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## Taxonomic implications of life cycle and basidium morphology of *Ochropsora ariae* and *O. nambuana* (Uredinales)

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**Abstract** *Ochropsora ariae* was found to host-alternate between *Anemone pseudo-altaica* and *Aruncus dioicus* var. *tenuifolius* and *Ochropsora nambuana* between *Anemone flaccida* and *Elaeagnus multiflora* var. *hortensis* in Japan. Both species produced a sessile, thin-walled, cylindrical probasidium (teliospore), which turned into a four-celled metabasidium by continuous apical elongation of the probasidium. Several probasidia of *O. nambuana* were produced from a basal basidiogenous cell in a sorus hymenium. Life cycle and probasidium/metabasidium morphology showed the taxonomic identity of *Ceraceopsora elaeagni* with *O. nambuana*. Developmental morphology of the basidium found in the two *Ochropsora* species raised a question against the taxonomic separation of *Ochropsora* and *Aplopsora*.

**Key words** *Anemone* · *Aruncus* · *Elaeagnus* · Probasidium · Rust fungus · Taxonomy

### Introduction

Genus *Ochropsora* consists of 4 species and is believed to have close phylogenetic and taxonomic affinity to genera *Aplopsora* (4 species), *Ceraceopsora* (1 species), *Chaconia* (7 species), *Goplana* (10 species), and *Olivea* (8 species). These genera are classified in the family Chaconiaceae together with *Achrotelium*, *Botryorhiza*, and *Maravalia* (Cummins and Hiratsuka 1983), although Ono and Hennen (1983) and Ono (1984) are hesitant to include the latter three genera in the Chaconiaceae.

The chaconiaceous genera (fide Ono and Hennen 1983; Ono 1984) are presumed to be basal in the phylogeny of the Uredinales (Ono 1978, 1984; Ono and Hennen 1983; Hart

1988). It is also suggested that life-cycle studies of species in the chaconiaceous genera would elucidate the process of early life cycle evolution in the Uredinales (Ono 2002). However, most species of the chaconiaceous genera are distributed in tropical or subtropical regions, and thus they have been poorly collected and insufficiently studied as to their geographical distribution, morphological variation, life cycle, and host specificity. Even *Ochropsora*, *Aplopsora*, and *Ceraceopsora*, which are distributed in temperate regions and have had a better chance to be studied than the tropical genera, are still circumscribed by putative host specificity with little critical evaluation of morphological characteristics. Therefore, the real nature of the chaconiaceous genera and species have been poorly understood and their phylogenetic relationships undetermined.

*Ochropsora*, *Aplopsora*, and *Ceraceopsora* are apparently closely related, and their taxonomic separation is based on the mode of probasidium (teliospore) production and metabasidium development (Cummins and Hiratsuka 1983, 2003). Because the probasidium and metabasidium are thin walled and fragile in species of *Ochropsora*, *Aplopsora*, and *Ceraceopsora*, however, the exact mode of the probasidium production and metabasidium development has not been determined in all species except *Ceraceopsora* (*C. elaeagni* Kakish. et al.: Kakishima et al. 1984; Kakishima and Sato 1984).

In the three genera, life-cycle studies have been done in only three species: *O. ariae* (Fuckel) Ramsb. host-alternates between *Anemone nemorosa* L. and *Aruncus*, *Pyrus*, and *Sorbus* species (Tranzschel 1904; Klebahn 1907; Fischer 1910), *O. kraunhiae* (Dietel) Dietel between *Corydalis incisa* (Thunb.) Pers. and *Wistaria floribunda* (Willd.) DC. (Hiratsuka and Kaneko 1978), and *Ceraceopsora elaeagni* Kakish. et al. between *Anemone flaccida* Fr. Schm. and *Elaeagnus* species (Kakishima et al. 1984; Kakishima and Sato 1984). No *Aplopsora* species is known for its full life cycle. *Anemone flaccida* and *A. pseudo-altaica* Hara are listed as spermogonial and aecial hosts of *O. ariae* (Hiratsuka et al. 1992).

To resolve taxonomic and phylogenetic relationships among species of *Ochropsora*, *Aplopsora*, and *Ceraceo-*

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*psora*, a life-cycle study is indispensable together with a basidium development study. This study examines the life cycle and developmental morphology of the probasidium and metabasidium in *O. ariae* and *O. nambuana* distributed in Japan and discusses the taxonomic relationships between *Ochropsora* and *Aplopsora*.

