Rust fungi (Pucciniales) forming the *Aecidium* state on *Meliosma* (Meliosmaceae) in Asia

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Abstract

Five *Phakopsora* species form the *Aecidium* state on plants of the genus *Meliosma* (Meliosmaceae) in temperate Asia; three are heteroecious with uredinial and telial stages on plants of the family Vitaceae and the two others are autoecious with all stages on *Meliosma* plants. Three unconnected *Aecidium* species occur on *Meliosma* plants in subtropical and tropical Asia. Light and scanning-electron microscopic observations revealed that aeciospores of the five temperate *Phakopsora* species are covered with nail-headed verrucae interconnected by buttress, the feature unique to them. Two of the three unconnected *Aecidium* fungi were found to form the same type of aeciospores as those of the five *Phakopsora* species. These observations support the assumption that these unconnected *Aecidium* fungi are the aecial anamorph of phakopsoroid species parasitic on vitaceous plants or of autoecious species on *Meliosma* in subtropical and tropical Asia.

Keywords – Aeciospore・*Phakopsora*・Taxonomy・Vitaceae・*Vitis*

Rust diseases of the vitaceous plants, including grapevine leaf rusts, are caused by *Phakopsora* species (Phakopsoraceae, Pucciniales) (Ono 2000; Ono et al. 2012). *Phakopsora meliosmae-myrianthae* (Henn. & Shirai) Y. Ono (= *P. euvitis* Y. Ono) is heteroecious and host-alternates between *Vitis* and *Meliosma myriantha* Siebold & Zucc. *Phakopsora vitis* P. Syd. is also heteroecious and host-alternates between *Parthenocissus* and *M. myriantha*. *Meliosma tenuis* Maxim. serves as the spermogonial and aecial host of heteroecious *P. montana* Y. Ono & Chatasiri, whose uredinial and telial stages are formed on *Vitis*. *Phakopsora myrianthae* Kusano and *P. orientalis* Chatasiri, Pota & Y. Ono are autoecious, forming spermogonial, aecial, uredinial and telial stages on *M. myriantha* and *M. tenuis,* respectively

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(Pota et al. 2013). These five rust species are closely related and probably share the most recent ancestor in their evolutionary history (Chatasiri and Ono 2008).

In addition to the five *Phakopsora* species, there are three unconnected *Aecidium* species parasitic on *Meliosma* in Southeast Asia, i.e. *A. hornotinum* Cummins (1937), *A. wareoense* Cummins (1941) and *A. painavuense* Hosagoudar (1987). A recent molecular phylogenetic study showed that two or more unidentified *Phakopsora* species are involved in grapevine leaf rust diseases in Southeast Asia and Australasia (Ono et al. 2012; Pota et al. 2013, 2015). Geographic association of unidentified phakopsoroid fungi with the unconnected *Aecidium* fungi in Southeast Asia suggest their possible life cycle connection.

This study aims at characterizing spermogonial and aecial morphology of eight rust fungi whose spermogonial and aecial stages are formed on *Meliosma* in Asia.

Dried herbarium specimens were selected for the study from those deposited in the Herbarium of Systematic Mycology, Faculty of Education, Ibaraki University, Japan (IBAR), the Mycological Herbarium, Botanic Gardens and Museum Berlin-Dahlem, Germany (B), the Arthur Herbarium, Purdue University, U. S. A. (PUR), and the Forest Herbarium, Department of National Parks, Wildlife and Plant Conservation, Ministry of Natural Resources and Environment, Thailand (BKF). Individual specimens studied are listed under each species description. Microscopic preparations was made and examined under a microscope with both bright-field and differential interference contrast equipment and a scanning electron microscope by the methods described by Ono et al. (2012) and Pota et al. (2013).

