokyo 55: 271 (Fig. 8).

≡ *Uropyxis arisanensis* (Hirats. f. and Hashioka) S. Ito and Murayama 1943

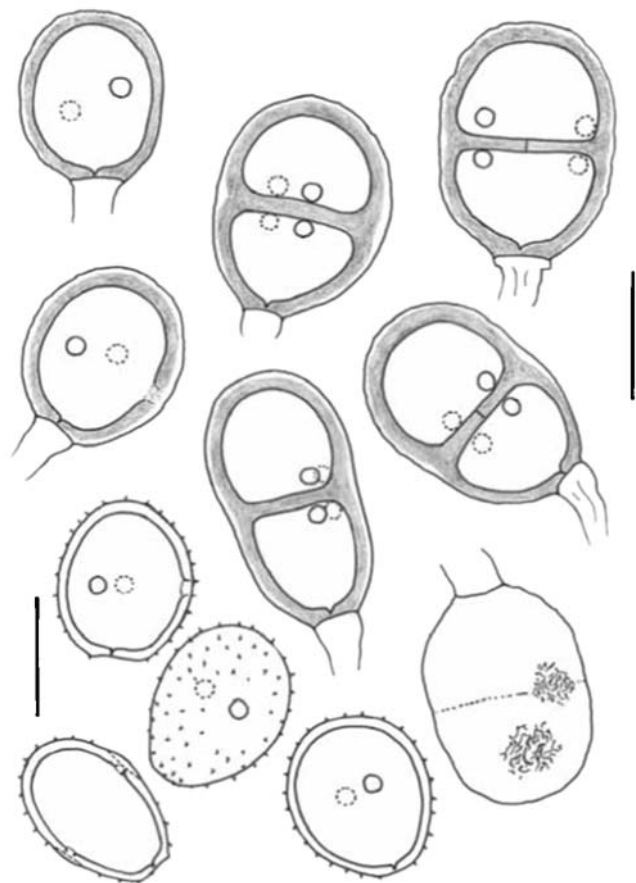
=? *Uredo zehneriae* Thümen 1877 (fide Hiratsuka 1941)

=? *Uredo cantonensis* Yates 1917 (fide Hiratsuka 1941)

Type on *Melothria mucronata* (Blume) Cogn., Taiwan.

Material studied: Taiwan, Prov. Tainan, Arisan (Mt. Ari), on *Melothria mucronata* (Blume) Cogn. (= *Zehneria mucronata* (Blume) Miq.), 16 Jan 1941, leg. Hiratsuka and Hashioka (type, Z+ZT)

**Urediniospores** obovoidal to subglobose, slightly compressed along the axis between the two opposite germ pores, 24–29.5 × 20–25 μm (mean for 25 spores 26.5 × 22.3 μm), spore wall ochraceous to light brown, 1–1.5 μm thick, a little thicker at the hilum, moderately dense and delicately echinulate, with an ill-defined smooth patch proximal to or around the germ pores, pores 2(3), more or less equatorial and opposite, sometimes with a flat, small papilla. **Teliospores** broadly ellipsoidal, or obovoidal, not or very slightly constricted at the septum, 29.5–40 (45.5) × 24–29.5 μm (mean for 25 spores 35.8 × 26.8 μm), spore wall orange–brown, rugulose with a fine dendritic to labyrinthine pattern or appearing almost smooth, 2.5–3.5 μm thick, inconspicuously to clearly two-layered, with a thin ochraceous outer layer that is often thickened at the septum, germ pores two per teliospore cell, close to the septum, more or less opposite in one teliospore cell, most often pairwise in the adjacent cells, papillae lacking, pedicels



**Fig. 8** *Puccinia arisanensis* (type), teliospores, one-celled mesospores and echinulate urediniospores. Bars (for uredinio- and telio- mesospores) 20 μm

hyaline, fragile, breaking off shortly from the hilum or up to almost as long as the spores. Mesospores scattered, with two germ pores, rarely three or one.

Ito (1950) reported 30–40 × 20–25 μm for the teliospores and 20–29 × 17–23 μm for the urediniospores. Jørstad (1959) observed that the teliospore cells had two germ pores and added *Melothria perpusilla* (Bl.) Cogn. as a new host from southern China.

It is probable that *U. cantonensis* on *Zehneria indica* (Lour.) Keraudren (= *Melothria indica* Lour.) from southern China (Guangzhou) is the same as *P. arisanensis*. *U. zehneriae* on *Zehneria scabra* (L. f.) Sond. from South Africa is morphologically similar but more likely belongs to *Puccinia rhytidoderma* R. Berndt described from Uganda on the latter host.

*Puccinia cephalandrae* Thümen 1876

Flora 59 (1876): 425 (Figs. 9 and 10).

= *Uredo cephalandrae* Thümen 1876

= *Aecidium cephalandrae* Cooke 1884 (fide Cooke 1884 and Doidge 1927)

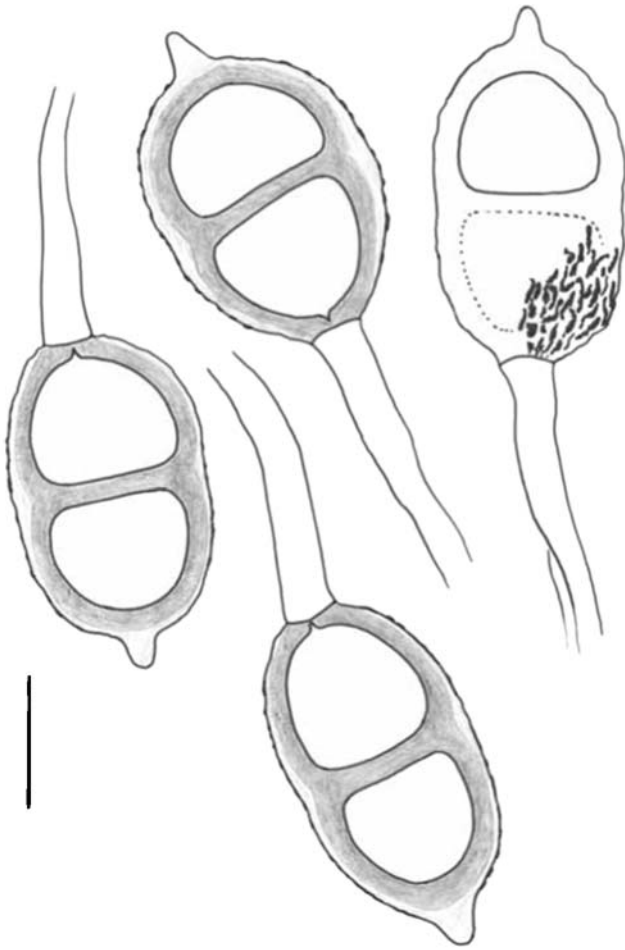


Fig. 9 *Puccinia cephalandrae* (type), teliospores. Bar 20  $\mu\text{m}$

Type on *Cephalandra quinqueloba* Schrad., South Africa, Eastern Cape Prov.

Material studied: South Africa, Eastern Cape Prov., near Somerset-East, at “Boschberg”, on *Cephalandra quinqueloba* Schrad. leg. Mac Owan (type, Thümen Mycotheca Univ. no. 1031, Z+ZT). South Africa, Promontory of Cape of Good Hope, leg. Mac Owan, 1875. (type, Thümen Mycotheca Univ. no. 1031, PUR F-7667). The location “Cape of Good Hope” on the label has probably been copied from the original description (“Promont. bonae-spei”), but this indication is an error as the “Boschberg” is in the Eastern Cape Province and not on Cape Peninsula. Africa, Northern Rhodesia [=Zambia], Western Prov., Naola District, Naola township, on *Coccinia* cf. *pubescens* Cogn. ex Harms, leg. A. Angus, Dec 1952 (PUR F-16057). South Africa, Free State Prov., Bloemfontein, on *Kedrostis punctulata* Cogn., 13 Apr 1917, leg. G. Potts (PREM 11301). South Africa, near Pretoria, Warmbaths Rd., on *Trochomeria ?macrocarpa*, leg. L.C.C. Liebenberg, Nov 1941 (IMI 56165). Africa, Uganda, Singo County, Mubende District, Mile 101 on the Kampala-Hoima Rd., on *Zehneria scabra* (L. f.) Sond., leg. H.B. Gjørnum, 16 Oct 1970 (no. 519/70). South Africa, Zululand,

Entumeni, on *Z. scabra* (*Melothria punctulata* (Thunb.) Cogn. according to a later annotation on label), June 1910(?), leg. W. Haygarth (PREM 14194 [II, III] and 1488 [0, I]).

**Urediniospores** broadly fusiform to lemon-shaped or ellipsoidal, (40)43–54(60)×20–26  $\mu\text{m}$  (mean 47.9×23.4  $\mu\text{m}$ ), spore wall golden–yellow, ca. 2  $\mu\text{m}$  thick, rather finely and moderately dense echinulate except for an indistinct smooth patch around the germ pores that is not always visible, germ pores two, equatorial to super-equatorial, opposite, without papillae. **Teliospores** mostly broadly ellipsoidal, not or scarcely constricted at the septum, 42–55(60)×25.5–33(36)  $\mu\text{m}$  (measured without apiculus, mean 46.2×31.6  $\mu\text{m}$ ), spore wall two-layered with an inner, orange–brown layer and a thinner, ochraceous outer layer that thickens considerably over the germ pores, more or less rugose, i.e. covered by very irregularly shaped flat, anastomosing warts, germ pores two per teliospore cell, close to the septum and generally opposite in a single cell, apiculus mostly present, very stout, normally 4–8  $\mu\text{m}$  long and 4–5.5  $\mu\text{m}$  wide, rarely lacking or shorter, pedicels subhyaline, stout, ca. 1–1.5 times as long as spores.

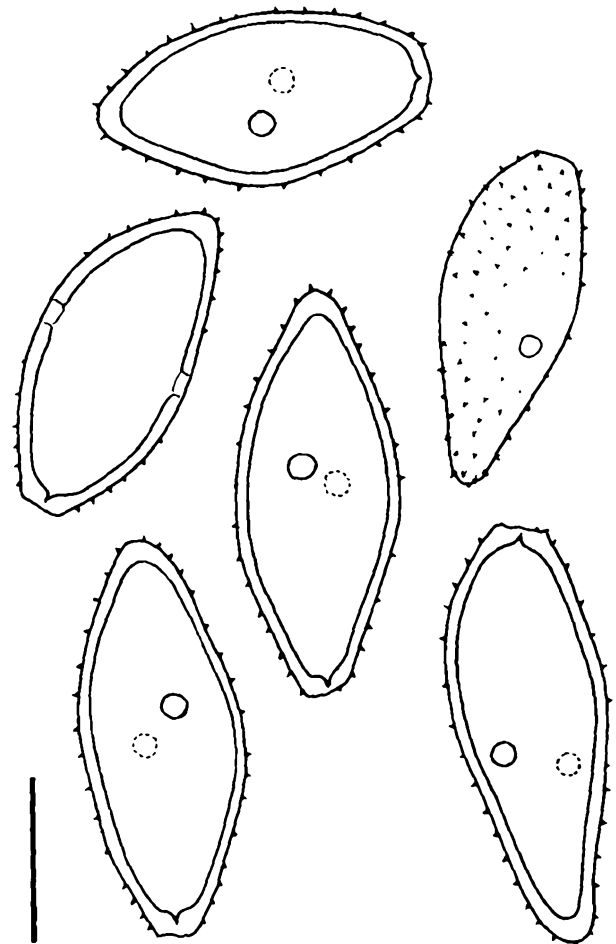


Fig. 10 *P. cephalandrae* (type), urediniospores. Bar 20  $\mu\text{m}$



When urediniospores are present, *P. cephalandrae* is unmistakable. No other known *Puccinia* species on cucurbits has such large urediniospores. The teliospores, however, are similar to those of other *Puccinias* and may easily be confused. Doidge (1950) listed *Coccinia* (= *Cephalandra*) (tribe Benincaseae), *Cucumis*, *Kedrostis*, *Melothria* (= *Zehneria*), *Trochomeria* (tribe Melothrieae) and *Momordica* (tribe Joliffieae) as host genera of *P. cephalandrae* and supposed that *P. momordicae* and *P. trochomeriae* were synonymous (Doidge 1927). The latter is incorrect as urediniospores unlike those of *P. cephalandrae* were discovered in the type specimens of *P. trochomeriae* (Sydow 1922) and *P. momordicae* (present work). The present investigation suggests that *P. cephalandrae* has a host range restricted to *Coccinia* and that reports from host genera of other tribes are due to misidentifications or the alleged synonymy with *P. momordicae* and *P. trochomeriae*: *P. cephalandrae* (PREM 14188 and 14194) on *Melothria punctata* (Thunb.) Cogn. is not *P. cephalandrae* but *P. hieroglyphica* described in the present paper. The host is nowadays assigned to *Zehneria*, as *Z. scabra* (L. f.) Sond. Gjørnum (1986) also assigned a specimen on *Z. scabra* from Uganda to *P. cephalandrae*. It is not *P. cephalandrae* either but *P. rhytidoderma* described in the present paper. *P. cephalandrae* on *Kedrostis punctulata* (PREM 11301) and on cf. *Momordica balsaminea* (PREM 26400) are also not this species but *P. arbor-miraculensis* described in the present paper.

IMI 56165 on *Trochomeria* revealed only teliospores. The specimen is labelled *P. cephalandrae* and listed by Doidge (1950) under this name. It was compared to the type of *P. trochomeriae* and belongs to the latter species.

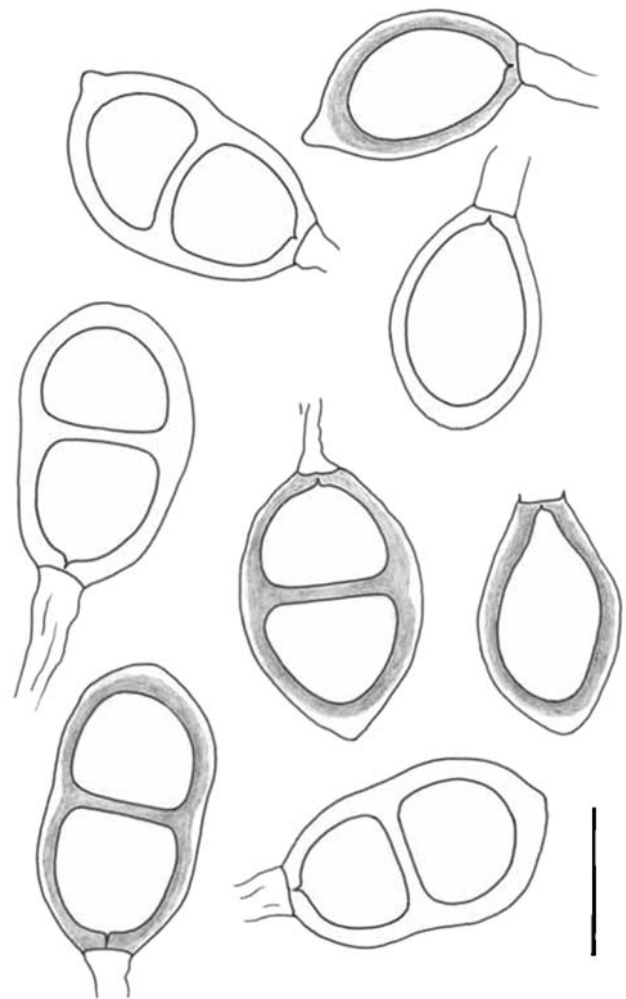
A specimen on *Coccinia* from Zambia labelled *P. cephalandrae* (PUR 16057) had only urediniospores, which measured only  $24\text{--}30 \times 18\text{--}22.5 \mu\text{m}$ , and therefore does not belong to the present species. It cannot be safely assigned to another species on its urediniospore characters but is morphologically similar to *P. arisanensis*, *P. ctenolepidis* and *P. windhoekensis* (the last one possibly on the same host genus).

#### *Puccinia cephalandrae-indicae* Syd. and P. Syd 1906

Ann. Mycol. 4: 433 (Fig. 11).

Type on *Cephalandra indica* (Wight and Arn.) Naud., India, Maharashtra State.

Material examined: India, Bombay Presidency, Nadiad, on *Cephalandra indica* (= *Coccinia indica* Wight and Arn.), leg. E.J. Butler, 12 Nov 1905 (type, B). India, Pusa, Bihar, on *Cephalandra indica* (= *Coccinia indica*), leg. E.J. Butler, 18 Dec 1911 (Herb. Crypt. Indiae Orient. Exsicc., Indian Uredinales, 2. fasc., no. 70, PUR F-15860). On the package spore stages II, III were indicated but aecia were included.