## Materials and methods

### Specimens examined

Most specimens for microscopic observations have been deposited in the Herbarium of Systematic Mycology, Ibaraki University (IBA). The type specimens of *Ochropsora* and *Ceraceopsora* species were loaned from the following herbaria: *O. ariae* (Fuckel, Fungi rhenani 2219) from the Mycological Herbarium of Conservatoire et jardin botaniques de la ville de Genève, Switzerland (G); *O. sorbi* (Rabenhorst, Fungi europei 1490) and *O. nambuana* (N. Nanbu 118) from the Mycological Herbarium of Botanischer Garten und Botanisches Museum Berlin-Dahlem, Freie Universität Berlin, Germany (B) and the isotype from the Mycological Herbarium of the University of Hokkaido (SAPA); and *C. elaeagni* (TSH-R411) from the Mycological Herbarium of the University of Tsukuba (TSH). An additional *O. sorbi* specimen on *A. dioicus* (Sydow, Uredineen No. 2838) was also loaned from B. *Ochropsora ariae* (Fuckel) Ramsb: Spermogonial and aecial stages on *Anemone pseudo-altaica* Hara, Tochigi, Shioya-gun, Fujiwara-machi (IBA-7334); Ibaraki, Mito (IBA-7754, originally from Fujiwara-machi and grown in Mito; IBA-8768, originally from Fujiwara-machi and grown in Mito); uredinal and telial stages on *Aruncus dioicus* (Walt.) Fern. var. *tenuifolius* (Nakai) Hara, Akita, Semboku-gun, Tazawako-machi (IBA-7910); Niigata, Nishikambara-gun, Yahiko-mura (IBA-6268); Fukushima, Minamiaizu-gun, Tateiwa-mura (IBA-7303); Tochigi, Nikko (IBA-6225); Ibaraki, Mito (IBA-7756, result of aeciospore inoculation; IBA-8819, result of aeciospore inoculation); on *A. dioicus* (Sydow, Uredineen No. 2838 in B), on *Sorbus aria* Cranz (Fuckel, Fungi rhenani 2219, holotype of *Melampsora ariae* Fuckel in G); on *S. aucuparia* L. (Rabenhorst, Fungi europei 1490, holotype of *Ochropsora sorbi* (Oudem.) Dietel = *Caoma sorbi* Oudem. in B). *Ochropsora nambuana* (Henn.) Dietel: Spermogonial and aecial stages on *Anemone flaccida* Fr. Schm., Tochigi, Nikko (IBA-5661), Haga-gun, Motegi-machi (IBA-6696); Ibaraki, Mito (IBA-5660, originally from Nikko and grown in Mito; IBA-6695, originally from Nikko and grown in Mito; IBA-6701, originally from Nikko and grown in Mito); Ibaraki, Kuji-gun, Daigo-machi (IBA-7333); uredinal and telial stages on *Elaeagnus multiflora* Thunb. var. *hortensis* (Maxim.) Servettaz, Ibaraki, Mito (IBA-7152, result of aeciospore inoculation; IBA-7340, result of aeciospore inoculation; IBA-7341, result of aeciospore inoculation; IBA-7683, result of urediniospore inoculation; IBA-7684, result of urediniospore inoculation; IBA-8735, result of

aeciospore inoculation; IBA-8736, result of aeciospore inoculation; IBA-8737, result of aeciospore inoculation; IBA-6716, result of aeciospore inoculation); on *Elaeagnus umbellata* Thunb., Ibaraki, Tsukuba (TSH-R411, holotype of *Ceraceopsora elaeagni* Kakish. et al.), Ibaraki, Tsukuba (IBA-2400), Niigata, Nishikambara-gun, Yahiko-mura (IBA-6295); Tokyo (N. Nanbu 118, holotype of *O. nambuana* in B, isotype in SAPA).

### Artificial inoculations

For aeciospore inoculations, *A. dioicus* var. *tenuifolius*, *Elaeagnus glabra* Thunb., *E. macrophylla* Thunb., *E. multiflora* var. *hortensis*, *Panax japonicus* C.A. Meyer, *Prunus buergeriana* Miq., and *P. grayana* Maxim. were planted in 18-cm clay pots with loam soil and maintained in a glasshouse to avoid possible natural rust infections. *Aruncus*, *Elaeagnus*, and *Panax* plants were chosen because they were either proven or potential hosts of *Ochropsora* species (Hiratsuka et al. 1992) and were readily available. *Prunus* species were chosen because *Tranzschelia* species were also expected to form the spermogonial/aecial stage on *Anemone* species (Hiratsuka et al. 1992).