Key to rust species (Pucciniales) that form *Aecidium*-type aecia on *Meliosma* (Meliosmaceae)

1. Aecia predominantly caulicolous and petiolicolous, occasionally foliicolous ……..... *Aecidium* sp.
1. Aecia foliicolous, occasionally petiolicolous ……..……..…….…….. 2
   2. Aecia predominantly epiphyllous ……..……...……..…….……. *Phakopsora meliosmae*
   2. Aecia predominantly hypophyllous ……..…...……..…..……...…….. 3
3. Aeciospore wall variously thickened ……..……..……..……... 4
3. Aeciospore wall evenly thin ……..……..……..……..... 6
   4. Aeciospore wall moderately thickened at the spore apex
      …… *Phakopsora meliosmae-myrianthae*
   4. Aeciospore wall prominently thickened ……...……..……...…….…….. 5
5. Verrucae on the wall columnar or conical, not interconnected by buttress
   ….……...……..…… *Aecidium wareoense*
5. Verrucae on the wall nail-headed interconnected by buttress
   ……...……..…..……...…….. *Aecidium hornotinum*

6. Aecia formed on *Meliosma myriantha* ……..……. *Phakopsora vitis*

6. Aecia formed on *Meliosma tenuis* ……. 7

7. Aeciospore small, 13–21 × 12–19 µm ……...……..… *Phakopsora montana*

7. Aeciospore large, 18–34 × 14–23 µm ……....……..… *Phakopsora orientalis*

Description of species

Aecidium* sp., aff. *painavuense Hosag., Curr. Sci. 56: 94, 1987.

Fig. 1, 1–4

Spermogoinal and aecial infection on shoots and petioles and causing hypertrophy and witches' broom symptom, occasionally on leaves. Spermogonia gregarious, intermixed in aecial clusters, subcuticular, dome-shaped or conical, 91–131 (–143) µm wide and 62–115 µm high. Aecia *Aecidium*-type with well-developed peridium; inner surface of peridial cells verrucose. Aeciospores catenulate, subglobose, broadly ellipsoid or oblong, often angular and 25–42 (–45) × 18–27 µm in size; wall hyaline, evenly 2.4–4.5 µm thick and verrucose; verrucae nail-headed and subtended by interconnecting buttress.

Specimen studied: On *M. simplicifolia* (Roxb.) Walp. THAILAND, Chiang Mai, Khun Woang, 5 April 1978, T. Smitinand (BKF-72734).

The symptom of hypertrophied and malformed shoots caused by the spermogonial and aecial infection on *M. simplicifolia* is similar to that reported for *A. painavuense* Hosag. (*as "painavuensis"*) on *M. arnottiana* (Wight) Walp. (as "*M. pinnata* (Roxb.) Walp. subsp. *arnottiana* (Wight) Beus.") (Hosagoudar 1987). *Aecidium painavuense* has been known only from the type locality in India. The *Aecidium* fungus under consideration and *A. painavuense* are similar in spermogonial and aecial morphology. However, the aeciospore wall of the latter fungus is described as apically thickened (6–8 µm thick) and pale yellow to cinnamon brown, while that of the former is evenly thick-walled (2.4–4.5 µm) and colorless. Because the type specimen of *A. painavuense* was not available for the study, biological and taxonomic identity of the *Aecidium* fungus under consideration with *A. painavuense* cannot be concluded.

Aecidium wareoense Cummins, Mycologia 33: 388, 1941. Fig. 1, 5–8

Spermogoinal and aecial infection on leaves and causing circular or irregular, hypertrophied lesions. Spermogonia epiphyllous, densely grouped, subcuticular, dome-shaped or conical, 105–178 µm wide and 62–99 µm high. Aecia surrounding spermogonia, deep-seated in host mesophyll, *Aecidium*-type with well-developed peridium; inner surface of peridial cells verrucose. Aeciospores catenulate, subglobose, broadly ovoid or broadly ellipsoid, often angular and 26–36 × 21–27 µm in size; wall hyaline, prominently thickened, 10–19 µm thick apically and verrucose; verrucae columnar and