**Fig. 11** *Puccinia cephalandrae-indicae* (type), teliospores and one-celled mesospores. The bilaminate spore wall is shown in some of the spores by shading. Bar 20  $\mu\text{m}$

**Aecia** lacking an ordinary peridium but isolated, thick-walled and coarsely warty peridial cells present, spore mass light cinnamon in herbarium specimen; **aeciospores** roundish, subangular, sometimes elongated and subapiculate,  $23\text{--}29 \times 21\text{--}25 \mu\text{m}$  (mean  $25.6 \times 22.5 \mu\text{m}$ ), spore wall light ochraceous, 1.5–2  $\mu\text{m}$  thick, occasionally much thicker at the apiculus or slightly thickened in the spore angles, finely and rather evenly verruculose. **Teliospores** ellipsoidal to broadly ellipsoidal (to subglobose), not or very slightly constricted at the septum,  $32\text{--}42 \times 24\text{--}29 \mu\text{m}$  (mean  $37.1 \times 27.1 \mu\text{m}$ ), spore wall 3–5(6)  $\mu\text{m}$  thick, two-layered with a thin, ochraceous to subhyaline, very finely subreticulate or rugulose outer layer that may form a short apiculus or thickening and a thicker, light brown inner layer, germ pores indistinct, probably two per teliospore cell, close to the septum. Mesospores numerous, mostly with 2, more or less equatorial germ pores.

In the original diagnosis, the Sydows described the teliospore wall to be ca. 2  $\mu\text{m}$  thick. I found the walls to be

considerably thicker. In the type specimen from B two urediniospores were discovered ( $30\text{--}31\times 24\text{--}25\ \mu\text{m}$ , with two equatorial germ pores, evenly echinulate except for an indistinct smooth patch at the germ pores). Ragunathan and Ramakrishnan (1973) described the urediniospores as  $24\text{--}31\times 22\text{--}26\ \mu\text{m}$  in size with 3–4 scattered germ pores. The latter character is unusual in the present group of rusts, where most species have two opposite and equatorial pores (except *P. citrullina* Ragun. and K. Ramakr. and *P. hieroglyphica* R. Berndt) and is in contradiction to my observation. The teliospore size ( $29\text{--}41\times 19\text{--}29\ \mu\text{m}$ ) and wall thickness (3–4  $\mu\text{m}$ ) observed by Ragunathan and Ramakrishnan agree well with my measurements. The aecial stage has not been reported hitherto. Its occurrence shows that *P. cephalandrae-indicae* is an autoecious macrocyclic rust. It may be distinguished from similar species by finely rugulose teliospores with indistinct pores and short apiculi. The characters of the uredinial stage are dubious.

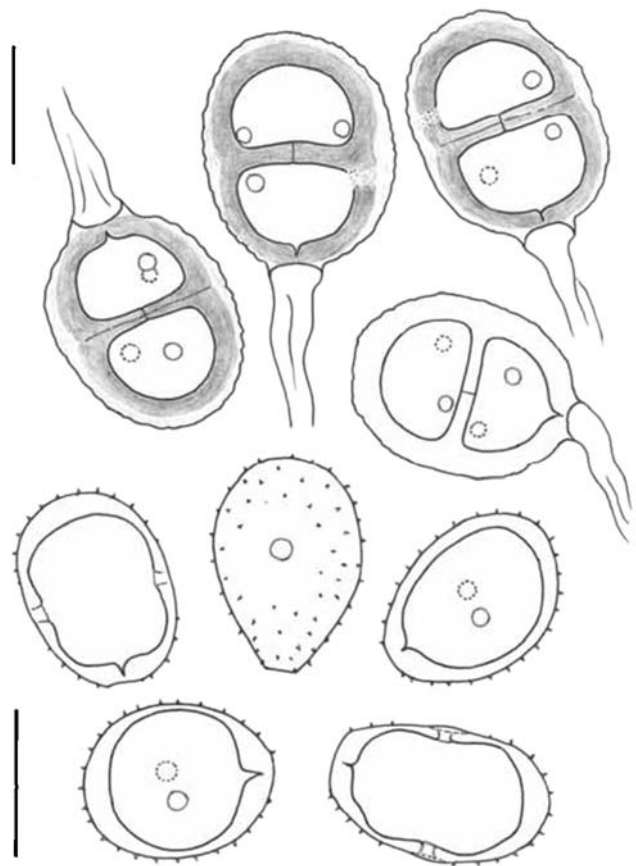
*Puccinia citrulli* Syd., P. Syd. and Butler 1912

Ann. Mycol. 10: 259 (Fig. 12).

Type on *Citrullus colocynthis* Schrad., India, Tamil Nadu State.

Material examined: India, Andhra Pradesh, Mahabubnagar Distr., Raghupathipet, Dundi river bed, on *Citrullus lanatus* (Thunb.) Matsum. and Nakai. (sub *Colocynthis citrullus* L.), leg. Ramachar and Rao, 23 Mar 1982 (PUR without no.). Pakistan, Sind, Landhi, on *Citrullus lanatus* (sub *Colocynthis citrullus*), leg. S.Z. Husnain, 25 Apr/May? 1949 (IMI 35568 and PUR F-11839). Pakistan, Karachi, on *Citrullus lanatus* (sub *Colocynthis citrullus*), leg. S.Z. Husnain, 28 Apr 1950 (IMI 136190). Yemen, Hodeidal, on *Citrullus lanatus* (sub *Colocynthis citrullus*), leg. M. Watt, 23 Apr 1973 (IMI 175048). Sudan, Red Sea coast, Tokar, on *Citrullus lanatus* (sub *Colocynthis citrullus*), leg. S.A.J. Tarr, 29 Jan 1955 (PUR F-15956 and IMI 59763). The location was adopted from Tarr (1963) as the locations indicated on the labels of the specimens from IMI and PUR were different and could not be found in geographic references.

**Urediniospores** obovoidal, more rarely broadly ellipsoidal or almost pyriform, slightly compressed along the axis between the opposite germ pores,  $25\text{--}32\times 20\text{--}26\ \mu\text{m}$  (mean for 25 spores,  $28.1\times 22.0\ \mu\text{m}$  [PUR F-15956]), cell wall light brown, rather finely and sparsely echinulate except for two smooth patches over the germ pores, 1.5–2.5  $\mu\text{m}$  thick laterally (around the germ pores), thicker at apex (ca. 3  $\mu\text{m}$ ) and around the hilum (3–5  $\mu\text{m}$ ), with two more or less equatorial, opposite germ pores that are sometimes covered by flat, inconspicuous papillae. **Teliospores** broadly ellip-



**Fig. 12** *Puccinia citrulli* (IMI 59763), teliospores and echinulate urediniospores. Bars (for telio- and urediniospores) 20  $\mu\text{m}$

soidal (to broadly obovoidal), not constricted at septum,  $33\text{--}45(49)\times 28\text{--}36\ \mu\text{m}$  (mean for 25 spores,  $38.2\times 30.8\ \mu\text{m}$  [PUR F-15956]), spore wall up to 7  $\mu\text{m}$  thick, occasionally laterally to 9  $\mu\text{m}$ , two-layered, with a 1–3  $\mu\text{m}$  thick ochraceous to pallid orange, rugose outer layer and a 3–4  $\mu\text{m}$  thick ferruginous inner layer that is not always sharply delimited from the outer one, germ pores indistinct and difficult to see, 2(3) per teliospore cell, close to the septum to almost equatorial, spores not apiculate. Meso-spores not observed.

Rizvi and Hasanain (1960) reported that *P. citrulli* was locally important as a pathogen on cultivated watermelons in Pakistan. The authors observed that colocynths (*Citrullus colocynthis* (L.) Schrad.) growing in fields with rust infected watermelons were not parasitised. Based on this observation, they proposed—invaldly—a new variety, var. *vulgari*, for the strains of *P. citrulli* infecting watermelons; the rust on colocynths they called *P. citrulli* var. *colocynthi*. They described the teliospores of the watermelon rust as smooth, having a single apical germ pore in the distal cell and one germ pore close to the septum in the proximal cell, observations contradictory to mine. Their measurements of

the uredinio- and teliospores tally well with my results. On the sheet of PUR F-11839, the uredinologist G.B. Cummins noted that he found teliospores with three pores per cell. Such teliospores are probably rare as I could not find a single one. In IMI 136190 a part of the urediniospore population had considerably thicker walls than the rest but did not differ in other characters. Such spores may represent a kind of “amphisporae” adapted to survive unfavourable conditions.

Ragunathan and Ramakrishnan (1972) reported *P. citrulli* on *Blastania garcini* Cogn. from India. *Blastania* is a synonym of *Ctenolepis* and belongs to another tribe (Melothrieae) than *Citrullus* (Benincaseae). It is possible that the specimen does not represent *P. citrulli* but the rather similar *P. ctenolepidis* Ramachar and Bagyanar.

*Puccinia citrullina* Ragunathan and K. Ramakr. ex Bagyanar. 1998

Mycotaxon 69: 478

≡ *Puccinia citrullina* Ragunathan and K. Ramakr. 1973 (nom. invalidum)

Type on *Citrullus lanatus* (Thunb.) Matsum. and Nakai., India, Tamil Nadu State.

**Spermogonia** and **aecia** unknown. **Uredinia** amphigenous, chiefly abaxial, brown, scattered; **urediniospores** obovoidal or broadly ellipsoidal,  $22\text{--}31 \times 17\text{--}22 \mu\text{m}$ , spore wall  $1\text{--}2 \mu\text{m}$  thick, cinnamon brown, echinulate, pores 3–4, scattered. **Telia** like the uredinia but blackish-brown; **teliospores** oblong or ellipsoidal,  $26\text{--}38 \times 17\text{--}26 \mu\text{m}$ , apex rounded, wall uniformly  $2\text{--}3 \mu\text{m}$  thick, chestnut brown, verrucose, pedicels hyaline, up to  $60 \mu\text{m}$  long.

As no material of *P. citrullina* could be obtained from herbaria, only the original description by Ragunathan and Ramakrishnan is repeated here. The species is distinguished from *P. citrulli* by smaller teliospores and urediniospores with 3–4 scattered germ pores. The latter character is unusual for the present group of rust, whose members generally have 2(3) opposite and equatorial pores. Ragunathan and Ramakrishnan (1973) depicted a single teliospore with one equatorial germ pore per cell. Considering that it is sometimes difficult to discern the germ pores, the delineated spore may not be representative.

*Puccinia ctenolepidis* Ramachar and Bagyanar. 1985

Mycologia 77: 981 (Figs. 13, 14 and 15).

Type on *Ctenolepis* sp., India, Andhra Pradesh State.

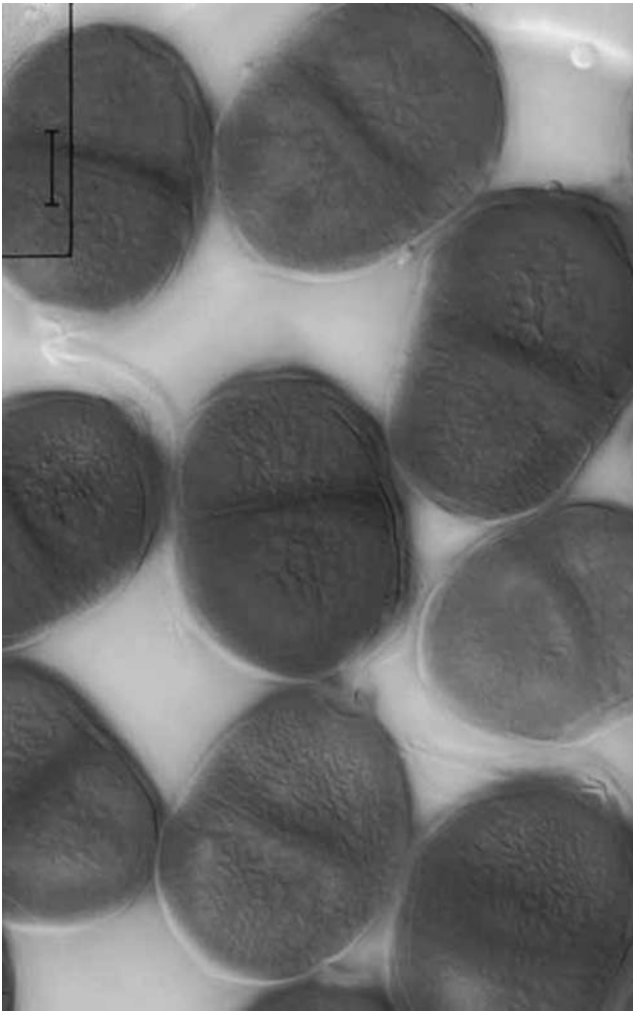
Material examined: India, Andhra Pradesh State, Mannanore Forest, on *Ctenolepis* sp., leg. K.N. Rao, 9 Feb 1982 (type).

**Spermogonia** weakly developed, adaxial, subepidermal, somewhat flattened, flask-shaped, with ostiolar paraphyses



Fig. 13 *Puccinia ctenolepidis* (type), teliospores. Bar  $10 \mu\text{m}$

(type 4); spermatia  $5\text{--}5.5 \mu\text{m}$  diam. **Aecia** amphigenous, weak peridium opening tardily and not recurving; peridial cells subcuboid,  $26 \times 22 \mu\text{m}$ , inner wall  $3.5\text{--}4 \mu\text{m}$  thick excluding shallow warts  $0.7 \mu\text{m}$  high  $\times 1 \mu\text{m}$  wide, outer wall  $5\text{--}5.5 \mu\text{m}$  thick and smooth; **aeciospores** broadly ovoidal,  $21\text{--}28(30) \times 17\text{--}21.5 \mu\text{m}$ , wall  $1\text{--}3.3 \mu\text{m}$ , light yellow, warts crowded  $0.3\text{--}0.8 \mu\text{m}$  diam., uneven but never bizonate, pores moderately conspicuous, 2–4(6), more or less scattered without internal annular thickening. **Uredinia** amphigenous; **urediniospores** ellipsoidal to obovoidal,  $23.5\text{--}32 \times 17\text{--}23.5 \mu\text{m}$  (mean for 18 spores  $27.5 \times 20.7 \mu\text{m}$ ), spore wall  $1.5\text{--}2 \mu\text{m}$  thick or slightly more near apex but often uniform, light yellow–brown to light chestnut, echinulate, echinulations  $1.7\text{--}5.5 \mu\text{m}$  spacing, except for generally completely smooth patch around pores, germ pores 2, approximately equatorial on flattened spore face, with slight ring of internal thickening. **Telia** amphigenous, black; **teliospores** ellipsoidal,  $35\text{--}48(50) \times 25\text{--}37(39) \mu\text{m}$  (excluding apiculus, mean  $44.5 \times 33.8 \mu\text{m}$ ), not or



**Fig. 14** *P. ctenolepidis* (type), teliospores. Focus on surface ornament. Bar 10  $\mu\text{m}$

very slightly constricted at septum, spore wall 4–6  $\mu\text{m}$  thick (mostly 5–5.5  $\mu\text{m}$ ), at germ pores generally swollen to 6–8  $\mu\text{m}$ , indistinctly bilaminate, the inner layer chestnut brown, the outer much thinner, yellow with chestnut tinge, rugose to rugulose, with irregular, sinuous, broken ridges or with very irregular warts often arranged in an almost labyrinthic pattern, at apex often forming a slenderly to broadly conical or cap-shaped apiculus up to 3–5  $\mu\text{m}$  high, germ pores inconspicuous, 2–3 per cell, those of distal cell 3/4 depressed to septal, those of proximal cell septal to 1/4 depressed, pedicel thin-walled, subhyaline, delicate, 60–110  $\mu\text{m}$  long, occasionally moderately offset, usually breaking near spore base.

The type of the species is not in IMI as indicated in the protologue. Through the courtesy of G. Bagyanarayana (Hyderabad, India) I obtained a fragment of the original collection. The material is scarce and does not contain the aecial stage. Therefore, the present description was based mainly on the diagnosis presented by Ramachar and Bagyanarayana supplemented by my own observations.

