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New records for pathogenic fungi on weedy or non-indigenous plants

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Abstract: A rust fungus, *Puccinia jaceae*, is reported for the first time in the United States on spotted knapweed, *Centaurea stoebe*. Powdery mildew (*Blumeria graminis*) of bulbous bluegrass, *Poa bulbosa*, is reported for the first time in western North America. *Ramularia nivosa* on *Penstemon palmeri*, *Albugo candida* on *Lunaria annua*, and *Pucciniastrum pustulatum* on *Epilobium brachycarpum*, are reported for the first time from Idaho. A *Golovinomyces* sp. on *Verbena bonariensis* is reported for the first time from Washington State. The basis for diagnosis for each disease is reported, accompanied by photomicrographs of the fungal pathogens, photographs of some of the diseases, and discussion of the implications of the findings.

Key words: *Albugo candida*, *Blumeria graminis*, *Centaurea stoebe*, *Epilobium brachycarpum*, *Golovinomyces*, *Lunaria annua*, *Penstemon palmeri* var. *palmeri*, *Poa bulbosa*, *Puccinia jaceae*, *Pucciniastrum epilobii*, *Pucciniastrum pustulatum*, *Ramularia nivosa*, rust, white rust, *Verbena bonariensis*

Introduction: Non-native (non-indigenous or exotic) plants growing in the absence of the co-evolved natural enemies of their home ranges are said to be in a state of enemy release; this state is common for non-native plants (Mitchell and Power 2003). Many invasion biologists hypothesize that enemy release drives non-native plant invasions (Keane and Crawley 2002). According to this hypothesis, it is the extent of enemy release, which can vary from total to negligible, that matters. Testing of this hypothesis has drawn heavily on host-pathogen records. For example, the hypothesis has been most comprehensively tested with the host-pathogen databases of the USDA Systematic Mycology and Microbiology Laboratory for an analysis published in *Nature* (Mitchell and Power 2003).

Enemy release may be steadily eroded over time as pathogens from the native range of the plant find their way to their host's invaded range. This outcome has been described as enemy reunion (Newcombe and Dugan, in press). Enemy release may also be eroded by pathogens that shift or jump from native plants (Shipunov *et al.* 2008). These changes in the extent of enemy release can affect the extent of plant invasions and thus their annual cost to the U.S. economy, estimated to be close to \$35 billion (Pimentel *et al.* 2005). Host-fungus records documenting new hosts or expanded ranges of pathogens also are useful for diagnosticians and other plant health professionals. Herein we focus on new records of pathogens of plants that are either non-native (*Poa bulbosa*, *Centaurea stoebe*, *Penstemon palmeri* var. *palmeri*, *Lunaria annua*, and *Verbena bonariensis*) or native but weedy (*Epilobium brachycarpum*) in Idaho and Washington. Whereas new pathogens on invasive *Poa bulbosa* and *Centaurea stoebe* can potentially reduce weed control costs, new pathogens on plants with ornamental value (*Penstemon palmeri* var. *palmeri*, *Lunaria*

annua, and *Verbena bonariensis*) may increase pathogen control costs.

Materials and Methods: Observations of microscopic characters were made and photographs taken with an Olympus BH-2 research microscope equipped with a DP-11 digital camera, or with a Zeiss Axioskop 2 equipped with a Nikon Coolpix digital camera. Microscopic structures were measured at 100-1000X while mounted in distilled water or, for *Puccinia jaceae*, *Blumeria graminis* and *Ramularia nivosa*, in lactoglycerol, or for *Golovinomyces* sp., in 3% KOH, and for *Albugo* and *Pucciniastrum*, 85% lactic acid. Free-hand sections of ascocarps were made when needed. Literature used for determination of identities of hosts and fungi, and place of deposit of vouchers, are specified in the text of each record.