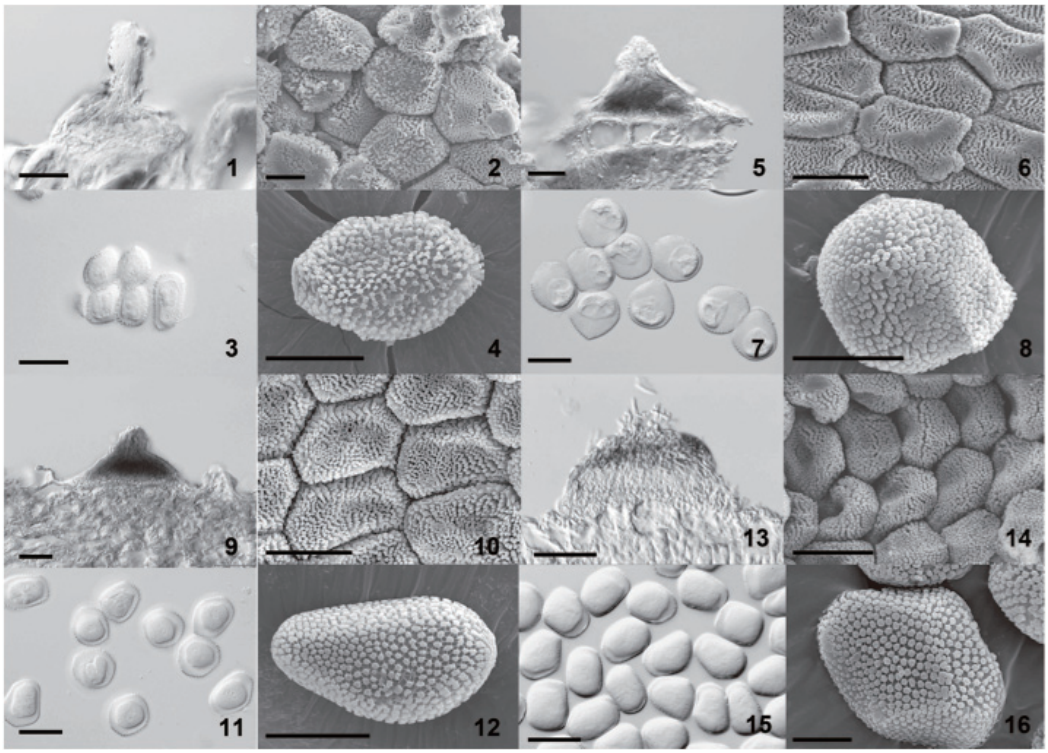

Fig. 1. Aecial morphology of four rust fungi with variously thick-walled aeciospores formed on *Meliosma* plants. 1–4. *Aecidium painavuense*: 1. Spermogonium. 2. Peridium. 3. Aeciospores. 4. Surface structure of aeciospore. 5–8. *Aecidium wareoense*: 5. Spermogonium. 6. Peridium. 7. Aeciospores. 8. Surface structure of aeciospore. 9–12. *Aecidium hornotinum*: 9. Spermogonium. 10. Peridium. 11. Aeciospores. 12. Surface structure of aeciospore. 13–16. *Phakopsora meliosmae-myrianthae*: 13. Spermogonium. 14. Peridium. 15. Aeciospores. 16. Surface structure of aeciospore. *Bars*: 50 µm in 1, 5, 9 and 13; 20 µm in 2, 3, 6, 7, 10, 11 and 15; 10 µm in 4, 8, 12, 14 and 16.

notched longitudinally or conical with blunt apex.

Specimens studied: On *M. ferruginea* Blume. PAPUA NEW GUINEA, Morobe, Wareo, 7 January 1936, M.S. Clemens (PURF-9925, holotype); Settleberg, 26 March 1936, M.S. Clemens (PURF-9926); Yunzaing, 29 June 1936, M.S. Clemens (PURF-9927). On *M. simplicifolia* (Roxb.) Walp. THAILAND, Phrae, between Ban Nam Krai and Pha Tuer, 16 April 1970, T. Smitinand and A.S. Cheke (BKF-46240).

The fungus was previously known only from Papua New Guinea. The new geographic distribution record in Thailand suggests broad distribution of this fungus in tropical Asia and Australasia.