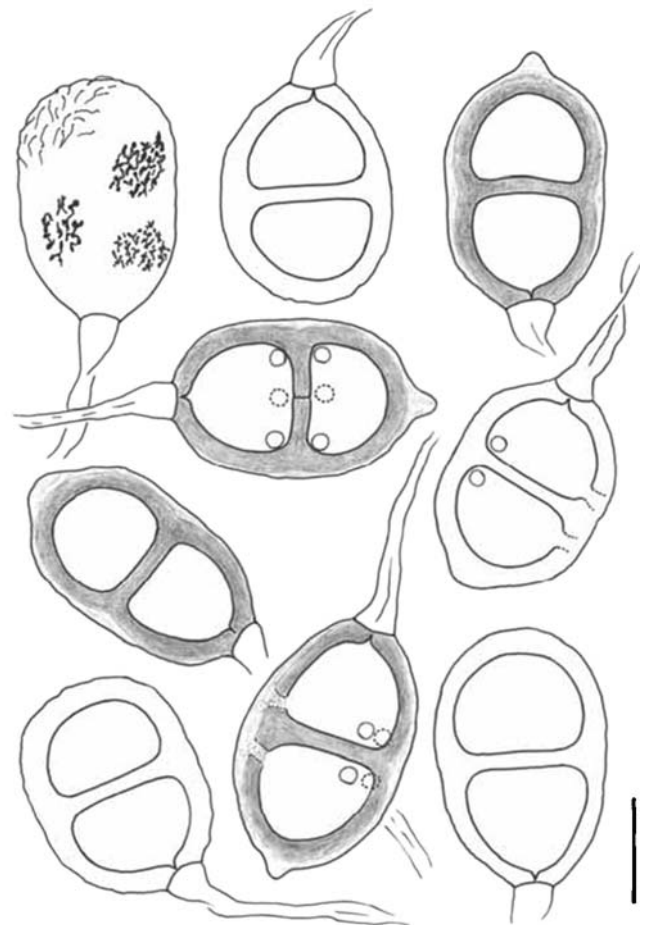
*P. windhoekensis* is very similar in all spore stages but can be distinguished by smaller teliospores with thinner and darker pigmented walls. *P. arbor-miraculensis* has teliospores lacking apiculi.

*Puccinia cucumeris* Henn. 1891

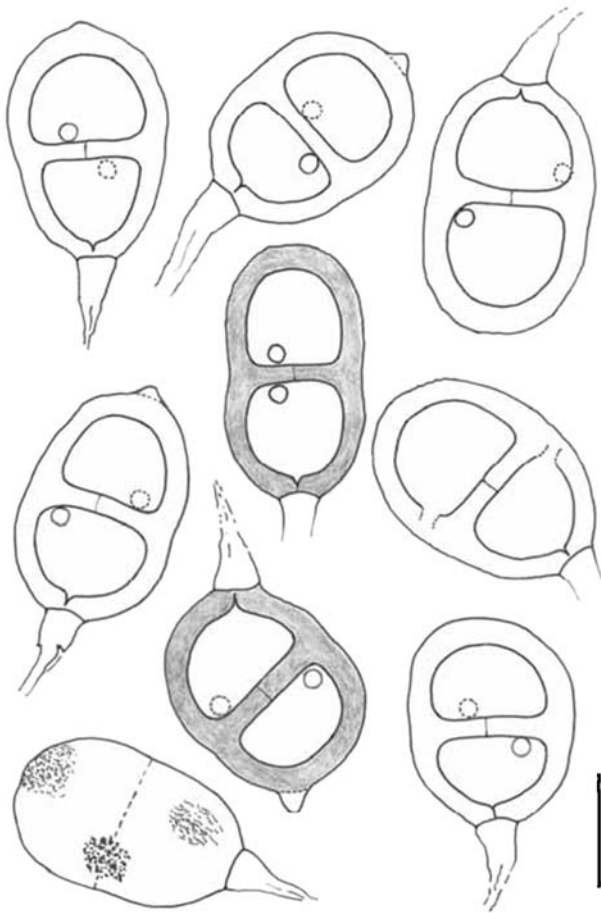
Engl. Bot. Jahrb. 14: 371 (Figs. 16 and 17).

Type on *Cucumis ficifolius* A. Rich., Africa, Eritrea.

Material examined: Africa, Abessinia, Colony Eritrea [=Eritrea], Keren, at the Dari brook, on *Cucumis ficifolius*, leg. G. Schweinfurth, 14 Mar 1891 (holotype and isotype, B). Brazil, Cantareira, S. P., on *Cucumis anguria* L., leg. S.C. Arruda, 19 Apr 1938 (PUR 88301). Brazil, Ceará State, Est. Exper. de Maraguape, Sto. Antonio, on *Cucumis anguria*?, leg. J. Weslander (sic?), Oct. 1938 (PUR F-18954). Brazil, IPEAN Bel-Pa., on *Cucumis anguria*, leg. F.C. de Albuquerque, 5 Jan 1971 (PUR 18955). Africa, Namibia, Caprivi Strip, at road from Rundu to Nkuremkuru, on *Cucumis anguria*, leg. A. Ritschel, det. R. Berndt, 2 May 2004 (PREM, Z+ZT).



**Fig. 15** *P. ctenolepidis* (type), teliospores. The surface ornament illustrated on a single spore represents various types of warts and the rugulose surface found on different spores. Bar 20  $\mu\text{m}$



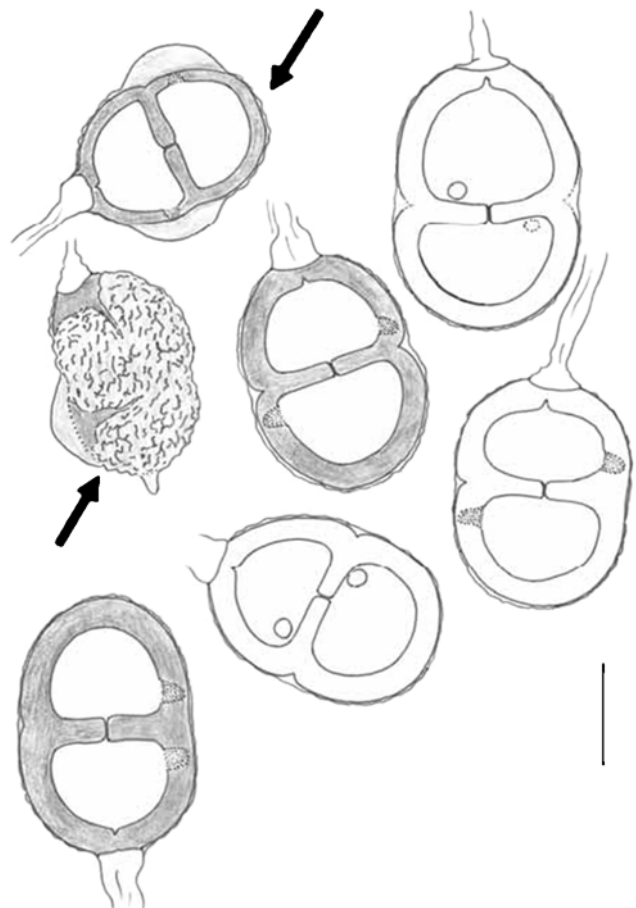
**Fig. 16** *Puccinia cucumeris* (Namibian specimen, Z+ZT), teliospores. The surface ornament illustrated on a single spore represents various types of warts found on different spores. Bar 20  $\mu\text{m}$

Africa, Nyasaland [=Malawi], Zomba, on *Cucumis* cf. *africanus* L. f., leg. P.O. Wiehe (no. 603), 17 Mar 1950 (PUR F-14516 and IMI 42563). Africa, Nigeria, University of Nigeria, village 3 miles N of Botany Dept., on *Coccinia barteri* (Hook. f.) Keay, leg. D. Eboh, 25 Feb 1977 (PUR F-18687).

**Aecia** amphigenous but predominantly abaxial, in dense, small groups on pallid yellow spots up to 3 mm diam., *Caecoma*-like, first bullate, then irregularly opening, pallid cinnamon; **aeciospores** often subangular, broadly ellipsoidal, subglobose or ellipsoidal, apically rounded to sub-apiculate, 18–31 $\times$ 16–26  $\mu\text{m}$  (mean 23.8 $\times$ 20.0  $\mu\text{m}$  [Namibian specimen], 24.6 $\times$ 18.9  $\mu\text{m}$  [PREM 40367]), spore wall subhyaline, 1–1.5  $\mu\text{m}$  thick, often slightly thickened apically, finely and evenly verruculose but often with scar-like bald lines; single bigger, thick-walled and moderately coarse verrucose cells resembling peridial cells occur among ordinary aeciospores. **Uredinia** amphigenous on leaves, apparently short-lived and giving rise to telia readily, probably not always formed, pulverulent, ferruginous; **urediniospores** obovoidal, ellipsoidal or broadly ellipsoidal, 23–30 $\times$ 20–24  $\mu\text{m}$  (mean 26.6 $\times$ 21.9  $\mu\text{m}$  [Namibian specimen], 25.8 $\times$ 21.4 [PREM 40367]), spore wall light brown,

uniformly 1–1.5  $\mu\text{m}$  thick, echinulate, spines about 2–3  $\mu\text{m}$  apart, with indistinct and ill-defined smooth patches over the mostly 2, more or less opposite and equatorial germ pores which are covered by flat, broad, hyaline papillae. **Telia** amphigenous, black; **teliospores** ellipsoidal, broadly ellipsoidal (to subglobose), not or slightly constricted at the septum, 40–50(54) $\times$ 30.5–37  $\mu\text{m}$  (mean 45.9 $\times$ 33.9  $\mu\text{m}$ ), spore wall (fully soaked with embedding fluid) light brown, almost smooth, 5–8(9)  $\mu\text{m}$  thick, not obviously layered but becoming lighter towards the outside, thinner, darker brown and with rugose surface when not wholly soaked, most often without apiculus, or with short, conical ochraceous apiculus, germ pores difficult to discern, one per teliospore cell (very rarely two), close to the septum. Mesospores and tricellular spores very rare.

The description of the aecial stage was partly adopted from Sydow and Sydow (1904) and supplemented or corrected by own observations. In the specimen from Namibia, the aeciospore wall was straw-coloured to golden, ca. 1  $\mu\text{m}$  thick, up to 2  $\mu\text{m}$  in angles or apically, finely, closely and rather evenly verruculose. As in the specimen from Malawi, thicker-walled cells that were more coarsely



**Fig. 17** *P. cucumeris* (PUR F-18954), teliospores. Two spores that are not fully soaked (arrows) are smaller and show blister-like swellings of the spore wall around the germ pores. Bar 20  $\mu\text{m}$

verrucose to partially smooth were interspersed and may represent vestigial peridial cells as indicated by the typical “rod-structure” of the spore wall.

While the observed teliospores of the type specimens lacked apiculi, apiculate teliospores occurred rarely in PUR F-18954 and scattered in the Namibian specimen (Fig. 16). The fully soaked teliospores are finely rugulose-reticulate to almost smooth. In the specimens from Namibia and Malawi, a uredinial stage was present that has been undescribed so far.

*P. cucumeris* is the only one of the species under consideration that is also reported from tropical America (Brazil) on cultivated *Cucumis* spp., among them *Cucumis anguria* L. (West Indian Gherkin). There is good evidence that, like all other *Cucumis* species, the latter is of African origin and was introduced to the Americas long ago (Puchalski and Robinson 1990; Kirkbride 1993; Garcia-Mas et al. 2004). One can assume therefore, that the parasite was also introduced to Brazil from Africa. In Africa it has been reported on *Cucumis* spp. from Eritrea and Malawi. In Namibia, the species has not been found hitherto.

A specimen from the Arthur Herbarium (PUR F-18687) on *Coccinia barteri* (Hook. f.) Keay (= *Physhedra barteri*) from Nigeria is not *P. cucumeris* as labelled but is most similar to *P. physedrae* known from Sierra Leone and Ghana. *P. cucumeris* reported on *Coccinia* from Kenya (Natrass 1961) and on *Cephalandra*, *Coccinia* and *Momordica* from Malawi (Bisby and Wiehe 1953) were not examined, but they too may represent other species.

*Puccinia gymnopetali-wightii* T.S. Ramakr., Srinivasan and Sundaram 1952

Proc. Indian Acad. Sci., sect. B, 36: 90 (as *P. gymnopetali-wightiae*) (Figs. 18 and 19).

Type on *Gymnopetalum wightii* G.A.W. Arnott, India, Tamil Nadu State.

Syn. *P. citrulli* Syd., P. Syd. and Butl. var. *gymnopetali-wightii* (T.S. Ramakr., Srinivasan and Sundaram) Ragunathan and K. Ramakr. 1972 (as var. *gymnopetali-wightiae*). Mysore J. Agric. Sci. 6: 453

Material examined: India, Tamil Nadu State, Pannaikadu, Palni Hills, on *Gymnopetalum wightii*, leg. N.V. Sundaram, 10 Dec 1951 (type, HClO 19913).

**Uredinia** amphigenous, mostly abaxial, subepidermal, erumpent, ferruginous, pulverulent; **urediniospores** pedicellate, obovoidal, ellipsoidal to broadly ellipsoidal or subglobose, slightly compressed along the axis between the two opposite, more or less equatorial germ pores, 26–34×20–25 µm (mean 29.8×23.0 µm), spore wall orange–brown, 2.5–3(3.5) µm thick, at germ pores ca. 1.5 µm thick,

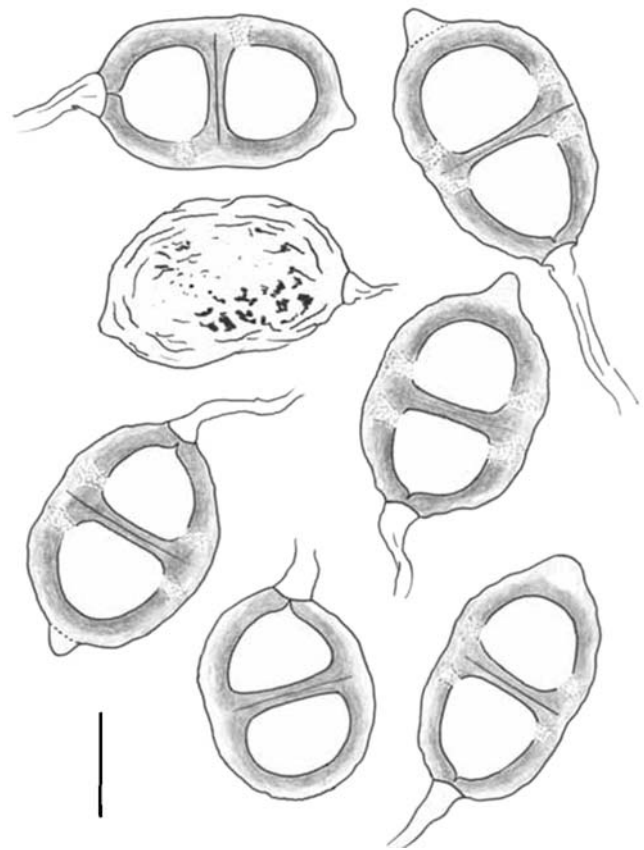


Fig. 18 *Puccinia gymnopetali-wightii* (type), teliospores. Bar 20 µm

echinulate by moderately fine spines spaced at ca. 2–3 µm except for two smooth patches around germ pores, pores without or with very small papillae. **Telia** blackish brown or black, amphigenous, mostly abaxial, subepidermal, pulverulent; **teliospores** usually two-celled, broadly ellipsoidal to ellipsoidal with rounded ends or, rarely, with a subacute distal cell, not to slightly constricted at septum, most often apiculate by an apical to subapical, stout ochraceous apiculus which is 2–6(8) µm long and broadly conical or elongated-conical, without apiculus 41–52×32–38 µm (mean 45.7×35.0 µm), spore wall 5–8 µm thick, to 10 µm thick over germ pores, orange brown, becoming lighter brown to the outside, indistinctly two-layered, the thin outer, ochraceous to straw-coloured layer blending into the inner one, with shallow ridges, rugose to rugose-subreticulate, “scabby” or almost smooth between ridges, germ pores indistinct, 2 per cell, more or less opposite and close to septum. In the single mesospore encountered three germ pores were present (according to diagnosis: mesospores rare, 25–31×19–25 µm).