Inoculations were performed with both the rust fungus of spotted knapweed, *Centaurea stoebe*, and with the fungus associated with leaf spots of *Penstemon palmeri* var. *palmeri*. For the former, seedlings were raised from seed of *C. stoebe* that had been collected in Moscow, Idaho, and from seed of *Centaurea diffusa*, diffuse knapweed, collected from four sites: Tygh Valley, Oregon; Portland, Oregon; Douglas County, Colorado; and Kittitas County, Washington. Forty seedlings of each species were grown; in the case of *C. diffusa* there were ten seedlings from each of the four sites. The eighty seedlings were grown outdoors in pots until they had developed full rosettes. Then they were misted with water and inoculated by wiping rust inoculum onto leaf surfaces with cotton swabs. At the time of this inoculation (29 September 2008), only teliospores appeared to be present on the naturally infected plants from Lapwai, Idaho (46° 20' 30.20" N, 116° 36' 39.60" W) that were used as the source of inoculum. Trays of the inoculated plants were inserted into large plastic bags to maintain leaf wetness overnight. The trays of inoculated plants were then placed near

uninoculated plants of *C. stoebe* that served as controls.

With respect to the leaf spot of *Penstemon palmeri* var. *palmeri*, potato dextrose agar (PDA) cultures of the fungus that sporulated freely on the leaf spots were first obtained from conidia of the fungus. Seeds of *Penstemon palmeri* var. *palmeri* were obtained from Seeds Trust (PO Box 596, Cornville, AZ 86325) and germinated to produce greenhouse plants. An aqueous suspension of fragmented mycelia from one-month-old PDA cultures (Ganley et al. 2008) was used to inoculate the three most basal perfoliate leaves of these plants. The suspension was simply poured into the cup formed by perfoliate leaves and allowed to remain there until it dried. The leaves of five plants were inoculated; another five plants were inoculated with sterile water alone.

Results: *Puccinia jaceae* Oth on *Centaurea stoebe* L. s. lat. (= *C. maculosa*, *C. pseudomaculosa*, *C. biebersteinii*, *C. micrantha*, spotted knapweed), 12 miles south of Lapwai along U.S. Highway 95, Nez Perce County, Idaho, 2 October 2007, 28 September 2008, and again 22 May 2009, collector G. Newcombe. Fall collections yielded dark-brown telia on stems and leaves (Fig. 1). Teliospores were 30-43 x 21-29 µm, often somewhat constricted at septum, with hyaline pedicels, warty and orange-brown walls when spores were observed singly with transmitted light (Fig. 2). A spring 2009 collection yielded uredinia only. Urediniospores were nearly spherical (Fig. 3), 25-33 µm x 23-31 µm, and echinulate except for smooth areas associated with germ pores. There were always two germ pores. A specimen was deposited in the U.S. National Fungus Collections (BPI 879147).

The inoculation of plants of *C. stoebe* and *C. diffusa* with teliospores in fall 2008 produced telia on leaves and stems 30 days later. Controls remained free of rust. A greater density of telia

developed on *C. stoebe* than on *C. diffusa* and on *C. stoebe* telia were initially associated with less chlorosis and necrosis, indicating a more susceptible infection type. Chlorotic areas were sometimes bordered by a purpling of leaf tissues. Teliospores from the potted *C. stoebe* plants were then used during the subsequent winter to periodically inoculate seedlings of *C. stoebe* in a greenhouse. In early spring 2009, uredinia were finally produced from an inoculation with teliospores, suggesting that an aecial state is unnecessary for this fungus. The greenhouse urediniospores were identical to those produced on collections from naturally infected plants in spring (Fig. 3).

The foremost students of the rusts of *Centaurea* and the *Cardueae* to date have undoubtedly been D.B.O. Savile and A.L. Guyot (Guyot 1965; Savile 1970). Both were candid about the manner in which the difficulty of their research problem was “compounded by the chaotic taxonomy of the hosts” (Savile 1970). *Centaurea* may comprise between 400 and 700 species and has long been one of the largest and most difficult genera of the Asteraceae (Garcia-Jacas et al. 2001), so Savile’s caution seems justified. With that caveat in mind, we considered the fact that Guyot recognized two species of *Puccinia* on *C. stoebe*: *P. centaureae-vallesiaceae* Hasler (related to *P. centaureae*), and *P. jaceae* Oth. Savile followed suit and stated that *P. centaureae* and its varieties are characterized by urediniospores with three germ pores, whereas *P. jaceae* and its varieties possess urediniospores with two germ pores. According to Savile, the teliospores of *P. centaureae* and *P. jaceae* are “easily confused”, so the urediniospore distinction is key.

The only report of any rust on *C. stoebe* in North America was from 1989 in British Columbia, Canada (Mortensen et al. 1991), where the rust was identified as *P. jaceae* var. *diffusae*. This variety specializes on *C. diffusa* and it was subsequently reported on this host in the United States (Dugan and Carris 1992; Palm et al. 1992).