Naturally *Aecidium*-infected *A. flaccida* and *A. pseudo-altaica* were collected from various locations in Japan and grown in Mito, Ibaraki. The aeciospores produced on these *Aecidium*-infected plants were used as inocula. The aeciospores were scraped from fresh sori and dusted on a small piece (~3 × 3 mm) of water-saturated filter paper. The spore-dusted pieces of filter paper were then placed on the abaxial surface of the apparently healthy leaves of the above-listed plants. Whenever possible, urediniospore inoculations were also conducted to determine the host range of the fungi concerned. All inoculations were done in Mito in 1991–2002 by the methods as described elsewhere (Ono 1995b; Ono and Azbukina 1997) at room temperature between 15°C and 22°C.

### Microscopic observations

To examine sorus structure and spore morphology, dried herbarium specimens were freehand-sectioned under a binocular dissecting microscope. Thin sections were mounted in a drop of lactophenol solution without staining on a microscopic slide. The slide preparations were observed under an Olympus BX50 microscope equipped with a differential interference contrast optic (DIC) unit. Photomicrographs were taken at a magnification of 670× on 35-mm Fuji Presto film (ISO 400) with an Olympus PM-20 automatic photomicrograph unit.

For scanning electron microscopy (SEM), rust spores were scraped from sori on dried herbarium specimens on double-adhesive tape on a specimen holder. The preparations were subsequently coated with platinum-palladium using a Hitachi E-1030 Ion Sputter and examined with a Hitachi S-4200 SEM at 15 kV.

## Results

### Artificial inoculations

In the 23 inoculation experiments undertaken in 1991–2002, only 9 inoculations were successful, i.e., 5 with aeciospores produced on *A. flaccida* and 4 with aeciospores on *A. pseudo-altaica* (Table 1). Aeciospores from *Aecidium*-infected *A. flaccida* collected at two sites each in Tochigi and Ibaraki were successfully inoculated onto *E. multiflora* var. *hortensis*, resulting in abundant production of uredinia and urediniospores on the abaxial surface of inoculated leaves, whereas other inoculated plants showed no sign of infection. However, aeciospores produced on *A. flaccida* collected at six additional sites in Ibaraki and Hokkaido did not infect any inoculated plants. Urediniospores produced on the *Elaeagnus* plants by the aeciospore inoculations were inoculated onto the same set of plants used for the aeciospore inoculations; and only *E. multiflora* var. *hortensis* plants was infected with abundant production of uredinia and urediniospores. No other plants inoculated showed any sign of infection. Structural and morphological characteristics of the sorus and spores produced on the *Elaeagnus* plants showed the taxonomic identity of the fungus with *O. nambuana*.

On the other hand, results of inoculations with aeciospores from *Aecidium*-infected *A. pseudo-altaica* were variable. Eight of the 12 inoculations were unsuccessful. Two inoculations with aeciospores produced on *A. pseudo-altaica* collected at two sites in Tochigi resulted in abundant production of uredinia and urediniospores on the abaxial surface of inoculated leaves of *A. dioicus* var. *ternuifolius* (see Table 1). No other plants inoculated showed any sign of infection. Urediniospores produced on the *Aruncus* plants by the aeciospore inoculations were inoculated onto the same set of plants that were used for the aeciospore inoculation. The inoculations were successful only on the *Aruncus* plants with abundant production of uredinia and urediniospores. Structural and morphological characteristics of the sorus and spores produced on *A. dioicus* var. *ternuifolius* showed the taxonomic identity of the fungus with *O. ariae*. On the other hand, two inoculations with aeciospores produced on *A. pseudo-altaica* collected at two sites in Ibaraki resulted in abundant production of uredinia and urediniospores on the abaxial surface of inoculated leaves of *P. buergeriana* (see Table 1). Uredinia and urediniospores were characteristic of *Tranzschelia* species.