The diagnosis given by Ramakrishnan et al. is rather short and does not comply with my observations in several respects. The authors described urediniospores with four super-equatorial germ pores and annotated that the teliospores resemble those of *Uropyxis* but that “the absence of

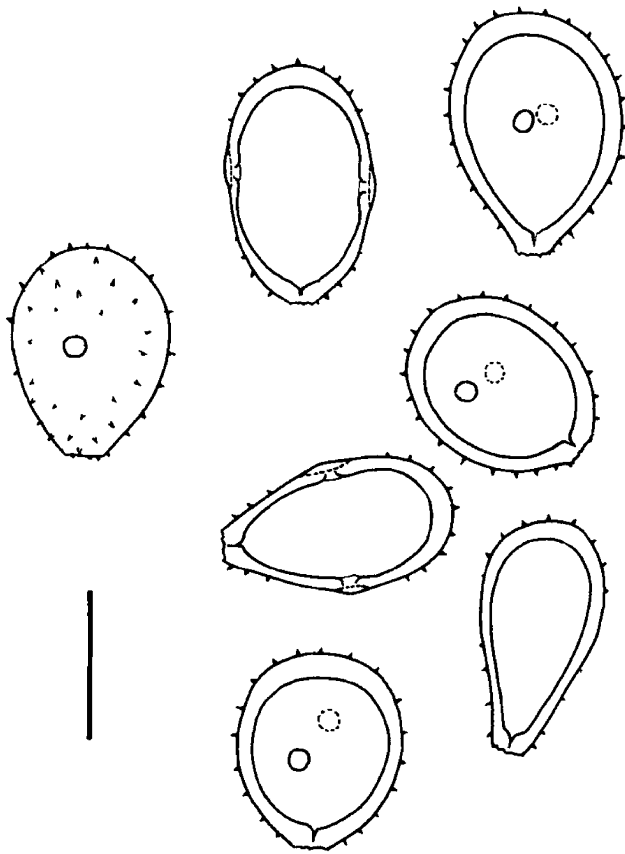


Fig. 19 *P. gymnopetali-wightii* (type), urediniospores. Bar 20  $\mu\text{m}$

two germ pores in each of the telial cells preclude the inclusion of this rust in this genus". In fact, the urediniospores and each teliospore cell have two germ pores. I found the teliospore wall to be thicker than described and irregularly rugose rather than verrucose. Ragunathan and Ramakrishnan (1972) wrote that they were "inclined to treat this species synonymous with *P. citrulli*". However, as they observed slightly shorter teliospores in *P. gymnopetali-wightii*, they reduced it to a variety of *P. citrulli*. According to my observations the teliospores are not shorter in *P. gymnopetali-wightii* but differ from those of *P. citrulli* mainly by the presence of apiculi and a more coarsely rugose spore surface. Because of these differences and the host affiliation, I prefer to keep both species separate.

*Puccinia hieroglyphica* R. Berndt, sp. nov.

Etymology: named after the irregularly shaped warts of the teliospore wall (Figs. 20, 21 and 22).

Syn. *Puccinia cephalandrae* auct., non Thümen 1876: Doidge, E.M. 1950. Bothalia 5: 405.

**Spermogonia** in pagina abaxiali folii dense aggregata. **Aecia** abaxialia, sparsa, peridio eburneo, primus cupulato, deinde aperto et breve cylindrico praedita; **aeciosporae**

saepe leniter deformes vel subangulares, obovoideae, late ellipsoideae vel prope rectangulares, 20–26 $\times$ 14–19.5  $\mu\text{m}$  (medium 22.9 $\times$ 17.3  $\mu\text{m}$ ), pariete hyalino, ca. 1–1.5  $\mu\text{m}$  crasso, apicaliter fortiter incrassato usque ad 4–9  $\mu\text{m}$ , proximaliter delicate, apicem versus grossiore verruculoso, cellulae peridii rhomboideae, intus sate grosse verrucosae, extus ornamento subtilissime labyrinthico vel verrucis delicatissimis et breviter striiformibus praeditae. **Uredinia** in pagina abaxiali folii sparsa, obsoleta, cinnamomea, pulverulenta; **urediniosporae** obovoideae, late ellipsoideae vel subgloboseae, 24–30 $\times$ 20–24  $\mu\text{m}$  (medium 26.5 $\times$ 21.8  $\mu\text{m}$ ), pariete ca. 1–1.5  $\mu\text{m}$  crasso, apicaliter et juxta hilum usque ad 2  $\mu\text{m}$  crasso, ochraceo vel dilute aurantiaco-brunneo, subtiliter echinulato spinis inter se ca. 2–3  $\mu\text{m}$  distantibus, poris germinationis (2)3(4), aequatorialibus vel supraequatorialibus, papillis parvis, hyalinis praeditis sed tonsura carentibus. **Telia** praecipue in pagina abaxiali folii sparsa, parva, atro-brunnea, pulverulenta; **teliosporae** late ellipsoideae, rariore ellipsoideae vel subgloboseae, utrinque rotundatae, circa septum non vel lenissime constrictae, sine apiculo 37–52(55) $\times$ (24)26–33(35)  $\mu\text{m}$  (medium 42.8 $\times$ 30.0  $\mu\text{m}$ ), basaliter pedicello hyalini, tenue tunicato, usque ad 55  $\mu\text{m}$  longo praeditae vel-rariore-sublateraliter pedicellatae, pariete ca. 4  $\mu\text{m}$  crasso, in poris germinationis saepe usque ad 7  $\mu\text{m}$

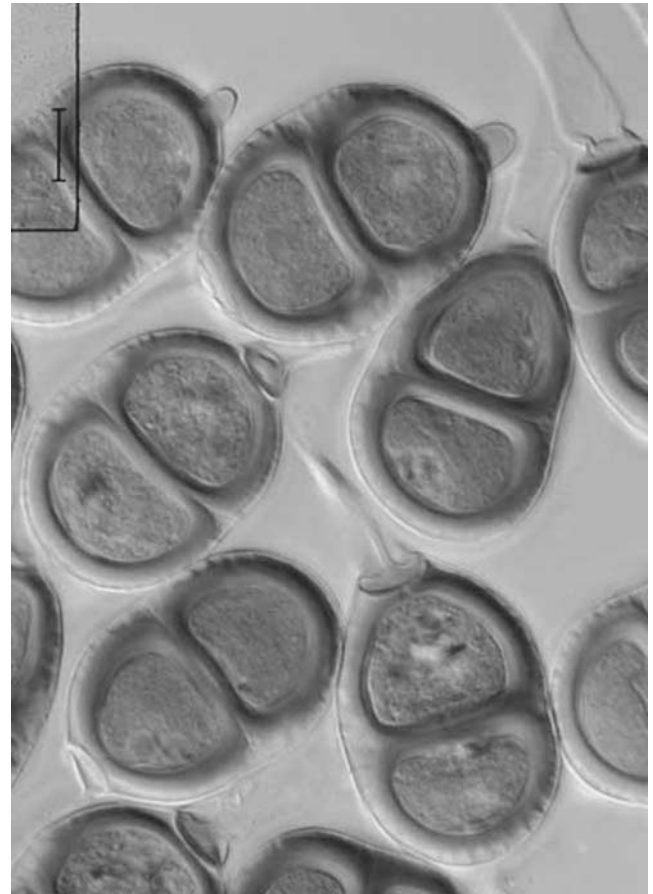
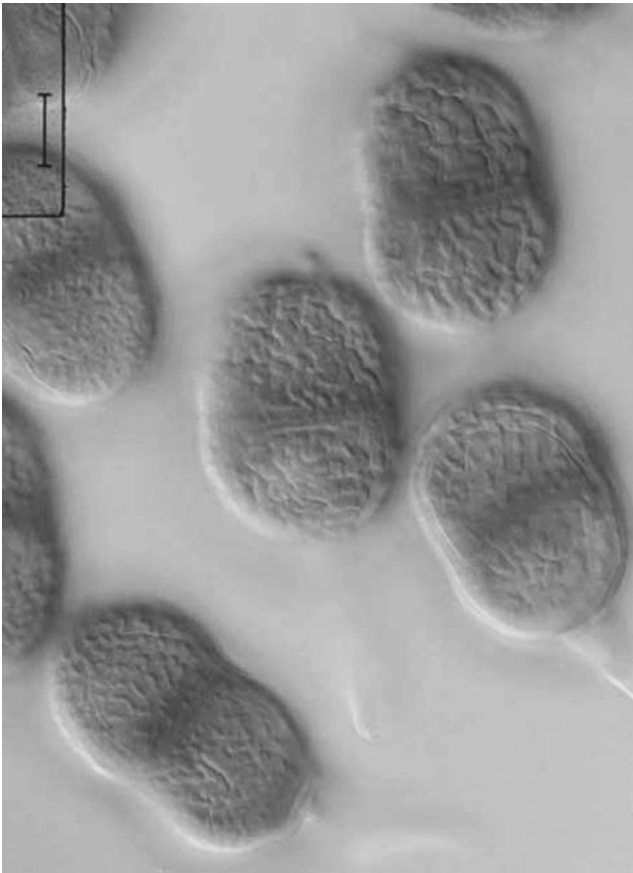


Fig. 20 *Puccinia hieroglyphica* (type), teliospores. Bar 10  $\mu\text{m}$



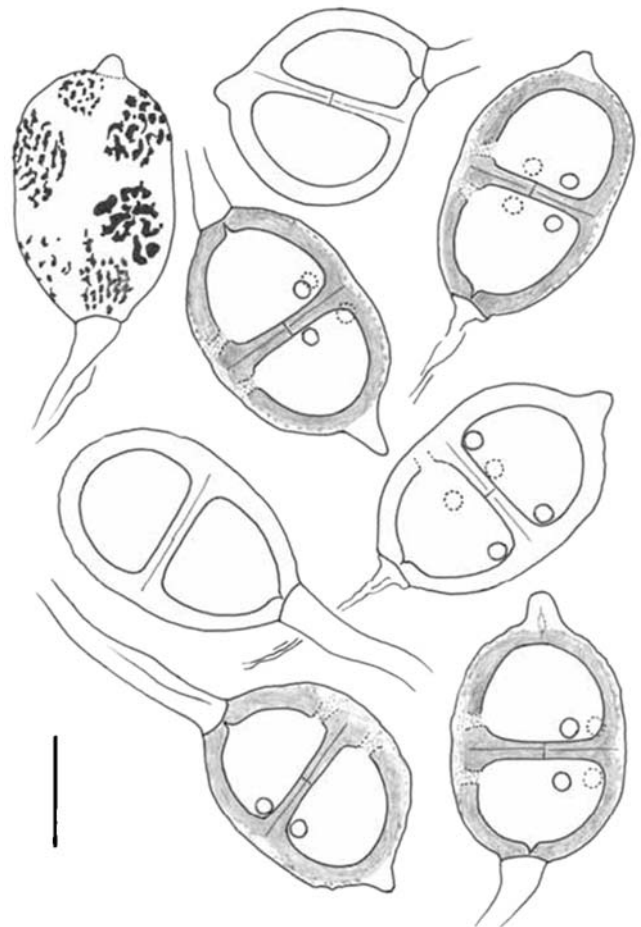
**Fig. 21** *P. hieroglyphica* (type), teliospores. Focus on surface ornament. Bar 10  $\mu\text{m}$

incrassato, indistincte vel distincte bilaminato, strato inferiori exteriori crassiore, aurantiaco-brunneo, strato exteriori stramineo ad ochraceo, praecipue apicaliter apiculum 2–6  $\mu\text{m}$  longum, late conicem facienti, verrucis irregularissimis, delicatis usque ad grossis dense vel laxe obsito, poris germinationis binis vel ternis, septum juxta. Mesosporae raras.

In foliis *Zehneriae scabrae* Sond.

**Spermogonia** in a dense group on abaxial leaf surface. **Aecia** scattered abaxially on a brownish decoloured area of the host leaf, peridium ebony, first closed and shortly dome-shaped, open shortly cylindrical and exposing the cream-coloured spore mass; **aeciospores** often slightly deformed and subangular, obovoidal, broadly ellipsoidal or almost rectangular, 20–26 $\times$ 14–19.5  $\mu\text{m}$  (mean 22.9 $\times$ 17.3  $\mu\text{m}$ ), spore wall hyaline, ca. 1–1.5  $\mu\text{m}$  thick, apically much thickened to 4–9  $\mu\text{m}$ , proximally rather finely verruculose, more coarsely verruculose towards apex; peridial cell rhomboidal, rather coarsely verrucose on inner side, with a very fine labyrinthine pattern or with very fine elongated warts on the outer side. **Uredinia** few, old, on abaxial side of leaves, cinnamon, pulverulent; **urediniospores** obovoidal, broadly ellipsoidal or subglobose, 24–30 $\times$ 20–24  $\mu\text{m}$  (mean 26.5 $\times$ 21.8  $\mu\text{m}$ ), cell wall ca. 1–1.5  $\mu\text{m}$  thick, apically and

around hilum to 2  $\mu\text{m}$  thick, ochraceous to light orange-brown, rather finely and evenly echinulate with spines ca. 2–3  $\mu\text{m}$  apart, germ pores (2)3(4), equatorial to super-equatorial, with a small and flat hyaline papilla, without a smooth patch. **Telia** predominantly abaxial on leaves, blackish brown, pulverulent, very small; **teliospores** broadly ellipsoidal, more rarely ellipsoidal or subglobose, rounded at both ends, at septum not or very slightly constricted, without apiculus 37–52(55) $\times$ (24)26–33(35)  $\mu\text{m}$  (mean 42.8 $\times$ 30.0  $\mu\text{m}$ ), spore wall about 4  $\mu\text{m}$  thick, at germ pores often swollen (to 7  $\mu\text{m}$ ), indistinctly to distinctly bilaminate, with a thicker, orange brown inner layer and a thinner, straw-coloured to ochraceous outer layer which is verrucose by very irregularly shaped coarse to rather fine, isolated to anastomosing warts and forms an apical or subapical, 2–6  $\mu\text{m}$  long, generally stout, straw-coloured apiculus, more rarely apiculus lacking, germ pores inconspicuous, 2–3 per teliospore cell, close to septum, spores basally stalked by a hyaline, thin-walled and collapsing pedicel up to 55  $\mu\text{m}$  long



**Fig. 22** *P. hieroglyphica* (type), teliospores. The surface ornament illustrated on a single spore represents various types of warts found on different spores. Bar 20  $\mu\text{m}$



but most often breaking off shorter, pedicel sometimes offset or rarely lateral. Mesospores rare.

On the leaves of *Zehneria scabra* Sond.

Holotype (PREM): South Africa, Zululand, Entumeni, on *Z. scabra* [*Melothria punctulata* (Thunb.) Cogn. according to a later annotation on the label], June 1910(?), leg. W. Haygarth, sub *P. cephalandrae* (PREM 14194 [II, III]). Paratype: same site, host and collector but without date (PREM 14188 [0, I]).

Aecia were not present on the holotype specimen but were in PREM 14188, which was collected at the same site and host by the same collector. It is reasonable to assume, therefore, that the aecia belong to the life cycle of *P. hieroglyphica*. As only very few aecidial cups were present, sections were not prepared but only some spores and a part of the peridium removed. Additional material will therefore be necessary to complement the description of the peridium. Among the Puccinias on cucurbits the presence of aecia with a well-developed peridium is remarkable. It is interesting to note that the only other species showing proper peridiate aecia is *P. rhytidoderma* occurring on the same host plant as *P. hieroglyphica*. Another unusual feature are the urediniospores, with generally three germ pores lacking a smooth patch. *P. citrullina* is the only other species described to have 3–4 scattered germ pores. The remaining species have predominantly two opposite, equatorial pores provided with a smooth patch.

*Puccinia melothriicola* Syd. and P. Syd. 1917

Ann. Mycol. 15: 172 (Fig. 23).

Type on *Melothria mucronata* Cogn., Philippines.

Material examined: Philippines, Luzon, Benguet Prov., between Camp 30 and Baguio, leg. M.S. Clemens (no. 5144), Feb 1925 (PUR F-7669).

**Spermogonia** amphigenous, subepidermal. **Aecia** amphigenous, subepidermal, in a small circle around the spermogonia, *Uredium*-like, cinnamon brown; **aeciospores** resembling urediniospores, ellipsoidal or globose, 29–37 × 24–31 μm, spore wall ca. 1.5 μm thick, sharply echinulate, with two opposite and super equatorial germ pores. **Uredinia** abaxial, occurring singly or in loose groups, tiny, soon naked, cinnamon to chestnut brown, pulverulent; **urediniospores** ellipsoidal or obovoidal, 30–38 × 20–26 μm, spore wall ca. 2 μm thick, yellow-brown or brown, distantly echinulate, with two equatorial germ pores. **Telia** abaxial, cinnamon brown, naked and compact, up to 1 mm diam., scattered or loosely aggregated, greyish pruinose by basidia after germination of spores; **teliospores** oblong or ellipsoidal, tapering towards the apex, both cells of similar length or the proximal slightly longer and narrower, slightly constricted at the septum, 45–58 × 18–22 μm, spore wall smooth, pallid

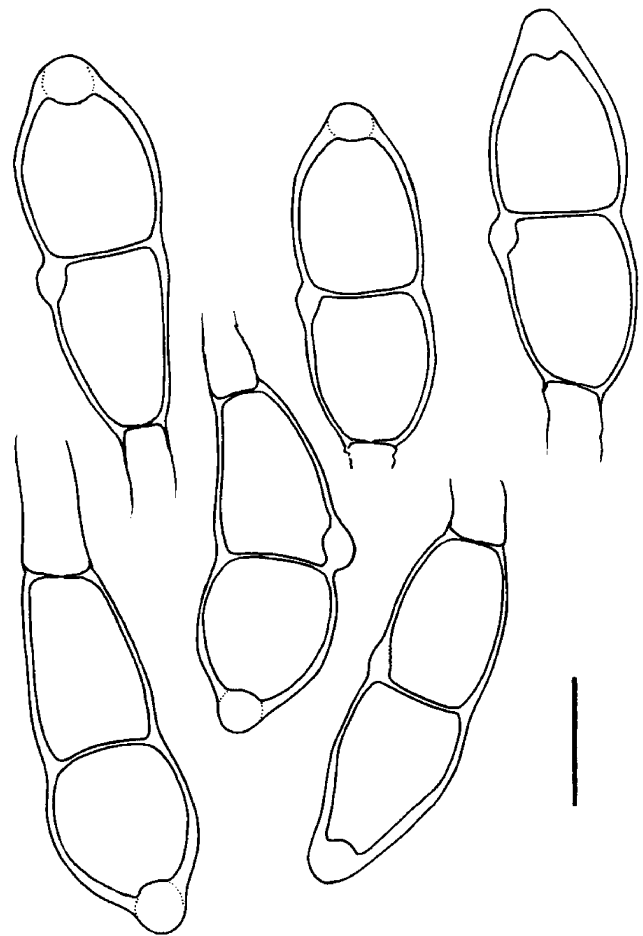


Fig. 23 *Puccinia melothriicola* (PUR F-7669), teliospores. Bar 20 μm

yellow-brown, ca. 1–2 μm thick, germ pores apical in the distal cell, at septum in the proximal cell, with a conspicuous, broadly ellipsoidal or globose wall thickening, spores germinating upon maturity, pedicels persistent, up to 80 μm long and 8 μm broad or breaking off shortly from the hilum.