However, *P. jaceae* var. *diffusae* also possesses limited virulence on *C. stoebe* (Mortensen et al. 1991). No variety of *P. jaceae* has been described to date that specializes on *C. stoebe*.

As the Lapwai rust fungus produced urediniospores with two germ pores, it would appear to be *P. jaceae* by Savile's criterion. However, the urediniospores of the Lapwai rust appear to be more nearly circular in outline (Fig. 3) than the broadly ellipsoid urediniospores of *P. jaceae* var. *diffusae*, *P. jaceae* var. *jaceae*, and *P. jaceae* var. *solstitialis* (Mortensen et al. 1989; Savile 1970). And, although our results are preliminary, it would appear that the rust of spotted knapweed in Lapwai is more virulent on *C. stoebe* than on *C. diffusa*. With further study, a new variety may be warranted for the fungus that we are reporting here. For now, however, we are reporting this rust of *C. stoebe* simply as *P. jaceae*. Our collections from three successive years show that this rust is capable of successful overwintering in the region.

If managed effectively, *P. jaceae* might contribute significantly to the biological control of *C. stoebe*, just as *Puccinia chondrillina* has to the control of *Chondrilla juncea* L., or rush skeleton weed, in Australia (Hanley and Groves 2002). *Centaurea stoebe* is such a serious invader in western North America that twelve insect species have been deliberately introduced for the purposes of classical biological control (Story et al. 2006). Increasing the number of enemies should decrease the invasiveness of the target plant, according to the enemy release hypothesis (Mitchell and Power 2003).

***Blumeria graminis* (D.C.) Speer on *Poa bulbosa* L. subsp. *vivipara* (Koel.) Arcang. (bulbous bluegrass), along Fall Creek above the middle fork of the Weiser River, Valley County, Idaho, 2 June 2008. A second collection was made in Moscow, Latah County, Idaho, 26 May 2009. Collector in both cases G. Newcombe. The**

asexual state of *B. graminis* was present on the leaves of both collections, and was largely as reported previously from *Festuca idahoensis* (Dugan and Newcombe 2007). Conidia were somewhat longer (Fig. 4), ranging from 26-36 µm. However, included in the second collection were chasmothecia in various stages of maturation (Fig. 5). A secondary mycelium including hyaline, thick-walled setae accompanied them (Fig. 6). Immature, clavate asci with short stalks were present in some chasmothecia. Specimens from the two collections were deposited in the U.S. National Fungus Collections (BPI 879148 and BPI 879151).

To our knowledge, *B. graminis* has only been found once on *Poa bulbosa* in North America (Farr et al. n.d.). A single specimen, BPI 563092, was collected in Washington, D.C., in 1916. In contrast, *B. graminis* appears to be common on *Poa bulbosa* throughout its native range in Eurasia, with records from many countries (Farr et al. n.d.). In western North America, where *Poa bulbosa* subsp. *vivipara* is invasive, *B. graminis* may have been present for some time at low levels, but this is the first report of its presence as far as we know. Many uninfected plants were observed near infected plants, and the powdery mildew of the latter was inconspicuous as it was mostly confined to leaves, particularly their adaxial surfaces. If reports of powdery mildew on *Poa bulbosa* are any indication, in its invaded range in North America this plant may still be benefiting from enemy release with respect to this pathogen. It is possible that relatively few virulent pathotypes of *B. graminis* have been introduced in the invaded range of *Poa bulbosa*, and that this fact explains the low infection frequency that we observed.

***Ramularia nivosa* (Ellis & Everh.) W.B. Cooke & C.G. Shaw on *Penstemon palmeri* var. *palmeri* (scented penstemon), the collector's garden, Moscow, Latah County, Idaho, 26 May 2009. Collector G. Newcombe. Produced on leaf spots (Fig. 7),**