### Morphology

#### *Ochropsora ariae*

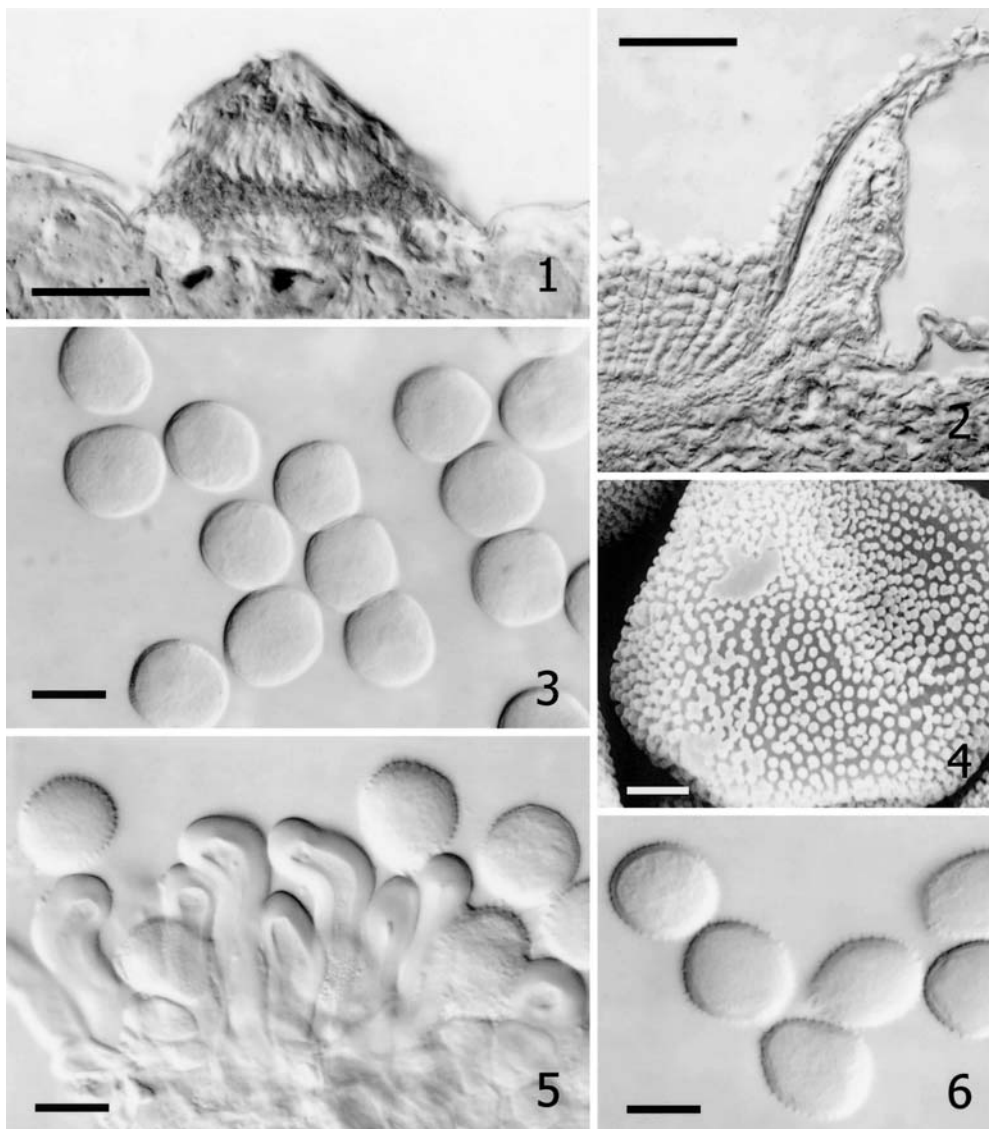
Spermogonial and aecial infection was systemic in *A. pseudo-altaica* plants and the infected stocks produced elongated leaves with narrow leaf segments: spermogonia were more or less evenly scattered on both leaf surfaces and aecia mostly on the abaxial leaf surface. Spermogonia were subcuticular, conical, 110–140 µm wide and 70–100 µm high

**Table 1.** Results of artificial inoculations with aeciospores produced on naturally infected *Anemone flaccida* and *A. pseudo-altaica*

Inoculum: fungus and host (locality, voucher specimen)	Successfully infected plant	Date of inoculation	Voucher specimen
<i>Ochropsora nambuana</i> (Henn.) Dietel			
<i>Anemone flaccida</i> Fr. Schm. (Tochigi, Nikko, IBA-6701)	<i>Elaeagnus multiflora</i> Thunb. var. <i>hortensis</i> (Maxim.) Servettaz	17 May 1993	IBA-6716
<i>A. flaccida</i> (Tochigi, Nikko, IBA-6701)	<i>E. multiflora</i> var. <i>hortensis</i>	13 May 1994	IBA-7152
<i>A. flaccida</i> (Tochigi, Moteji, IBA-6696)	<i>E. multiflora</i> var. <i>hortensis</i>	29 April 1995	IBA-7340
<i>A. flaccida</i> (Ibaraki, Mt. Yamizo, IBA-7333)	<i>E. multiflora</i> var. <i>hortensis</i>	1 May 1995	IBA-7341
<i>A. flaccida</i> (Ibaraki, Mito, no voucher)	<i>E. multiflora</i> var. <i>hortensis</i>	May 2001	IBA-8735-7
<i>Ochropsora ariae</i> (Fuekel) Ramsb.			
<i>Anemone pseudo-altaica</i> Hara (Tochigi, Fujiwara, IBA-7754)	<i>Aruncus dioicus</i> (Walt.) Fern. var. <i>tenuifolius</i> (Nakai) Hara	25 April 1996	IBA-7756
<i>A. pseudo-altaica</i> (Tochigi, Fujiwara, IBA-8768 = IBA-7334)	<i>A. dioicus</i> var. <i>tenuifolius</i>	7 April 2002	IBA-8819
<i>Tranzschelia</i> sp.			
<i>A. pseudo-altaica</i> (Ibaraki, Daigo, IBA-8668)	<i>Prunus buergeriana</i> Miq.	16 April 2001	IBA-8675
<i>A. pseudo-altaica</i> (Ibaraki, Mt. Gozenyama, IBA-8670)	<i>P. buergeriana</i>	18 April 2001	IBA-8676