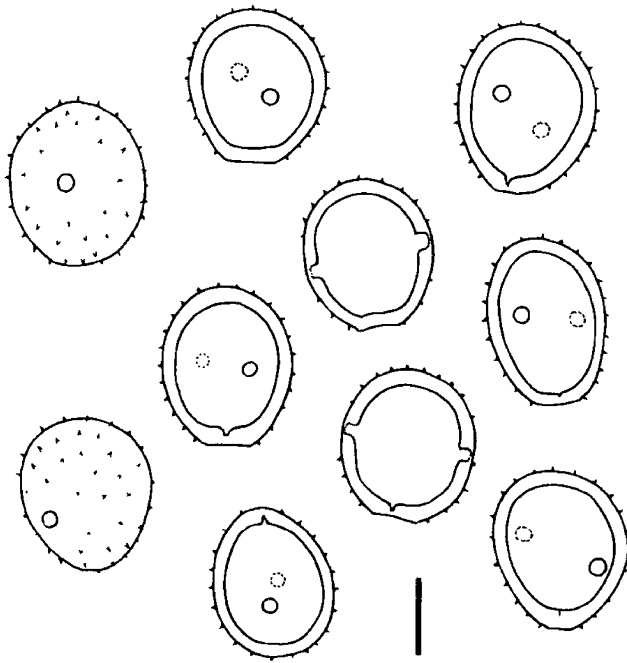
The description was compiled from the diagnosis, Arthur and Cummins (1937), and my own observations. Together with *P. vanderystii* Henn., this is the only of the autoecious Puccinias on cucurbits with leptosporic teliospores (i.e. teliospores germinating with a basidium upon maturity). It is uncertain whether it is related to the species with resting spores as it differs not only by teliospore morphology but also by *Uredium*-like aecia.

*Puccinia momordicae* Kalchbr. and Cooke 1882

Grevillea 11: 24 (Figs. 24, 25 and 26).

Type on *Momordica cordifolia* Sond., South Africa, Natal.

Syn. *Puccinia cephalandrae* auct., non Thümen 1876: Doidge, E.M. 1950. Bothalia 5: 405.



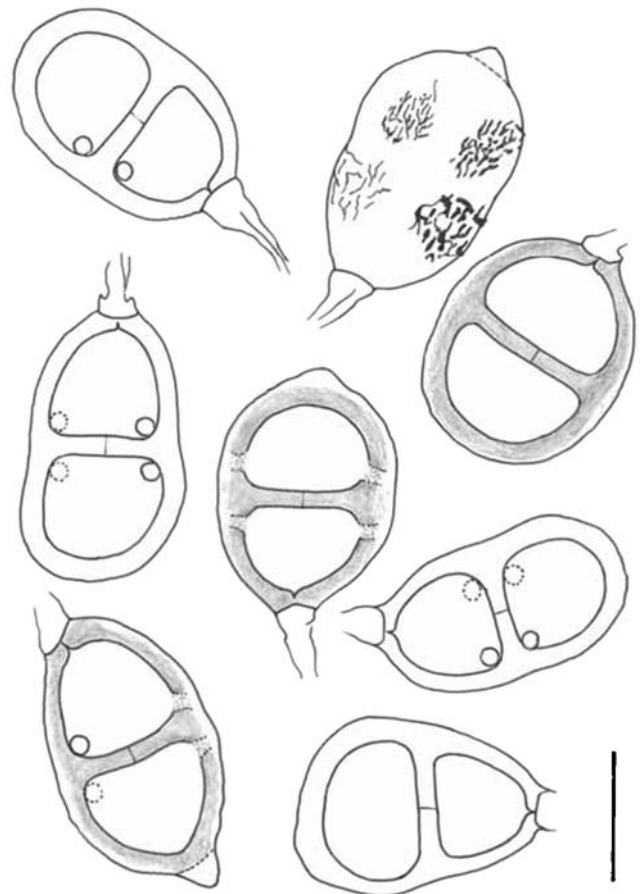
**Fig. 24** *Puccinia momordicae* (HeRB 5169), urediniospores. Bar 10  $\mu\text{m}$

Material examined: Republic of South Africa, Natal, on *Momordica cordifolia*, leg. et det. J.M. Wood 1878 (type, issued in Parasitic Fungi of Natal no. 141; Berlin, B 70 000 8486, Stockholm, S F28569 and F28570). Zimbabwe, 5.5 km S Morondera along Musape road, alt. ca. 1,660 m, 18°14'24"S/31°33'50"E, on *Momordica* sp., leg. C. and K. Vánky, det. R. Berndt, 20 Feb 1999 (HeRB 5169, at Z+ZT).

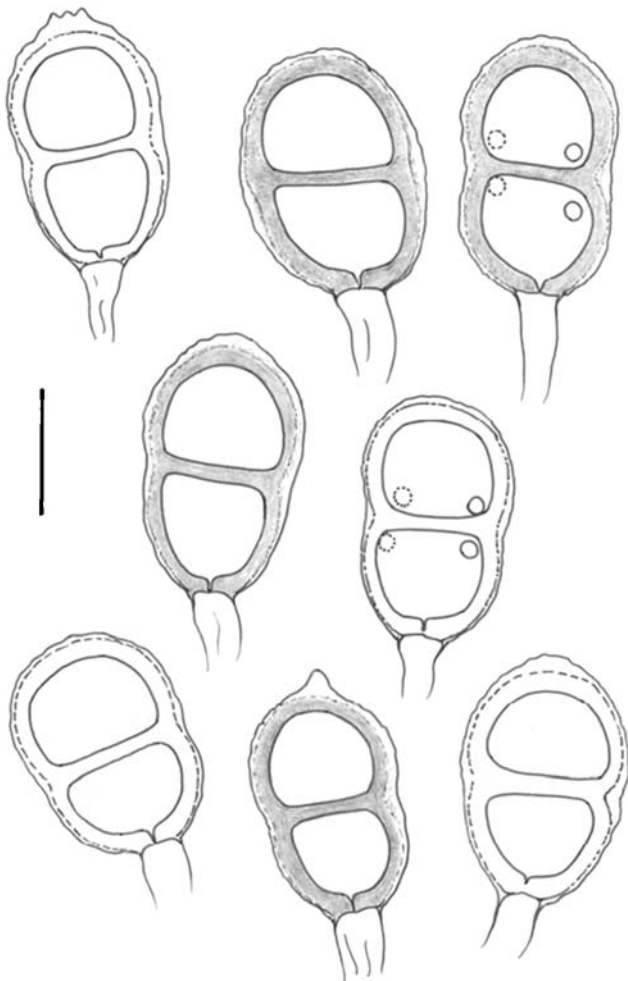
**Uredinia** not found in type specimens; **urediniospores** subglobose, broadly obovoidal (to globose), 21–24 $\times$ 19–22  $\mu\text{m}$  (mean 22.2 $\times$ 20.5  $\mu\text{m}$  for 28 spores), spore wall light brown with orange tinge, (1.5)2–2.5  $\mu\text{m}$  thick, up to 3.5  $\mu\text{m}$  thick around hilum, finely and sparsely echinulate, very sparsely echinulate in equatorial region but no distinct smooth patches observed, germ pores two, opposite and equatorial. **Telia** predominantly scattered on abaxial side of leaves, subepidermal, mostly 0.3–0.6 mm diam., dark chestnut brown to blackish brown; **teliospores** broadly ellipsoidal, obovoidal to ellipsoidal, not or very slightly constricted at septum, 33.5–44 $\times$ 23–28(31)  $\mu\text{m}$  (mean 37.8 $\times$ 26.4  $\mu\text{m}$ ), spore wall orange–brown to light chestnut brown, often with an indistinct, thin, straw-coloured outer layer that may form an apiculus 2–4  $\mu\text{m}$  high, spore wall 3–4.5  $\mu\text{m}$  thick or slightly thicker at the germ pores, rugose by a pattern of dendritic to subreticulate shallow ridges or warts, germ pores 2 per teliospore cell, most often pair-wise in adjacent and opposite in the same cell, close to the septum, spores stalked basally or slightly laterally by a delicate, subhyaline pedicel breaking off shortly from the hilum.

Urediniospores of *P. momordicae* have not been described so far, but a few old ones were discovered in type specimens kept in B and S. Uredinia were found in a specimen from Zimbabwe. They were mainly abaxial, rarely adaxial, cinnamon brown, early naked, flatly bullate and pulverulent, ca. 0.3–0.7 mm diam., later replaced by telia; the urediniospores were subglobose to obovoidal or broadly ellipsoidal, 20–24 $\times$ 18–21  $\mu\text{m}$ , the spore wall light brown, 2–3  $\mu\text{m}$  thick, very delicately and rather sparsely echinulate, with 2(3) more or less equatorial germ pores.

Doidge (1927) considered *P. momordicae* to be synonymous to *P. cephalandrae* and *P. trochomeriae* based on teliospore morphology. This is incorrect, as the urediniospores are different. The species is also very similar to *P. citrulli* and *P. ctenolepidis* with regard to teliospore characters but differs by smaller urediniospores with a thicker spore wall. To my knowledge, this is the first report of *P. momordicae* for Zimbabwe.



**Fig. 25** *P. momordicae* (type), teliospores. The surface ornament illustrated on a single spore represents various types of warts found on different spores. Bar 20  $\mu\text{m}$



**Fig. 26** *P. momordicae* (HerB 5169), teliospores. Bar 20  $\mu\text{m}$

*Puccinia physedrae* Syd. 1938

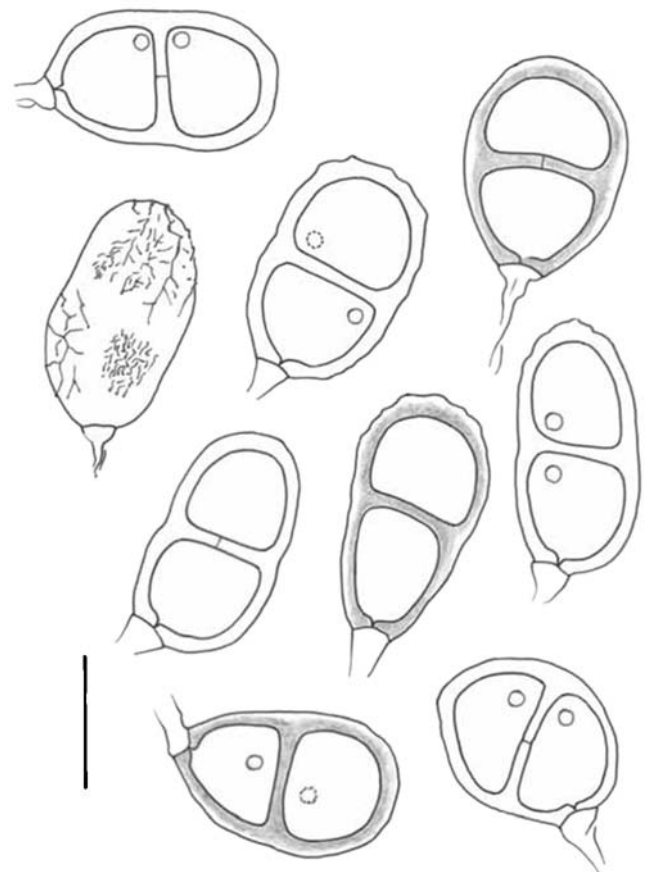
Ann. Mycol. 36: 156 (Figs. 27 and 28).

Type on *Physedra barteri* (Hook. f.) Cogn., Africa, Sierra Leone.

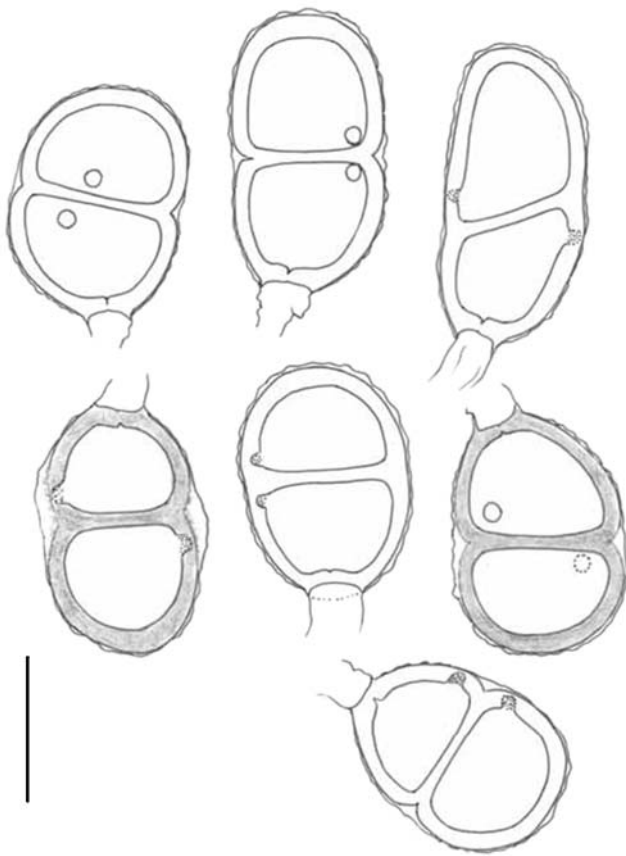
Material examined: Africa, Sierra Leone, Mange, on *Physedra barteri*, leg. F.C. Deighton, 1 Feb 1939 (PUR F-9691 [II, III]). Africa, Gold Coast [=Ghana], Aburi, E. Province, on *Physedra* sp. aff. *barteri*, leg. F.C. Deighton, 27 Jul 1937 (syntype, Flora of Gold Coast, ex herb. H. Owen no. 510; S F-27870 [I, III]). Africa, Nigeria, Univ. of Nigeria, village 3 miles N Botany Dept., on *Coccinia barteri* (Hook. f.) Keay (= *Physedra barteri*), leg. D. Eboh 25 Feb 1977. (PUR F-18687, sub *P. cucumeris* [II, III]).

**Aecia** mostly abaxial, often on leaf veins, or on petioles, forming groups of 2–4 mm diam. or elongated groups, tiny (100–130  $\mu\text{m}$  diam.), pustulate, a long while closed, lacking a typical peridium, but with isolated or loosely adherent cells with thickened walls and coarse warts otherwise resembling

aeciospores, transitional forms present; **aeciospores** globose to broadly ellipsoidal, 20–32  $\times$  17–24  $\mu\text{m}$  (mean 26.3  $\times$  20.8  $\mu\text{m}$  for 20 spores), spore wall 1.5–2  $\mu\text{m}$  thick, subhyaline, rather densely verrucose by shortly cylindrical delicate or moderately delicate warts. **Uredinia** not observed; **urediniospores** on telia, subglobose, ellipsoidal or ovate, 26–31.5  $\times$  22.5–26  $\mu\text{m}$  (mean 28.0  $\times$  23.6  $\mu\text{m}$  for 18 spores [PUR F-9691]) [according to Sydow: 23–29  $\times$  17–21  $\mu\text{m}$ ], spore wall ca. 1.5  $\mu\text{m}$  thick, brown, echinulate by very delicate spines, with two equatorial germ pores. **Telia** amphigenous, but predominantly adaxial, mostly in small irregular groups, sometimes in bigger groups with up to 5 mm diam. or coalescing to more or less concentric rings, ferruginous, early naked and surrounded by the torn epidermis, pulverulent; **teliospores** broadly ellipsoidal, ellipsoidal, ovate or almost oblong, rounded on both sides or proximal cell tapering towards the pedicel, not or hardly constricted at the septum, (25)28–37.5  $\times$  18–26  $\mu\text{m}$  (mean 32.4  $\times$  23.0  $\mu\text{m}$ ), spore wall light brown, 2.5–3.5  $\mu\text{m}$  thick, at germ pores to 5.5  $\mu\text{m}$  thick, indistinctly bilaminate with a thin outer, straw-coloured layer, almost smooth to rugose (“wrinkled”) by a pattern of linear to labyrinthine low and



**Fig. 27** *Puccinia physedrae* (type), teliospores. The surface ornament illustrated on a single spore represents various types of warts and the rugose-ridged surface found on different spores. Bar 20  $\mu\text{m}$



**Fig. 28** *P. physedrae* (Purdue F-9691), teliospores. Bar 20  $\mu$ m

sharp ridges, one germ pore per teliospore cell, most often close to the septum, pair-wise or opposite in adjacent cells, pedicel inserted basally or shifted slightly to the side, subhyaline, delicate and breaking off shortly from the hilum.