Aecidium hornotinum Cummins, Ann. Mycol. 35: 103, 1937. Fig. 1, 9–12

Spermogoinal and aecial infection on leaves and petioles and causing hypertrophied lesions.

Spermogonia amphigenous, densely grouped, subcuticular, dome-shaped or conical, 101–154 µm wide and (50–) 78–122 µm high. Aecia amphigenous, surrounding spermogonia, *Aecidium*-type with well-developed peridium; inner surface of peridial cells verrucose. Aeciospores catenulate, subglobose to broadly ellipsoid, often angular and 25–41 × 21–31 µm in size; wall hyaline, prominently thickened, 6–14 µm thick apically and verrucose; verrucae nail-headed and subtended by interconnecting buttress.

Specimens studied: On *Meliosma* cf. *multiflora* Merr. THE PHILIPPINES, Luzon, Benguet, Mt. Sant Tomas, 26 March 1935, M.S. Clemens (PURF-9911, holotype). On *M. pendula* Merr. THE PHILIPPINES, Luzon, Benguet, Bontoc Trail, December 1926, M.S. Clemens (PURF-9212). On *M. arnottiana* (Wight) Walp. subsp. *oldhami* (Maxim.) H. Ohba, JAPAN, OKINAWA, Taketomi, Iriomote, Mt. Tedu, Ishigaki, 9 May 2013, Y. Ono (IBAR-10434); 7 Apr 2014, Y. Ono (IBAR-10582 & 10583); along the Otomi Nature Trail, 7 April 2014, Y. Ono (IBAR-10587); along the Urauchi Nature Trail, 7 April 2014, Y. Ono (IBAR-10589); Ishigaki, Mt. Omoto, 9 April 2014, Y. Ono (IBAR-10590).

Phakopsora meliosmae-myrianthae (Henn. & Shirai) Y. Ono, in Ono, Chatasiri, Pota & Yamaoka, Journ. Gen. Plant Pathol. 78: 345, 2012. Fig. 1, 13–16

Spermogoinal and aecial infection on leaves and causing more or less circular, diffused, discolored lesions. Spermogonia epiphyllous, gregarious, subcuticular, conical, 98–151 µm wide and 54–133 µm high. Aecia hypophyllous, *Aecidium*-type with well-developed peridium; inner surface of peridial cells verrucose. Aeciospores catenulate, subglobose to broadly ellipsoid, often angular and 13–24 × 9–18 µm in size; wall hyaline, 0.9–1.7 µm thick laterally, 1.9–7.0 µm thick apically and evenly verrucose; verrucae nail-headed and subtended by interconnecting buttress.

Specimens studied: On *M. myriantha* Siebold & Zucc. JAPAN, IBARAKI Mito, 9 June 1992, Y. Ono (IBAR-6045 & 6046); 8 June 1993, Y. Ono (IBAR-6708–6710); 10 May 1994, Y. Ono (IBAR-7142); 30 May 1998, Y. Ono (IBAR8104); 8 June 2006, Y. Ono and S. Kodato (IBAR-9679); 8 June 2006, Y. Ono and S. Kodato (IBAR-9680 & 9784); TOCHIGI, Nikko, July 1897, M. Shirai (one of the two syntypes of *Aecidium meliosmae-myrianthae* Henn. & Shirai in herb B).

Phakopsora melisomae Kusano, Bot. Mag. (Tokyo) 18: 148, 1904; emend. Chatasiri, Pota & Y. Ono, in Pota, Chatasiri, Ono, Yamaoka & Kakishima, Mycoscience 54: 26, 2013. Fig. 2, 1–4

Spermogoinal and aecial infection on leaves and forming small, irregular-shaped lesion on adaxial leaf surface. Spermogonia amphigenous, gregarious, subcuticular, conical, 68–158 µm wide and 60–157 µm high. Aecia amphigenous, more on adaxial leaf surface, *Aecidium*-type with well-developed peridium; inner surface of peridial cells smooth. Aeciospores catenulate, subglobose to broadly ellipsoid and 17–37 × 14–26 µm in size; wall hyaline, evenly 0.9–2.1 µm thick and verrucose; verrucae nail-headed and subtended by interconnecting buttress.