**Figs. 1–4.** *Ochropsora ariae* on *Anemone pseudo-altaica*, IBA-5659. **1** Spermogonium. **2** Right half of vertical section of aecium. **3** Aeciospores. **4** Aeciospore surface structure. Bars **1, 2** 40  $\mu\text{m}$ ; **3** 10  $\mu\text{m}$ ; **4** 2.5  $\mu\text{m}$

**Figs. 5,6.** *Ochropsora ariae* on *Aruncus dioicus* var. *tenuifolius*, IBA-7756. **5** Uredinial paraphyses. **6** Urediniospores. Bars **5, 6** 10  $\mu\text{m}$



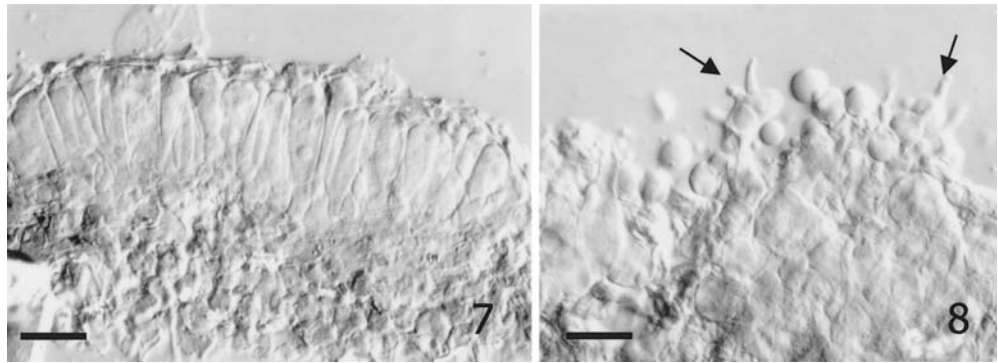
(Fig. 1). Aecia were surrounded by well-developed peridium, thus appearing cupulate (Fig. 2). Aeciospores were produced in chains, subglobose or broadly ellipsoid, often angular and 14–21  $\times$  13–18  $\mu\text{m}$  in size (Fig. 3). The wall was thin, colorless, and densely warted (Fig. 4). Uredinia produced on the abaxial leaf surface were minute and surrounded by thick-walled, incurved paraphyses. Paraphyses were variable in size, 37–70  $\mu\text{m}$  high and 9–16  $\mu\text{m}$  wide in Japanese specimens (Fig. 5), 29–47  $\mu\text{m}$  high and 8–13  $\mu\text{m}$  wide in Rabenhorst, *Fungi europei* 1490 (B), and 39–77  $\mu\text{m}$  high and 9–19  $\mu\text{m}$  wide in Fuckel, *Fungi rhenani* 2219 (G). Urediniospores were broadly ellipsoid or obovoid and 21–28  $\times$  17–23  $\mu\text{m}$  in size (Fig. 6). The wall was colorless, evenly 1.5–2  $\mu\text{m}$  thick, and completely echinulate. Probasidia were produced beneath the host epidermis, sessile, thin walled, and oblong to cylindrical (Fig. 7). The size of the probasidia varied from 27–36  $\times$  11–15  $\mu\text{m}$  in Rabenhorst, *Fungi europei* 1490 (B), 36–46  $\times$  9–16  $\mu\text{m}$  in Fuckel, *Fungi rhenani* 2219 (G), to 38–47  $\times$  10–18  $\mu\text{m}$  in Japanese specimens.

The exact mode of the probasidium production was not determined because they were thin walled and fragile. Metabasidium development was observed in Japanese specimens. The apex of the probasidium seemed to continuously elongate immediately after maturation; different developmental phases were observed within the same sori as well as among different sori and, thus, no delimitation was possible between the probasidium and the metabasidium in their development. The apical elongated part, then, became four-celled by horizontal septum formation (Fig. 8). Basidiospores were produced on an apiculus developed from a metabasidial cell.