The description was adopted from the diagnosis and the protologue and complemented or corrected by my own observations. PUR F-9691 and S F-27870 did not tally with several of the teliospore characters observed by Sydow. He described the spore wall as being 1.5–2  $\mu$ m thick, evenly and delicately punctate-verruculose, appearing almost smooth, with the germ pore being apical or subapical in the distal cell, at the septum or to 1/3 depressed in the proximal cell. The measurements of the uredinio- and teliospores coincide well, however.

Sydow listed two specimens in the protologue, of which I studied one (S F-27870). He did not designate a holotype and it is necessary, therefore, to select a lectotype. As I was unable to locate and study the other syntype (Sierra Leone, Segbwema, on *Physedra barteri*, leg. F.C. Deighton, 11 Dec 1937) I shall not do this here.

PUR F-18687 is labelled *P. cucumeris*. It is certainly not this species. The teliospore characters and the presence of uredinia suggest that it belongs to *P. physedrae*, but the

urediniospores are bigger than in the other specimens studied [(27)29–36(38) $\times$ 21–26  $\mu$ m; mean 31.3 $\times$ 23.0  $\mu$ m].

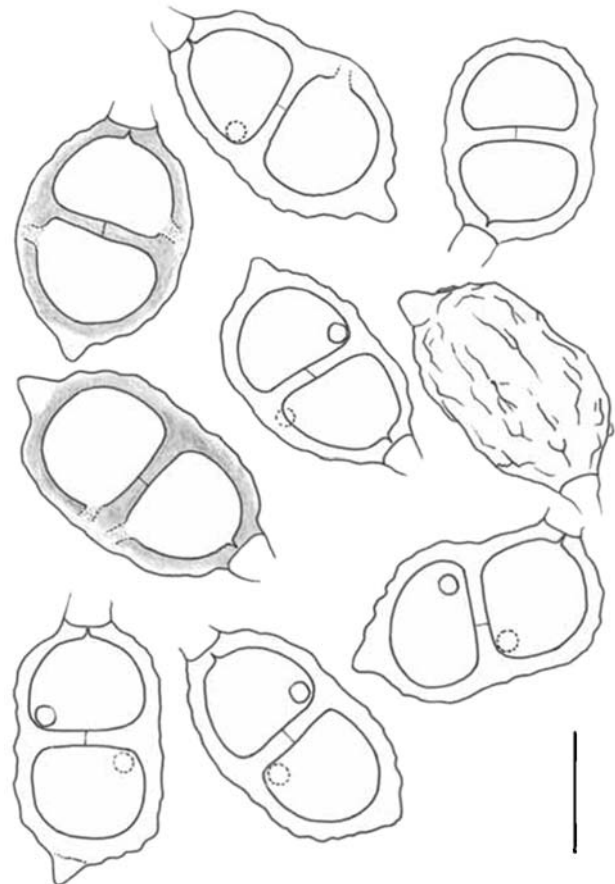
*Puccinia rhytidoderma* R. Berndt, sp. nov.

**Etymology:** named after the wrinkled surface of the teliospores (Figs. 29, 30 and 31).

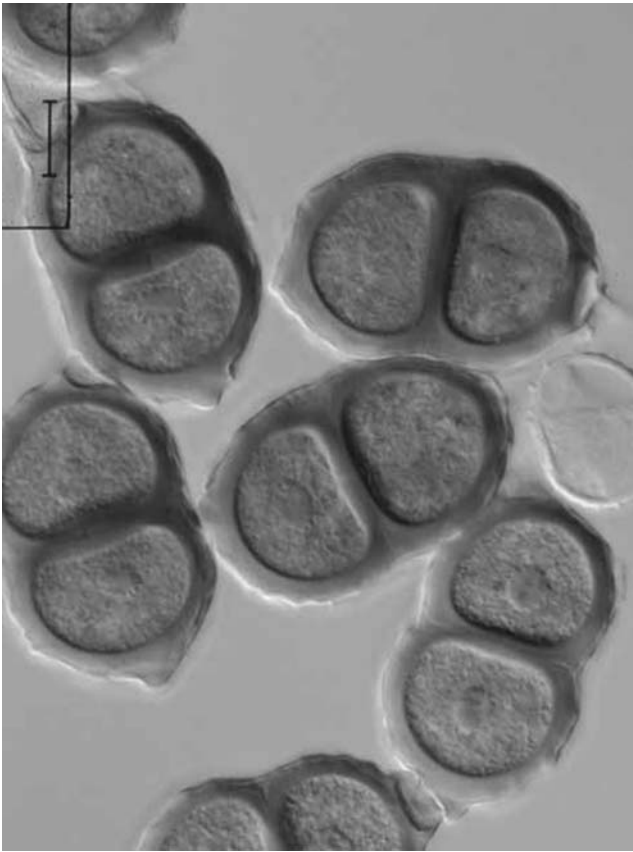
$\equiv$  *P. cephalandrae* auct., non Thümen. Gjørnum, H.B. 1986. Mycotaxon 27: 520

$=?$  *Uredo zehmeriae* Thümen 1877

**Aecia** foliicola, abaxialia, in gregibus parvis, peridio albo praedita; **aeciosporae** subgloboasae vel obovoideasae, 21–25(32) $\times$ 17–23  $\mu$ m, pariete 1–1.5  $\mu$ m crasso, hyalino, verruculoso, poris germinationis nonnunquam cum granulis lucem refringentem (obtumentis pororum). **Uredinia** foliicola, abaxialia, subepidermalia, ferruginea, pulverulenta, postea telios evolventia; **urediniosporae** obovoideasae, late ellipsoideasae (ad subgloboasae), 23–28 $\times$ 19–22.5  $\mu$ m (medium 25.2 $\times$ 20.6  $\mu$ m), pariete luteo-brunneo, ca. 1–1.5  $\mu$ m crasso, moderate laxe echinulato, spinis delicatis inter se 2.5–3  $\mu$ m distantibus, poris germinationis duobus aequatorialibus et oppositis, papillis parvis, humilibus



**Fig. 29** *Puccinia rhytidoderma* (type), teliospores. Bar 20  $\mu$ m



**Fig. 30** *P. rhytidoderma* (type), teliospores. Bar 10  $\mu\text{m}$

inconspicuis et tonsuris praeditis. **Telia** nigro-brunnea vel nigra, pulverulenta; **teliosporae** ellipsoideae ad late ellipsoideae, non vel leniter constrictae ad septum, utrinque rotundatae, plerumque apicaliter vel subapicaliter apiculo late conico, 3–7  $\mu\text{m}$  longo praedita, sine apiculo (34)36–40 (42.5) $\times$ 25–29.5  $\mu\text{m}$  (medium 38.1 $\times$ 26.9  $\mu\text{m}$ ), pariete spadiceo ad ferrugineo, in septo obscuriori, apiculo et strato exteriori parietis-ubi distinguibili-aureo vel ochraceo, (2.5) 3–4  $\mu\text{m}$  crasso, in poris germinationis leniter incrassato et dilutiori, ob plicas ramificantes et subanastomosantes pannuceo ad ruminato, poris germinationis singulis, septum juxta, saepe plusminusve oppositis vel binatim locatis, pedicellis basaliter vel oblique insertis, subhyalinis, tenue tunicatis et fragilibus.

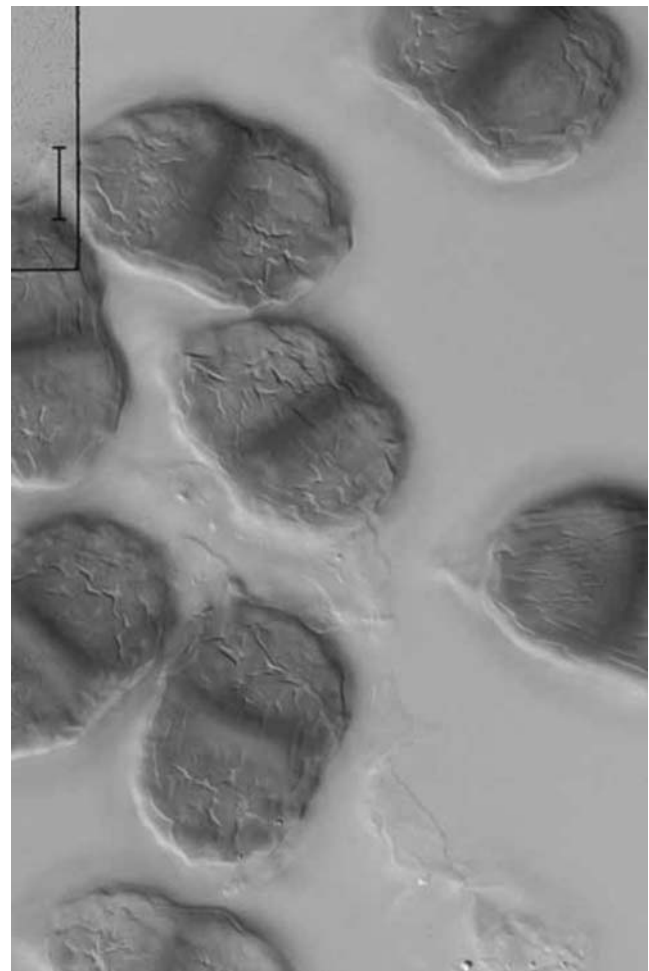
In foliis *Zehneriae scabrae*.

**Aecia** abaxial on leaves, in small groups; peridium white, **aeciospores** subglobose or obovoidal, 21–25(32) $\times$ 17–23  $\mu\text{m}$ , spore wall 1–1.5  $\mu\text{m}$  thick, hyaline, verruculose, some pores with light refracting granules. **Uredinia** on abaxial leaf surface, subepidermal, ferruginous and pulverulent, later replaced by telia; **urediniospores** obovoidal, broadly ellipsoidal (to subglobose), 23–28 $\times$ 19–22.5  $\mu\text{m}$  (mean 25.2 $\times$ 20.6  $\mu\text{m}$ ), spore wall evenly light brown with yellow tinge, ca. 1–1.5  $\mu\text{m}$  thick, evenly and moderately sparsely echinulate (ca. 2.5–3  $\mu\text{m}$  between spines) by sharp

spines except for inconspicuous smooth patches around the two, more or less equatorial and opposite germ pores that are provided with small and flat, inconspicuous papillae. **Telia** blackish-brown to black, pulverulent; **teliospores** ellipsoidal to broadly ellipsoidal, slightly or hardly constricted at the septum, rounded at both ends, apically or subapically most often with a stout, broadly conical, 3–7  $\mu\text{m}$  long apiculus, without apiculus (34)36–40(42.5) $\times$ 25–29.5  $\mu\text{m}$  (mean 38.1 $\times$ 26.9  $\mu\text{m}$ ), spore wall yellow–brown with orange tinge, septum slightly darker coloured, apiculus and outer wall layer—where visible—golden yellow to ochraceous, (2.5)3–4  $\mu\text{m}$  thick, at germ pores slightly lighter and thicker, surface shrivelled and rugose with broken and branching ridges and folds, one germ pore per teliospore cell located close to the septum, often more or less opposite or pair-wise in adjacent cells, pedicels inserted basally or slightly shifted sideways, subhyaline and thin-walled, breaking off shortly from the hilum.

On leaves of *Zehneria scabra*.

Holotype (Z+ZT): Africa, Uganda, Singo County, Mubende District, Mile 101 on the Kampala-Hoima Rd.,



**Fig. 31** *P. rhytidoderma* (type), teliospores. Focus on surface ornament. Bar 10  $\mu\text{m}$

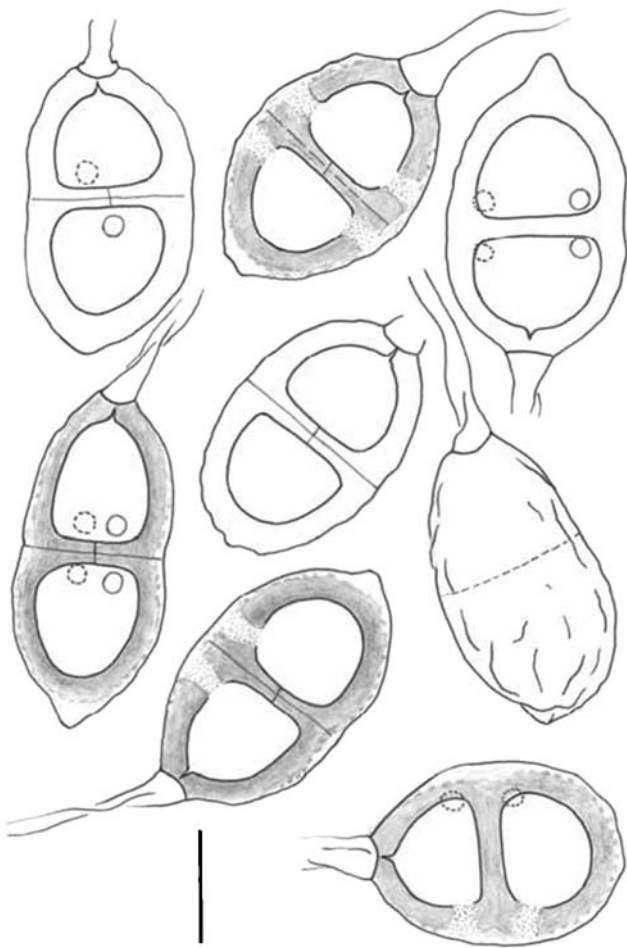


Fig. 32 *Puccinia trochomeriae* (type), teliospores. Bar 20  $\mu\text{m}$

on *Zehneria scabra* (L. f.) Sond., leg. H.B. Gjørum, 16 Oct 1970 (no. 519/70).

The description of the aecial stage was adopted from Gjørum (1986). He measured 23–28 $\times$ 18–25  $\mu\text{m}$  for the urediniospores and 37–47 $\times$ 27–33  $\mu\text{m}$  for the teliospores. *P. rhytidoderma* differs from other species by its coarsely rugose teliospores with a conspicuous stout apiculus and one germ pore per teliospore cell. It may not be distinguishable from similar species if only the uredinal stage is present. *Uredo zehneriae* was described on the same host from South Africa. Its urediniospores are described as similar to those of the present species and I assume it to be synonymous to *P. rhytidoderma* rather than *P. arisanensis* as supposed by Hiratsuka (1941). An interesting feature is the presence of peridiate aecia; in most other species of this group typical peridia are lacking or vestigial.

Most of the material of the present rust (containing also the aecial stage) was sent to Makerere University Herbarium in Uganda but was apparently lost. I am indebted to H.B.

Gjørum (Ås, Norway) for sending me a remaining fragment and donating it to Herbarium turicense.

*Puccinia trochomeriae* Cooke 1881

Grevillea 10: 125 (Fig. 32).

Type on *Trochomeria sagittata* Benth. and Hook. f., Africa, South Africa, Natal.

Syn. *Puccinia cephalandrae* auct., non Thümen 1876: Doidge, E.M. 1950. Bothalia 5: 405.

Material examined: South Africa, Natal Province, Inanda, on *T. sagittata* (Harv.) Cogn., leg. J.M. Wood, June 1881 (type, PREM 10513). South Africa, near Pretoria, Warmbaths Rd., on *Trochomeria? macrocarpa*, leg. L.C.C. Liebenberg, Nov 1941 (IMI 56165, sub *P. cephalandrae*).