conidia were hyaline, catenulate, and minutely echinulate (Fig. 8) with single, medial septa. Conidia varied in length from 19 to 32 μm , and were produced on conidiophores from 32 to 80 μm in length, with several conidiogenous loci (Fig. 9). This fungus fit the description of *Ramularia nivosa* (Savile 1968; Braun 1998). The leaf spots have been described previously (Braun 1998); each lesion was typically necrotic, concentric, and bounded by a darker periphery. Savile noted that conidia and conidiophores of *R. nivosa* can vary considerably in length. Specimens were deposited in the U.S. National Fungus Collections (BPI 879149). Inoculations of greenhouse seedlings of *P. palmeri* var. *palmeri* with mycelium from the culture made from conidia of *R. nivosa* produced leaf spots like those seen in the field (Fig. 7) on all fifteen leaves; all control leaves remained free of spots. When moist-incubated these leaf spots supported characteristic sporulation of *R. nivosa* from which a new culture was obtained that was very similar to the culture from conidia from the garden. This appears to be the first successful completion of Koch's Postulates for *R. nivosa*.

This single species of *Ramularia*, *R. nivosa*, and no other, specializes on species of *Penstemon* (Farr et al. n.d.; Savile 1968; Braun 1998). But not all species of *Penstemon* have been recorded as hosts. Braun (1998) does list *P. palmeri* in Utah as a host but does not state which of the two varieties of *P. palmeri* there, var. *palmeri* or var. *eglandulosus* (USDA n.d.), hosted *R. nivosa*. Thus, it is possible that this is the first report of *R. nivosa* on *P. palmeri* var. *palmeri*. But it is equally possible that we are only reporting *R. nivosa* on *P. palmeri* var. *palmeri* for the first time in Idaho, and it is this more cautious alternative that is presented in the Abstract.

The three varieties of *P. palmeri* are all native to the American Southwest, although some introduced populations of *P. palmeri* var. *palmeri* are naturalized in southern Idaho (Cronquist et al. 1984). In 2002, the first author

introduced seedlings into his garden in Moscow which is farther north than the just-mentioned, naturalized populations of southern Idaho. The reason for the introduction was the beauty of the flowers (Fig. 10) and their scent. For three years these plants and their seedlings grew without *Ramularia* leaf spot. For the past five years (including 2009), however, *R. nivosa* has appeared each year in mid-May on new leaves (Fig. 7). *Ramularia* leaf spot appears to be limiting the local naturalization of *P. palmeri* in this garden; plants are short-lived and new seedlings frequently die before flowering.

Oddly, leaf lesions have not been seen in the garden on *P. digitalis*, *P. strictus*, and *P. albertinus*, all of which have been recorded before as hosts of *R. nivosa* (Farr et al. n.d.). *P. davidsonii* var. *menziesii* is also present and unaffected in the garden; however, this species has never been recorded as a host of *R. nivosa*. The source of the initial inoculum is unknown but four species of *Penstemon* grow wild on nearby Moscow Mountain, and three of them have been recorded as hosts of *R. nivosa*: *P. confertus*, *P. fruticosus*, and *P. wilcoxii* (Farr et al. n.d.).

***Albugo candida* (Pers.) Roussel on *Lunaria annua* L. (annual honesty, money plant), Moscow, Latah County, Idaho, 20 August 2008, collector R. Gaylord.**

Sporangia (sporangiospores) (Fig. 11) were subglobose, hyaline, thin-walled, smooth to slightly punctate, 15.5-18 x 13.5-17.5 μm , borne on smooth, hyaline, typically straight sporangiophores, 22-31 x 11-14 μm . Dimensions of sporangia differed slightly from, but were overlapping with, dimensions from Glawe et al. (2004) and Mukerji (1975); sporangiophores from our specimens and those of Glawe et al. (2004) were shorter than those described in Mukerji (1975). Sori were as described and illustrated in Glawe et al. (2004) from disease incidents in Willamette Valley, Oregon, and Seattle and Tacoma, Washington. *Albugo* spp. (Albuginaceae, Peronosporales) are often called

"white rusts" because of the appearance of the sori, which in our instance were conspicuous, often in semi-concentric patterns, becoming quite dense and numerous. Plants with larger numbers of sori were stunted relative to those with fewer sori. The collection is represented by WSP 71638. *Albugo candida* has been recorded on numerous hosts, mostly in the Brassicaceae (Choi et al. 2009; Farr et al. n.d.).