#### *Ochropsora nambuana*

Spermogonial and aecial infection was partially systemic in *A. flaccida* plants and infected stocks produced both healthy normal leaves and infected, distorted leaves with a

**Figs. 7,8.** *Ochropsora ariae* on *Aruncus dioicus* var. *tenuifolius*, IBA-6225. **7** Probasidia aligned in a basidiosorus. **8** Metabasidia (arrows). Bars 10µm



long petiole: spermogonia were more or less evenly scattered on both surfaces and aecia mostly on the abaxial surface of the infected leaves. Spermogonia were subcuticular, conical, 160–200µm wide, and 100–156µm high (Fig. 9). Aecia were surrounded by well-developed peridium, thus appearing cupulate (Fig. 10). Aeciospores were produced in chains, subglobose or broadly ellipsoid, often angular and 16–24 × 14–20µm in size (Fig. 11). The wall was thin, colorless, and densely warted (Fig. 12). Uredinia were produced on the abaxial leaf surface, minute and surrounded by thin-walled, incurved paraphyses. Paraphyses were 27–47µm high and 7–11µm wide (Fig. 13). Urediniospores were broadly ellipsoid or obovoid and 21–28 × 16–21µm in size (Fig. 14). The wall was colorless, evenly 1.5–2µm thick, and completely echinulate. Probasidia were produced beneath the host epidermis, sessile, thin-walled, oblong to cylindrical, and 46–73 × 11–19µm in size (Fig. 15). Several probasidia were successively produced from a basal basidiogenous cell (Figs. 15, 16). The mode of metabasidium development in *O. nambuana* was the same as in *O. ariae*: the apex of the probasidium continuously elongated to become a four-celled metabasidium (Fig. 16), and no delimitation was possible between the probasidium and the metabasidium development. Basidiospores were produced on an apiculus developed from a metabasidial cell.

The type specimen of *C. elaeagni* (TSH-R411) was compared with the type specimens of *O. nambuana* (N. Nanbu 118 in B and SAPA) as well as the specimens derived from inoculation experiments. No appreciable differences were observed in the uredinial morphology and the basidial development between the type specimens of *O. nambuana* and *C. elaeagni*.

## Discussion

The genus *Ochropsora* was proposed by Dietel (1895) with the basionym of “*Melampsora sorbi* (Oudem.)” (Winter 1884). Winter (1884) seems to be the first to describe the “internal mode” of metabasidium production; thus, the proper citation of the type species is considered to be *O. sorbi* (G. Winter) Dietel (as accepted by Cummins and