**Uredinia** not observed; **urediniospores** among teliospores, globose to ellipsoidal, 24–27 $\times$ 20–25  $\mu\text{m}$ , spore wall ca. 1.5–2  $\mu\text{m}$  thick, delicately echinulate, with 2–3 germ pores. **Telia** abaxial, scattered, ca. 0.5–1 mm diam., rather long covered by the lead-grey epidermis, moderately

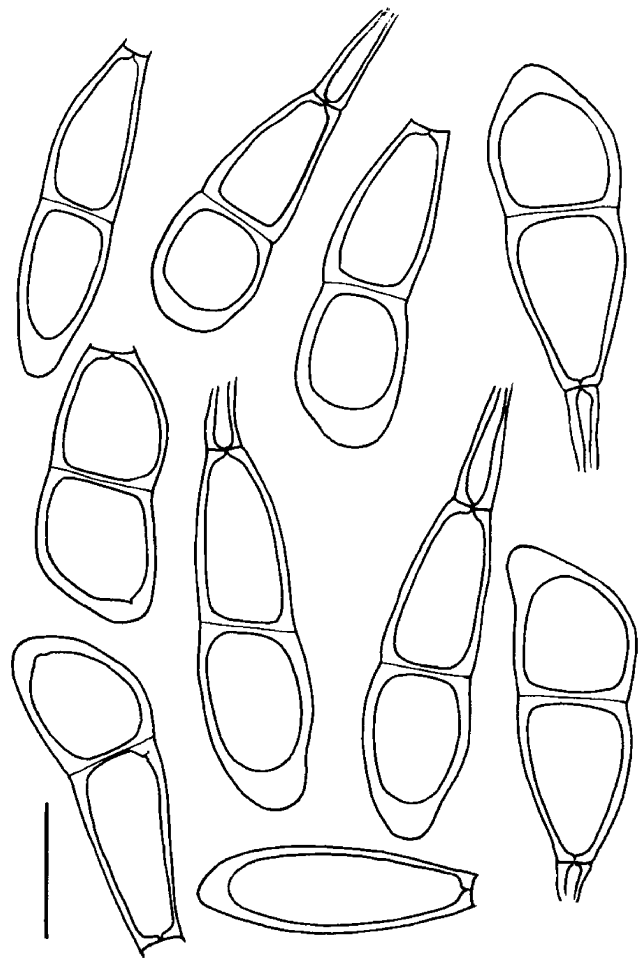
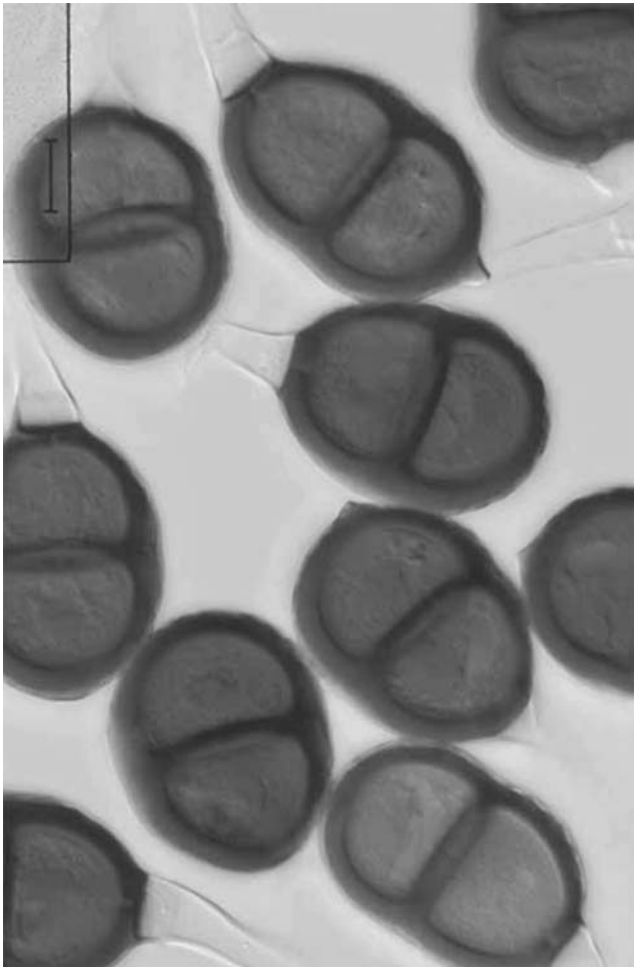


Fig. 33 *Puccinia vanderystii* (type), teliospores, a single mesospore at the bottom. Bar 20  $\mu\text{m}$



**Fig. 34** *Puccinia windhoekensis* (type), teliospores. Bar 10  $\mu\text{m}$

pulverulent, dark to blackish-brown; **teliospores** broadly ellipsoidal, broadly obovoidal, rarely ellipsoidal, not or very slightly constricted at the septum, or even slightly swollen because of a thickened wall above germ pores, rounded at both ends, or distal cell up to subacute,  $38\text{--}52 \times 28\text{--}36 \mu\text{m}$  (mean  $45.4 \times 31.3 \mu\text{m}$ ), spore wall  $4\text{--}5.5 \mu\text{m}$  thick, over germ pores thickened up to  $8 \mu\text{m}$ , indistinctly bilaminar, with a thin, straw-coloured, outer layer and a thicker orange-brown inner layer, rugose to wrinkled, sometimes appearing irregularly verrucose, apically quite often with a straw-coloured, stout but low papilla that may attain a length of  $4\text{--}5 \mu\text{m}$  more rarely, or with a cap-like or flatly conical thickening of the outer wall layer, germ pores indistinct, 2 per cell, close to septum and normally pairwise in the adjacent cells, spores basally stalked by a hyaline, thin-walled, collapsing pedicel up to  $70 \mu\text{m}$  long, but most often breaking shorter, sometimes pedicel offset or spores stalked laterally.

In IMI 56165 no urediniospores were found, in PREM very few, mostly old ones. Their description was therefore adopted

from Sydow (1922) prepared on type material from Kew. Doidge (1927) considered *P. trochomeriae* to be synonymous to *P. cephalandrae*. This is not correct as both species have entirely different urediniospores. IMI 56165 is assigned to the present species though it did not contain urediniospores. The teliospores are indistinguishable from the type, however, with short or without apiculi and two germ pores per teliospore cell. The teliospores *P. trochomeriae* are very similar to those of *P. cephalandrae*, which have generally much stouter and longer apiculi.

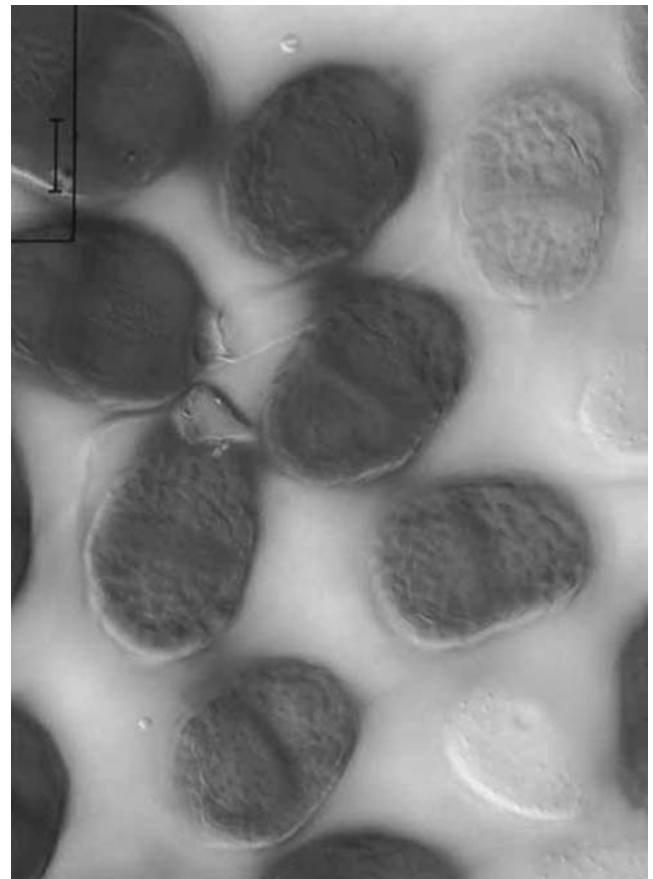
*Puccinia vanderystii* Henn. 1907

Annales du Musée du Congo (Botanique) 2, fasc. 2: 91 (Fig. 33).

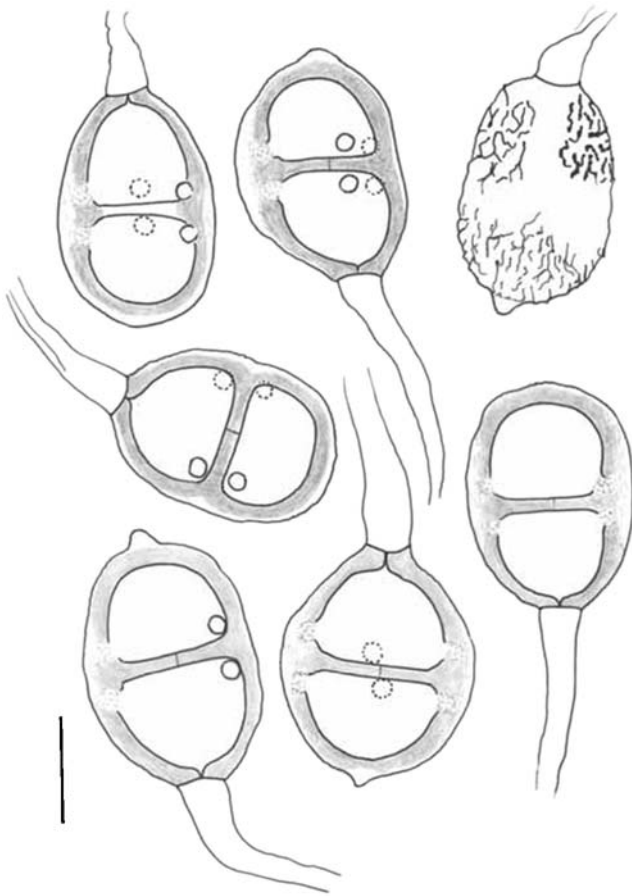
Type on Cucurbitacea sp., Africa, Congo.

Syn. *Puccinia momordicae* auct., non Kalchbr. and Cooke 1882: Mogk and Hindorf 1971. Nova Hedwigia 21: 497.

Material examined: Africa, Congo, Kwango, Kisantu, on Cucurbitacea, leg. Vanderyst, May 1906 (type, B 700010783). Africa, Kenya, Kiambu, on *Momordica*



**Fig. 35** *P. windhoekensis* (type), teliospores. Focus on surface ornament. Bar 10  $\mu\text{m}$



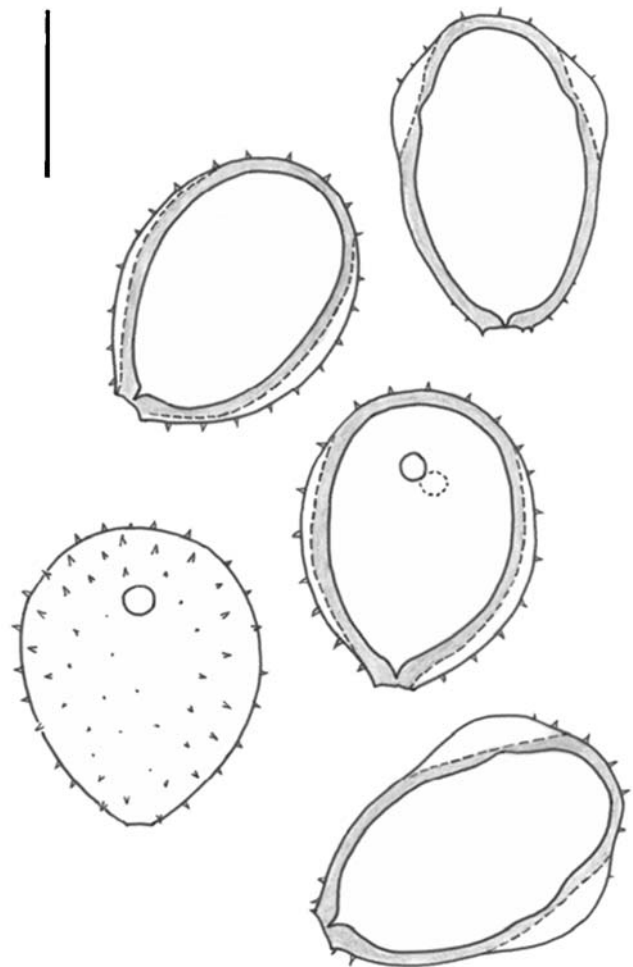
**Fig. 36** *P. windhoekensis* (type), teliospores. The surface ornament illustrated on a single spore represents various types of warts and the rugulose surface found on different spores. Bar 20  $\mu\text{m}$

*foetida* Schumach., leg. H. Hindorf, 25 Jul 1967 (IMI 148621, sub *Puccinia momordicae*).

**Spermogonia**, **aecia** and **uredinia** not observed. **Telia** predominantly on abaxial side of leaves, on almost circular, ochraceous spots with blurred margins (ca. 3–7 mm diam.), sori subcompact, densely aggregated, pulvinate (ca. 0.2–0.4 mm diam. or confluent), with flakes of surrounding or uplifted epidermis; **teliospores** bicellular, occasionally three-celled, ellipsoidal, subclavate, spindle-shaped or oblong, slightly constricted at septum, apex rounded, conical to subacute, proximal cell tapering into the pedicel, often a bit longer than the distal cell, (32)34–57(62)×13–20  $\mu\text{m}$  (mean 48.2×16.1  $\mu\text{m}$ ), spore wall ochraceous or pallid golden, subhyaline at germ pores, smooth, laterally ca. 1–1.5  $\mu\text{m}$  thick in proximal, 1.5–2  $\mu\text{m}$  in distal cell, apically thickened to 4–8  $\mu\text{m}$ , germ pores apical and close to the septum, without papillae but often with a narrowly conical pit in the wall, pedicels straw-coloured, persistent, slightly thick-walled but often compressed, about 0.5–0.7 times as long as spores, often breaking much shorter or close to septum. Mesospores scattered.

To my knowledge, the present species has been known only from the type collection. A specimen from Kenya published by Mogk and Hindorf (1971) as *P. momordicae* is identical with *P. vanderystii*. Well developed telia were orange–brown to ferruginous or slightly pruinose after germination of the teliospores. Telia were often aborted, however, and visible as tiny dark brown crusts (like telia of *Melampsora* or *Phakopsora*) among or next to well-developed telia. The teliospores were slightly broader than in the type (mean 45.0×18.0  $\mu\text{m}$ ) and had germ pores with more distinct conical pits. They germinated upon maturity. As the Kenyan specimen is growing on *Momordica* it is possible that the undetermined host of the type of *P. vanderystii* could also belong to this genus.

*P. vanderystii* is a new member of the Kenyan rust mycobiota. The only other known leptosporic *Puccinia* species on Cucurbitaceae, *P. melothriicola*, differs by conspicuously papillate germ pores of the teliospores. It is known from the Philippines, where it grows on *Melothria* spp.



**Fig. 37** *Uredo melothriae* (type), urediniospores. Bar 20  $\mu\text{m}$



*Puccinia windhoekensis* Mennicken, Maier and Oberw. 2005

Mycol. Progr. 4: 60 (Figs. 34, 35 and 36).

Type on *Coccinia rehmannii* Cogn., Africa, Namibia.

Material examined: Africa, Namibia, Windhoek, on *Coccinia rehmannii*, leg. M. Mennicken, 5 Apr 2002 (type, TUB, to be deposited in PREM).

**Spermogonia** of type 4. **Aecia** small, ca. 0.2–0.4 mm diam., bullate, in smaller to larger loose or dense groups, opening with a rather regular round and wide porus, without a visible peridium, spore mass pallid cinnamon; **aeciospores** irregularly rounded, subglobose to broadly ellipsoidal, 22.5–28×18.5–24 µm (mean 24.3×20.8 µm), spore wall ochraceous to light brown, ca. 1–1.5 µm thick, up to 2.5 µm in angles or restricted wall areas, more or less evenly rather fine and densely verruculose (rarely with small smooth patches), germ pores indistinct, scattered, 4–6?, among the ordinary spores scattered cells occur that have thicker walls and coarser warts, probably cells of a rudimentary peridium. **Uredinia** amphigenous on leaves, on shoots and—more rarely—on tendrils, scattered or sometimes slightly confluent, ferruginous, ca. 0.3–0.8 mm diam., more or less round, pulvinate and pulverulent, later often being replaced by telia; **urediniospores** obovoidal, broadly ellipsoidal (to subglobose), 24–29.5×19.5–23 µm (mean 26.7×20.7 µm), spore wall ca. 1–1.5 µm thick, light brown, echinulate with moderately delicate spines spaced ca. 2.5–3.5 µm, germ pores 2(3), more or less equatorial and opposite, without papillae but with a conspicuous smooth patch. **Telia** like uredinia, black; **teliospores** broadly ellipsoidal, ellipsoidal, sometimes subglobose, not or hardly constricted at the septum, (34.5)36–45(48)×(25.5)27–32 µm (mean 40.2×29.7 µm), spore wall chestnut brown, 3–4.5 µm thick, swelling to 7 µm in restricted areas, rugose, with a labyrinthine-dendritic pattern, indistinctly two-layered but often with a more or less distinct, broad yellow-brown thickening over the germ pores, germ pores 2–3 per cell, mostly equidistant/opposite and close to the septum, often with a short, up to 4 µm long, conical, yellow-brown apiculus, pedicels thin-walled, persistent, up to 80 µm long, but usually breaking off shorter.