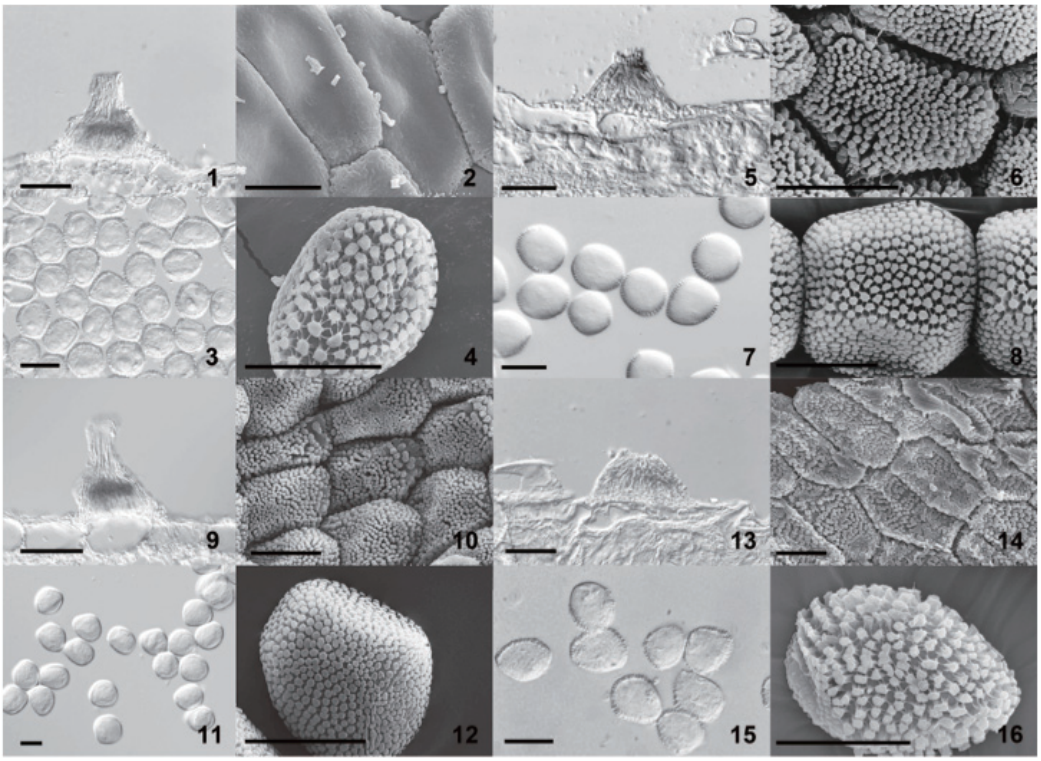

Fig. 2. Aecial morphology of four rust fungi with evenly thin-walled aeciospores formed on *Meliosma* plants. 1–4. *Phakopsora meliosmae*: 1. Spermogonium. 2. Peridium. 3. Aeciospores. 4. Surface structure of aeciospore. 5–8. *Phakopsora vitis*: 5. Spermogonium. 6. Peridium. 7. Aeciospores. 8. Surface structure of aeciospores. 9–12. *Phakopsora montana*: 9. Spermogonium. 10. Peridium. 11. Aeciospores. 12. Surface structure of aeciospore. 13–16. *Phakopsora orientalis*: 13. Spermogonium. 14. Peridium. 15. Aeciospores. 16. Surface structure of aeciospore. *Bars*: 50 µm in 1, 5, 9 and 13; 20 µm in 2, 3, 7, 11, 14 and 15; 10 µm in 4, 6, 8, 10, 12 and 16.