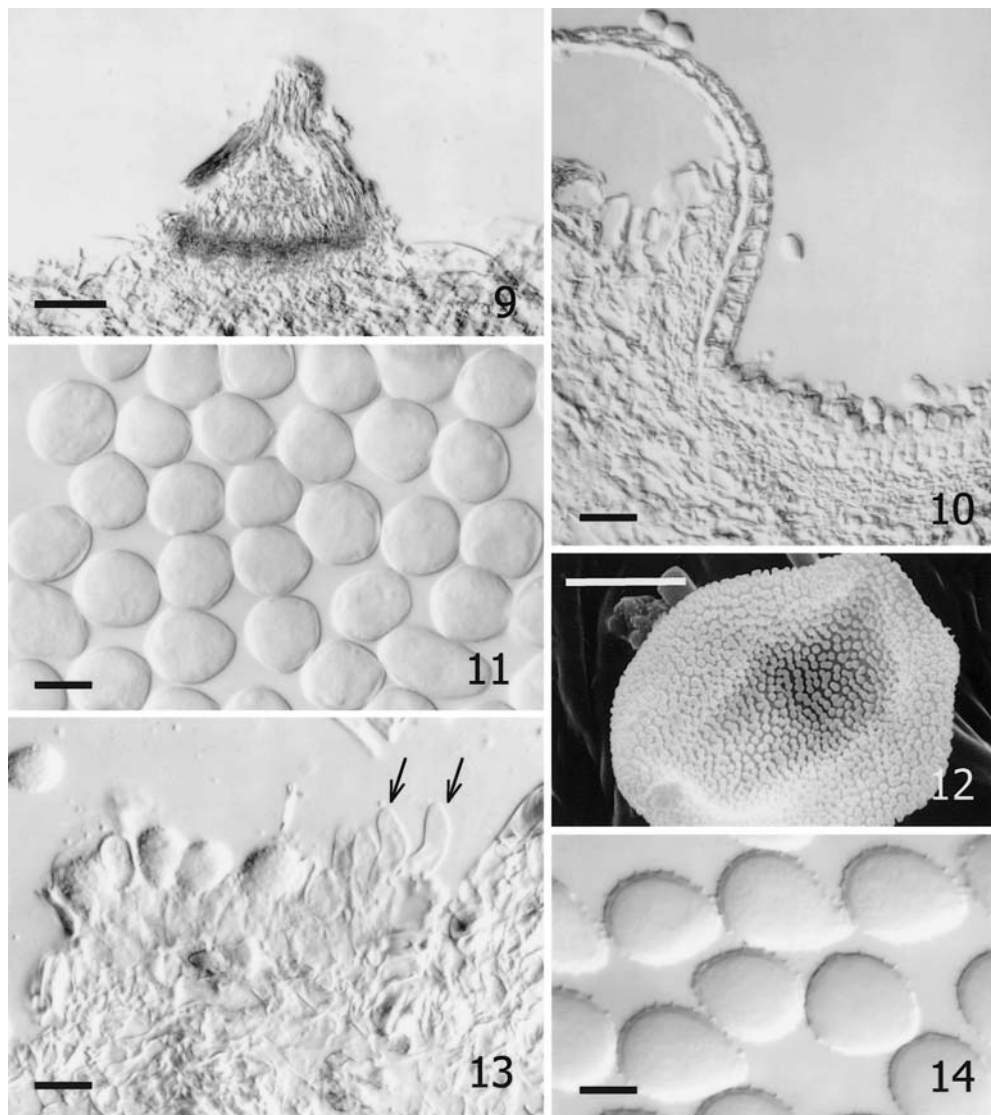
Hiratsuka 2003) instead of *O. sorbi* (Oudem.) Dietel (as accepted by Gäumann 1959). This typification has caused the nomenclatural difficulty of the genus, however. The life-cycle studies described below show that the fungus on *S. aria* originally named as *Melampsora ariae* Fuckel (Fuckel 1869, cited from Ramsbottom 1914) is conspecific with *O. sorbi*. Because *M. ariae* predates *O. sorbi*, Ramsbottom (1914) proposed to replace *O. sorbi* with *O. ariae* (Fuckel) Ramsbottom as the correct name of the type species of the genus *Ochropsora*. The name *O. ariae* (Fuckel) Ramsbottom is hereafter used as the correct name of the fungus concerned (as accepted by Wilson and Henderson 1966). *Ochropsora ariae* (Fuckel) P. Syd. & Syd. (Sydow and Sydow 1915; Cummins and Hiratsuka 1983) is the synonym of *O. ariae* (Fuckel) Ramsbottom.

The heteroecious life cycle of *O. ariae* was first proven by Tranzschel (1904), who successfully connected the spermogonial/aecial stage (*Aecidium leucospermum* DC.) on *Anemone nemorosa* L. with the uredinial/telial stage (*O. ariae*) on *Sorbus aucuparia* L. Fischer (1904, 1910), and Klebahn (1907) confirmed the heteroecism of the fungus onto *S. americana* L., *S. aria* (L.) Crantz, *S. aucuparia*, *S. fennica* (Kalm.) Fr., *S. torminalis* (L.) Crantz, *Pyrus communis* L., and *Pyrus malus* L. *Aruncus sylvester* Kostel. [= *A. dioicus* (Walt.) Fern] was also successfully infected with aeciospores from *A. nemorosa* (Fischer 1910). In addition, *Amelanchier asiatica* Endl., *Aruncus dioicus* (Walt.) Fern. var. *tenuifolius* (Nakai) Hara (= *Aruncus vulgaris* Raff.), *Malus sylvestris* (L.) Mill., *Prunus avium* L., *P. padus* L., *Sorbus hybrida* L., *S. latifolia* (Lam.) Pers., and *S. suecica* (L.) Krok & Amq. are listed as uredinial/telial hosts (Gäumann 1959; Hiratsuka et al. 1992).

In Japan, *Ochropsora*-infected *Aruncus* plants are widespread and commonly observed, whereas the rust infection on *Amelanchier asiatica* seems limited. *Anemone flaccida* and *A. pseudo-altaica* are said to be spermogonial/aecial hosts (Hiratsuka et al. 1992). However, this perspective has not been verified by inoculation experiments.