I studied the type of the fungus and observed that many teliospores had three germ pores per teliospore cell and not only two as stated in the diagnosis. In all spore stages, the fungus is very similar to *P. ctenolepidis* and is probably closely related. It differs by slightly smaller teliospores with thinner walls, more conspicuous germ pores and a darker colour. The host was determined as *Coccinia rehmannii*, which belongs to another tribe (Benincaseae) than *Ctenolepis* (Melothriaceae). The host specimen of *P. windhoekensis* is sterile. I compared it to

the specimens of *Coccinia rehmannii* available in Z+ZT but was unable to confirm its identity. It might also represent *Kedrostis africana* (L.) Cogn. Affiliation of the host with *Kedrostis* would support a close relationship between *P. windhoekensis* and *P. ctenolepidis*, as both host genera belong to the same tribe.

Uredinial stages with uncertain affinity

I have knowledge of three *Uredo*-anamorphs described on Old-World cucurbits and not assigned to a teliomorph genus: *Uredo melothriae* (Henn.) R. Berndt, *U. momordicae* Petch and *U. trichosanthis* Petch. The description of *U. trichosanthis* on *Trichosanthes palmata* L. is too short to link this rust to any of the species considered here (Sydow and Sydow 1924). *U. momordicae* on *Momordica charantia* L. has larger urediniospores than other rusts on this host genus and two basal germ pores (Sydow and Sydow 1924). *U. melothriae* is a new combination for *Uromyces melothriae* Henn. on *Melothria tomentosa* L. from Ethiopia. Sydow and Sydow (1908) recognised that *Uromyces melothriae* is based on a uredinial stage and thus an illegitimate name. As they did not make the necessary recombination, I propose *Uredo melothriae* (Henn.) R. Berndt as a new combination and give an improved description of the fungus based on the holotype (B):

*Uredo melothriae* (Henn.) R. Berndt, comb. nov.

≡*Uromyces melothriae* Henn. 1893. Englers botanische Jahrbücher 17: 13. Bulletin de l'Herbier Boissier 1: 108 (Fig. 37).

**Uredinia** on leaves, mainly abaxial, subepidermal, ferruginous and pulverulent; **urediniospores** asymmetrical and slightly compressed along axis between the germ pores, broadly ellipsoidal to subglobose in front view upon germ pores, 33–39×28–32.5 µm (mean 35.9×30.4 µm), spore wall very light brown, 1.5–2 µm thick, with two thickened bands (up to 4.5 µm thick) stretching from the hilum towards the subapical part of the spores, bilaminar in the thickened areas with a subhyaline outer layer, rather distantly and coarsely echinulate (ca. 3–4.5 µm between spines) except for two almost smooth large patches proximal to the super-equatorial to subapical, opposite germ pores which are covered by prominent broad and high subhyaline papillae.

*U. melothriae* is markedly different from the uredinial stages of the described *Puccinia* species on cucurbits. Its urediniospore morphology suggests that it may not belong to the group of *Puccinias* treated in the present work.

## Key and host index to the species of *Puccinia* on Cucurbitaceae

The key includes the *Puccinia* species described above. An index of the host genera with their known rust species has been added to facilitate the determination.

- 
- 1 Teliospores germinating upon maturity, smooth; spore wall not bilaminate, 1 germ pore per teliospore cell  
 2 germ pores with conspicuous, subhyaline papillae *P. melothriicola*
- 2\* germ pores without papillae, with or without conical pits *P. vanderystii*
- 1\* Teliospores germinating after dormancy; wall rugose, rugulose, verrucose or rough, sometimes appearing smooth, often bilaminate, with 1 or 2(3) germ pores per teliospore cell
- 3 Urediniospores with 3–4 (super)equatorial or scattered germ pores
- 4 Teliospores 26–38×17–26 μm, wall 2–3 μm thick, verrucose, not apiculate; number of germ pores uncertain, urediniospores with 3–4 scattered pores *P. citrullina*
- 4\* Teliospores bigger, wall ca. 4 μm thick, very irregularly verrucose, generally apiculate, with 2–3 germ pores per cell; urediniospores with mostly 3 (super)-equatorial pores *P. hieroglyphica*
- 3\* Urediniospores with 2(3) more or less equatorial and opposite germ pores, generally surrounded by a smooth patch, or uredinial stage lacking
- 5 Teliospores normally with 1 germ pore per cell
- 6 Teliospores mostly with stout and conspicuous apiculi, wall conspicuously rugose and shrivelled *P. rhytidoderma*
- 6\* Teliospores without apiculi or with small apiculi, wall almost smooth to rugulose-subreticulate
- 7 Teliospores 40–54×30–38 μm, wall 4–5(9) μm thick, almost smooth to inconspicuously reticulate-rugulose, not or very indistinctly layered, not apiculate or with a short conical apiculus *P. cucumeris*
- 7\* Teliospores smaller, 28–37×18–26 μm, wall 2.5–3.5 μm thick, at germ pores to 5.5 μm, wall almost smooth to rugose, indistinctly bilaminate, not apiculate *P. physedrae*
- 5\* Teliospores generally with 2 or 3 germ pores per cell, or germ pores indistinct
- 8 Urediniospores large, 36–54×20–26 μm *P. cephalandrae*
- 8\* Urediniospores smaller, generally ranging within 23–32×18–26 μm
- 9 Mesospores scattered to common
- 10 Teliospores often apiculate, apiculi rather small, wall ca. 3–5 μm thick, finely reticulate-rugulose germ pores indistinct *P. cephalandrae-indicae*
- 10\* Teliospores without apiculi, wall ca. 2.5–3.5 μm thick, rugulose, germ pores distinct, 2 per cell *P. arisanensis*
- 9\* Mesospores absent or only rarely present
- 11 Aecial stage known, aecia usually present (if absent, both alternatives should be followed)

- 12 Teliospores lacking apiculi, teliospore wall irregularly verrucose and with a wrinkled surface, ferruginous to light chestnut, on *Momordica* or *Kedrostis* (host identity uncertain) *P. arbor-miraculensis*
- 12\* Teliospores often or predominantly with apiculi
- 13 Teliospores often with short, conical apiculi
- 14 Teliospore wall 4–6 μm thick, mostly about 5 μm, chestnut brown, on *Ctenolepis* *P. ctenolepidis*
- 14\* Teliospore wall ca. 3–4.5 μm thick, dark chestnut brown, on (?)*Coccinia* *P. windhoekensis*
- 13\* Teliospores predominantly with long and slender to stout apiculi, on *Dactyliandra* *P. antennata*
- 11\* Aecia unknown
- 15 Urediniospores range mainly between 23–31×20–26 μm
- 16 Urediniospore wall ± evenly 1.5–2 μm thick, teliospores apiculate or not, rugulose, wrinkled or verrucose *P. trochomeriae*
- 16\* Urediniospore wall laterally ca. 1.5–2 μm thick, apically to 3 μm and up to 5 μm thick at the hilum
- 17 Teliospores without apiculi, rugulose *P. citrulli*
- 17\* Teliospores often with stout apiculi, rugose *P. gymnopetalii-wightii*
- 15\* Urediniospores smaller, 20–24×18–22 μm, wall 2–3 μm thick; teliospores delicately reticulate-rugulose, apiculi lacking or conical and up to 4 μm high *P. momordicae*
- 

Index of host genera, listed by tribes, with their known *Puccinia* species and *Uredo*-anamorphs of unknown affiliation:

(*Puccinia* species reported from hosts belonging to different tribes are underlined; the respective type specimens are indicated by “(type)”)

### Benincaseae

- Citrullus* *P. citrulli* (type)  
*P. citrullina*  
*Coccinia* *P. cephalandrae*  
 (=Cephalandra, =Physedra) *P. cephalandrae-indicae*  
*P. cucumeris*  
*P. physedrae*  
*P. windhoekensis* [host determination uncertain, may be *Kedrostis*]

### Melothriaceae

- Cucumis* *P. cucumeris* (type)  
*Ctenolepis* *P. ctenolepidis*  
 (=Blastania) *P. citrulli*  
*Dactyliandra* *P. antennata* (type)  
*Kedrostis* *P. arbor-miraculensis* [host determination uncertain, may be *Momordica*]  
*Melothria* *P. arisanensis*  
*P. melothriicola*  
*Uredo melothriaceae*  
*Trochomeria* *P. trochomeriae*  
*Zehneria* *P. hieroglyphica*  
*P. rhytidoderma*

**Joliffieae**

<i>Momordica</i>	<i>P. cucumeris</i>
	<i>P. momordicae</i>
	<i>P. vanderystii</i>
	<i>Uredo momordicae</i>
<b>Trichosantheae</b>	
<i>Gymnopetalum</i>	<i>P. gymnopetali-wightii</i>
<i>Trichosanthes</i>	<i>Uredo trichosanthis</i>
<b>Undetermined Cucurbitaceae</b>	<i>P. antennata</i> (paratype)
	<i>P. vanderystii</i> (type)

**Discussion**

With one exception, all *Puccinia* species on Cucurbitaceae are autoecious, either macrocyclic or known only as sporophyte. *P. isiacae* Winter is the only species with a proven heteroecious life cycle in which the sporophyte parasitises *Phragmites* (Poaceae) and the gametophyte a broad range of unrelated hosts, among them *Bryonia dioica* Jacq. from the Cucurbitaceae (González Fragoso 1924). I did not consider *P. isiacae* in the present work as its different morphology, life cycle and distribution indicate that it is unrelated to the rusts under consideration.

The present study showed that two morphologically distinct groups of *Puccinia* species occur on Cucurbitaceae: (1) *P. melothriicola* and *P. vanderystii* with smooth, leptosporic teliospores with a single germ pore per cell, one located at the spore apex the other close to the septum, and (2) the remaining majority of the species, which are similar with their thick, often bilaminate teliospore walls with a more or less rugose or wrinkled surface and often by the presence of an apiculus and two to three germ pores per cell located close to the septum.

Each of the teliospore characters observed in the second group may occur in other *Puccinia* species. Their combination, however, together with the restriction to cucurbitaceous hosts is unique within the genus and indicates that these rusts represent a monophyletic group that evolved on the host family Cucurbitaceae. Because of their different morphology it is uncertain whether the species of the first group are closely related to those of the second, but the “standard” morphology of their teliospores does not allow linking them to other lineages of *Puccinia* either.

**Determination and species delimitation**

The determination of a *Puccinia* species on Cucurbitaceae can be difficult. This is due to the fact that most species have very similar telio-and/or urediniospores and that certain characters are easily overlooked or tend to be variable. In many of the original descriptions, important morphological traits, such as the number of germ pores of

the teliospore cells or details of the spore ornament, were not considered. Some characters that are used to distinguish species can vary within a single collection and are quantitative rather than qualitative features, e.g. the presence and number of one-celled mesospores in a spore population, the ratio of teliospores with or without apiculi or of teliospore cells with two or three germ pores. Certain characters, like spore wall thickness and appearance of the ornament, may even be influenced by the embedding fluid and its ability to penetrate and soak the wall. Isolated telial or uredinial stages may therefore not be reliably determinable. This difficulty has led to misidentifications, and consequently rust–host connections and geographical reports listed in literature need to be critically evaluated.

Some of the difficulties encountered are highlighted in the “*P. ctenolepidis*-complex” comprising the very similar *P. ctenolepidis*, *P. antennata*, *P. arbor-miraculensis* and *P. windhoekensis*. These species are distinguishable in direct comparison by differences of the teliospore ornament, the colour of the spore wall and traits of the apiculi, but the characters are difficult to key out. Because of the similarity of these species, and as they are represented by only one or two collections that may not display the entire variability, one might be inclined to regard them as one variable species. Data from host plants are equivocal: *P. windhoekensis* was described on a member of the tribe Benincaseae, but this could not be verified and an affiliation of the host with Melothrieae is also possible. The remaining species are on members of Melothrieae though the host of *P. arbor-miraculensis* has been determined to belong to either Melothrieae or Joliffieae. As will be discussed below, the *Puccinias* on cucurbits are probably restricted to hosts belonging to a single tribe. I consider it preferable, therefore, to keep the discussed species separate until more specimens have been studied and until certainty about the host identity warrants a taxonomic change.

**Host affinities and distribution**

Four tribes of Cucurbitaceae, subfam. Cucurbitoideae, are infected by *Puccinia* species (number of reported rust species in brackets): Benincaseae (7), Melothrieae (10), Joliffieae (3) and Trichosantheae (1). Except for three species of *Luffa*, all members of Benincaseae are from the Old World. Members of Melothrieae are distributed pantropically, but the *Puccinia*-hosts *Ctenolepis*, *Cucumis*, *Dactyliandra*, *Kedrostis*, *Trochomeria* and *Zehneria* are restricted to the palaeotropics. The tribes Joliffieae and Trichosantheae are also restricted to the Old World.

As mentioned above, it is difficult to assess the host spectra of the rust species because of the difficulties in determining them correctly. Reports from literature have to be considered with caution as they may include

misidentifications or suppositions on the synonymy of species. However, most of the parasites are not known to occur on more than one host tribe or even genus. A prominent exception appears to be *P. cephalandrae*, which has been reported from no less than six different host genera belonging to three tribes. Doidge (1950) listed *Coccinia* (Benincaseae), the host genus of the type, *Cucumis*, *Kedrostis*, *Zehneria* (sub *Melothria*), *Trochomeria* (all *Melothrieae*) and *Momordica* (*Joliffieae*) as host genera. The latter two are the host genera of *P. trochomeriae* and *P. momordicae* originally described as distinct species but regarded as synonyms of *P. cephalandrae* by Doidge. In the present paper it was proven that *P. trochomeriae* and *P. momordicae* are distinct from *P. cephalandrae*. This fact eliminates *Joliffieae* as a host tribe of *P. cephalandrae* and *Trochomeria* from the *Melothrieae* as a host genus. The report on *Kedrostis* is due to a misidentification of *P. arbor-miraculensis*, those on *Zehneria scabra* (= *Melothria punctata*) represent *P. hieroglyphica* or *P. rhytidoderma*. I presume that Doidge's report of *P. cephalandrae* on *Cucumis* also represents another species.

Other *Puccinia* species with a possible trans-tribal occurrence are *P. citrulli* reported from *Citrullus* and *Blastania* (= *Ctenolepis*) and *P. cucumeris* on *Cucumis*, *Cephalandra*, *Coccinia* and *Momordica*. Although not proven, I assume that the rust on *Blastania* may be *P. ctenolepidis* misidentified as *P. citrulli*. In my opinion, the trans-tribal presence of *P. cucumeris* is also uncertain.

*Puccinia* species on Cucurbitaceae are restricted to the Old World, where they occur mainly in tropical to subtropical regions. There is one exception, *P. cucumeris*, which is known from Brazil on *Cucumis anguria* L. It was almost certainly introduced to the Neotropics with the host, which seems to be an African native (Kirkbride 1993). *Puccinia melothriae* Stevens (1907) described on *Melothria pendula* L. from the southeastern United States is in reality *P. spegazzinii* De Toni on *Mikania*, Asteraceae (Arthur and Jackson 1922).

It is difficult to estimate the geographical distribution of individual species as only a few collections are available and any new finding might completely change the picture. Nevertheless, certain patterns can already be discerned. Most of the known species occur in a broad band ranging from India through the southern Arabian Peninsula, eastern Africa to South Africa. Southern Africa with seven and India with five species appear to be the centres of diversity. The easternmost representatives are *P. arisanensis* and *P. melothriicola* from Taiwan and the Philippines. *P. physedrae* is the only member of the group known from West Africa and marks the western limit of the natural distribution.

Despite several open questions, one can make the following generalisations: (1) there is a unique group of morphologically similar *Puccinia* species growing on cucurbits in the Old World. They exhibit differences, which justify

regarding them as separate species, but they are so similar that it is reasonable to assume that they represent a natural and perhaps young relationship. (2) The present data suggest that at least the majority of these rusts are host specific and restricted to a single host genus or tribe. *P. citrulli* and *P. cucumeris* may cross tribal boundaries and infect members of Benincaseae and Melothrieae; this needs to be verified, however. (3) All *Puccinia* species considered here occur on hosts from tribes or at least genera restricted to the Old World. One can assume that these rusts evolved on groups of Cucurbitaceae restricted to or most diversified in semi-arid, open habitats of southern Africa to India.

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