Specimens studied: on *M. myriantha* Siebold & Zucc. JAPAN, FUKUSHIMA, Futaba-machi, Mt. Goshayama, 27 June 2009, Y. Ono (IBAR-10078); GUMMA, Minakami-machi, Hoshi-onsen, 18 June 1973, Y. Ono (IBAR-1592); IBARAKI, Daigo-machi, Mt. Yamizo, 2 June 1995, Y. Ono (IBAR-7582); Kitaibaraki, Hanazono, 4 July 1992, K. Higuchi et al. (IBAR-6629); Mito, Ibaraki Univ., 3 July 2008, Y. Ono (IBAR-10037 & 10038); 21 May 2009, Y. Ono (IBAR-10064); 5 June 2009, Y. Ono (IBAR-10065); Satomi-mura, 8 June 1990, Y. Ono (IBAR-4798); Tsukuba, Mt. Tsukuba-san, June 1979, M. Kakishima (IBAR-1801); TOKYO, no locality data (probably collected at Mt. Takao-san on 11 July 1899), S. Kusano (IBAR-7798, probably part of the designated holotype of *Aecidium meliosmae*, originally labeled as "*meliosmatis* Dietel").

Phakopsora vitis P. Syd., Hedwigia 38 (Beibl.): (141) , 1899. Fig. 2, 5–8

Spermogoinal and aecial infection on leaves and causing more or less circular, diffused, discolored lesions. Spermogonia amphigenous, gregarious, subcuticular, conical, 60–100 µm wide and 53–85 µm high. Aecia hypophyllous, *Aecidium*-type with well-developed peridium; inner surface of peridial cells verrucose. Aeciospores catenulate, subglobose to broadly ellipsoid, often angular and 16–21 × 13–17 µm in size; wall hyaline, evenly 0.9–1.9 µm thick and verrucose; verrucae nail-headed and subtended by interconnecting buttress.

Specimens studied: On *M. myriantha* Siebold & Zucc. JAPAN, IBARAKI, Mito, 10 May 1994, Y. Ono (IBAR-7134); 20 May 1994, Y. Ono (IBAR-7144); 20 May 1995, Y. Ono (IBAR-7338); 30 May 1998, Y. Ono (IBAR-8105); Kuji-gun, Daigo-machi, 9 May 1998, Y. Ono and K. Ishimiya (IBAR-8047).

Phakopsora montana Y. Ono & Chatasiri, in Ono, Chatasiri, Pota & Yamaoka, Journ. Gen. Plant Pathol. 78: 344, 2012. Fig. 2, 9–12

Spermogoinal and aecial infection on leaves and causing more or less circular, diffused, discolored lesions. Spermogonia epiphyllous, gregarious, subcuticular, conical, 69–162 µm wide and 51–129 µm high. Aecia hypophyllous, *Aecidium*-type, surrounded by well-developed peridium; inner surface of peridial cells verrucose. Aeciospores catenulate, angularly subglobose to broadly ellipsoid and 13–21 × 12–19 µm in size; wall hyaline, 0.9–1.7 µm thick and verrucose; verrucae nail-headed and subtended by interconnecting buttress.

Specimens studied: On *M. tenuis* Maxim. JAPAN, GUMMA, Hoshi-onsen, 14 July 1963, N. Hiratsuka and K. Sugimoto (IBAR-3600); IBARAKI, Mito, 30 May 2010, Y. Ono (IBAR-10258 & 10260), 7 June 2011, YO (IBAR-10365 & 10366); TOCHIGI, Nikko, Miyori, 14 June 1995, Y. Ono (IBAR7588); Nikko, Yunishigawa, 14 June 1995, Y. Ono (IBAR7591), 18 August 2005, Y. Ono et al. (IBAR9545 & 9547), 21 July 2006, Y. Ono et al. (IBAR-9682), 7 July 2007, Y. Ono et al. (IBAR-9861); TOTTORI, Mt. Daisen, 25 July 1976, N. Hiratsuka and S. Okubo (IBAR-7790); Mt. Hyonosen, 5 July 1982, S. Kaneko and A. Kudo (IBAR-7791).