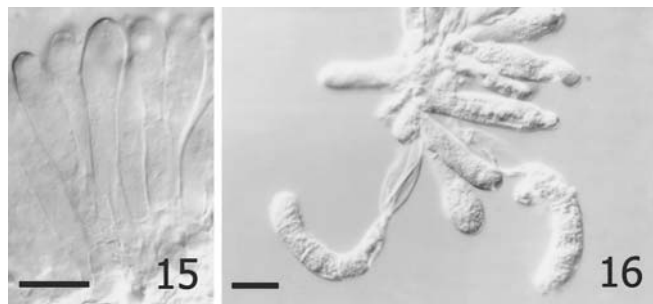
Because no *Aplopsora* species has been known to its full life cycle, the only characteristic that separates *Ochropsora* and *Aplopsora* is the mode of metabasidium development, i.e., “internal” in the former and “external” in the latter genus. Line drawings of *O. ariae* (Sydow and Sydow 1915; Soong 1939; Savlescu 1953 cited from Gäumann 1959;

**Figs. 9–12.** *Ochropsora nambuana* on *Anemone flaccida*, IBA-6701. **9** Spermogonium. **10** Left half of vertical section of aecium. **11** Aeciospores. **12** Aeciospore surface structure. **Bars 9, 10** 40  $\mu\text{m}$ ; **11** 10  $\mu\text{m}$ ; **12** 5  $\mu\text{m}$   
**Figs. 13,14.** *Ochropsora nambuana* on *Elaeagnus multiflora* var. *hortensis*, IBA-7340. **13** Vertical section of uredinium with peripheral paraphyses (arrows). **14** Uredinisporos. **Bars 13** 20  $\mu\text{m}$ ; **14** 10  $\mu\text{m}$



Wilson and Henderson 1966; Cummins and Hiratsuka 1983, 2003) and *O. nambuana* (Ito 1938) illustrate the development of the four-celled metabasidium from the one-celled probasidium with little morphological change. In contrast to the two species, a line drawing of *Aplopsora nyssae* (Cummins and Hiratsuka 1983, 2003) and a photomicrograph of *A. corni* (Ono and Harada 1994) illustrate the development of the metabasidium by continuous apical elongation of the probasidium.

Microscopic examinations of *O. ariae* on *A. dioicus* var. *tenuifolia* and *O. nambuana* on *E. multiflora* var. *hortensis* showed that both fungi produce one-celled, oblong or cylindrical probasidia in a single horizontal layer beneath the host epidermis. The basidiosori (telia) of the two fungi seem to become naked quickly as they mature; and the apical portion of the probasidium continuously elongates to turn into the four-celled metabasidium. Although metabasidium development was not observed in the type materials of *O. ariae*, the “external” mode of metabasidium development was observed in the holo- and isotypes of *O. nambuana*.



**Figs. 15,16.** *Ochropsora nambuana*. **15** Probasidia, IBA-7683. **16** Metabasidia developed by continuous apical elongation of probasidia, Nanbu 118 in B. **Bars** 10  $\mu\text{m}$

This unexpected observation necessitates the comparison of *O. nambuana* with *C. elaeagni*, because the latter fungus host-alternates between *A. flaccida* and *Elaeagnus* spp. and because it is separated from *Ochropsora* only by the mode of probasidium production and metabasidium development

(Kakishima et al. 1984; Cummins and Hiratsuka 2003). However, the probasidium morphology and the metabasidium development observed in the type materials and other herbarium specimens of *O. nambuana* and *C. elaeagni* are the same (Fig. 16; see figs. 11 and 12 of Kakishima et al. 1984). Therefore, it is concluded that *O. nambuana* and *C. elaeagni* are conspecific and that *Ochropsora* and *Ceraceopsora* are congeneric.

Although the samples examined in this study do not represent the entire variation range of each of the two species, the results raise a question against the taxonomic separation of *Ochropsora* and *Aplopsora*. The previously stated difference in the mode of metabasidium production seems to be a matter of degree of apical elongation of the probasidium during maturation. Wilson and Henderson (1966) described that “teleutospores” (=probasidia) are at first unicellular, then becoming four celled, up to 70 µm long. This description does not disagree with the observations on Japanese specimens. Size variations in the probasidium among the holotypes of *Ochropsora sorbi* and *Melampsora ariae* and Japanese specimens reflect the degree of probasidium maturation or, in other words, different transitional phases in the development of the metabasidium from the probasidium. There is no clear morphological delimitation between the probasidium and the metabasidium. Thus, the taxonomic separation of the two genera is questioned. In addition, three species in a poorly circumscribed genus *Cerotelium* have been suggested to belong to *Aplopsora* because of the similarity in probasidium morphology and a mode of metabasidium production (Ono et al. 1992; Ono 1995a). Preliminary field survey and inoculation experiments have shown that some *Aplopsora* species produce their spermogonial and aecial stages on *Anemone* species in Japan. All the observations indicate the taxonomic identity of *Aplopsora* with *Ochropsora*. However, any taxonomic conclusion must wait until the morphological variations and the life cycles of the fungi concerned are fully resolved.

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