Phakopsora orientalis Chatasiri, Pota & Y. Ono, in Pota, Chatasiri, Ono & Yamaoka, Mycoscience 54: 26, 2013. Fig. 2, 13-16

Spermogoinal and aecial infection on leaves and forming small, irregular-shaped lesions on adaxial leaf surface. Spermogonia amphigenous, gregarious, subcuticular, conical, 45–121 µm wide and 50–118 µm high. Aecia amphigenous, more on adaxial leaf surface, *Aecidium*-type with well-developed peridium; inner surface of peridial cells verrucose. Aeciospores catenulate, subglobose to broadly ellipsoid, often angular, 18–34 × 14–23 µm; wall hyaline, evenly 0.9–1.9 µm thick and verrucose; verrucae nail-headed and subtended by interconnecting buttress.

Specimens studied: On *M. tenuis* Maxim. JAPAN, IBARAKI, Mito, 10 June 1996, Y. Ono (IBAR-7758); Tsukuba, 19 April 2010, S. Pota (IBAR-10253 & 10254); 22 April 2010, S. Pota (IBAR-10256).

Notes

Symptoms on host shoots and leaves caused by spermogonial and aecial infection, peridial surface structure, aeciospore size, aeciospore wall thickness and aeciospore wall surface structure characterize the spermogonial and aecial stages of the five *Phakopsora* and three *Aecidium* species. These morphological circumscriptions of the species correspond with the differences in their life-cycle pattern and actual or putative host preference. *Aecidium hornotinum* and *Aecidium* sp. aff. *painavuense* are distributed in East and Southeast Asia where unidentified *Phakopsora* species on *Vitis* also occur. These two *Aecidium* species share characteristic nail-headed structure of aeciospore wall with three heteroecious *Phakopsora* species on vitaceous plants. The host relationships, geographic association and morphological similarity suggest either one or two of the *Aecidium* species can be the *Aecidium* state of unidentified grapevine leaf rust fungus (or fungi).

Otherwise, they may be autoecious in the life cycle although their uredinial and telial stages have not been confirmed due to the lack of controlled inoculation experiments. *Aecidium hornotinum* has been reported on *M. arnottiana* subsp. *oldhami* (as *M. rhoifolia* Maxim. or *M. oldhami* Miq.) in the Ryukyu Islands (Hiratsuka and Shimabukuro 1955; Shimabukuro 1961; Shimabukuro and Tamori 1962; Hiratsuka et al. 1985). *Phakopsora meliosmae* has also been reported to occur on the same *Meliosma* species in the same geographic area. It is likely that the *Aecidium*-morph and *Phakopsora*-morph, reported as distinct species, constitute a holomorph of a single fungus. If this is proven, the fungus is distinct from two autoecious *Phakopsora* species, i.e. *P. meliosmae* and *P. orientalis*, on *Meliosma*. Assumed differential host preference on *M. arnottiana* subsp. *oldhami* and geographic distribution in subtropical and tropical region of the fungus support this perspective.

Acknowledgments

The type material of *Aecidium meliosmae-myrianthae* was loaned from the Mycological Herbarium, Botanic Gardens and Museum Berlin-Dahlem, Germany (B); and the types of *A. hornotinum* and *A. wareoense* from the Arthur Herbarium, Purdue University, U. S. A. (PUR). Small portion of *Aecidium*-infected shoot was detached from *Meliosma simplicifolia* specimens deposited in the Forest Herbarium, Department of National Parks, Wildlife and Plant Conservation, Thailand (BKF). We thank directors and curators of these herbaria for the loan of the specimens. We also thank Ms. Nannapat Pattharahirantricin for her help in examining phanerogamic specimens at BKF. This study was supported, in part, by a Grant-in-Aid for Scientific Research No. 07640921 from Ministry of Education, Science and Culture, Japan and Nos. 18570081 & 25450058 from Japan Society for the Promotion of Science (YO).

Disclosure

The authors declare no conflict of interest. The Thai rust specimens were imported under the permissions from the Ministry of Agriculture, Forestry and Fishery, Japan.

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