Lunaria annua is not indigenous to North America, but is widely cultivated as an ornamental annual and recognizable by its distinctive, coin-shaped silicles (Hitchcock and Cronquist 1973). It can be weedy in disturbed areas (DiTomaso and Healy 2007), but is also a candidate crop for oilseed (e.g., Walker et al. 2003). *Albugo candida* had not been reported on *L. annua* in North America prior to Glawe et al. (2004), and, to our knowledge, this is the first report of *A. candida* on *L. annua* in Idaho.

***Pucciniastrum pustulatum* Dietel (= *Pucciniastrum epilobii* G.H. Otth) on *Epilobium brachycarpum* C. Presl (= *Epilobium paniculatum* Nutt. ex Torr. & A. Gray, tall annual willowherb, panicle willowweed), University of Idaho Arboretum, Moscow, Latah County, Idaho, 14 July 2008, collector F.M. Dugan.**

Urediniospores (Figs. 12, 13) were somewhat irregularly obovate or oval, with orange-yellow contents; colorless wall ca. 1.5 µm thick, echinulate (spines ca. 0.2 µm tall, separated by ca. 1.5 µm); 17-22.5 x 13-16.5 µm. Uredinia were (Fig. 14) spherical, orange, mostly hypophyllous, ca. (80-)110-240 µm, opening by an apical pore, densely to sparsely distributed, and accompanied by varying degrees of leaf chlorosis, being more intense with greater numbers of uredinia at time of collection. Urediniospores of our specimens were slightly wider and with a slightly larger minimum length than those of Arthur (1962), and closer to dimensions in Ziller (1974). The host, a "ruderal native" that "can be weedy" (DiTomaso and Healy 2007), was identified by the keys in

Hitchcock and Cronquist (1973). The collection is represented by WSP 71639.

The life cycle of the rust, including alternate hosts (*Abies* species) and other host species of *Epilobium*, is discussed in Arthur (1962), Hotson (1934) and Ziller (1974). Ziller referenced the opinions of several prominent uredinologists (J.C. Arthur, G.B. Cummins, Y. Hiratsuka, W. Tranzschel and others) that *P. pustulatum* and *P. epilobii* were conspecific, but accepted D.B.O. Savile's opinion that the species were distinct, with *P. pustulatum* occurring on *Epilobium* species in section *Lysimachion*. *Epilobium brachycarpum* (as *E. paniculatum*) had been traditionally placed in this section (Just 1891; Trelease 1891), although Ziller (1974) did not specify this species in a short list of other species in *Lysimachion*. Faull (1938) failed to obtain infection in cross inoculations when using *Pucciniastrum* isolates from *Epilobium* species then classified in *Lysimachion* or *Chamaenerion*. *Epilobium paniculatum* was later made the type of a new section in *Epilobium*, *Xerolobium* (Raven 1976). Index Fungorum (www.indexfungorum.org) treats *P. pustulatum* and *P. epilobii* as conspecific, and provides additional synonyms. We infer that knowledge of the taxonomy and host ranges of the rusts infecting *Epilobium* spp. is incomplete.

Numerous *Epilobium* spp. are listed as hosts of *P. epilobii* and/or *P. pustulatum* (Farr et al. n.d.). In addition to records from North America, there are numerous reports of *Pucciniastrum pustulatum* on *Abies* spp. and/or *Epilobium* spp. in Eurasia (Azbukina 1974; Kuprevich and Tranzschel 1957). *Pucciniastrum pustulatum* and/or *E. epilobii* are recorded in Idaho from other species of *Epilobium* and from *Abies* spp. (Farr et al. n.d.), but to our knowledge this is the first report for infection of *P. brachycarpum* in Idaho.

***Golovinomyces* sp. on *Verbena bonariensis* L. (purpletop vervain, tall**

vervain), Lawson Gardens, Pullman, Whitman County, Washington, 27 September 2007, 14 October 2008, collector F.M. Dugan. Conidia were hyaline, in chains of up to four, oval to ellipsoid (more rarely cylindrical-ellipsoid), 25-33.5 (-37.5) x 12.5-18 µm, lacking fibrosin bodies, on conidiophores with straight foot-cells generally 39-67 x 10-13 µm and followed by (1-)2-3(-4) shorter cells (Figs. 15-17). Appressoria were papillate (Fig. 18). Conidia germinated sub-apically. Chasmothecia were not seen. Colonies on leaves (primarily abaxial) and stems were spreading, off-white, becoming gray, without any conspicuous chlorosis at the time. The collections are represented by WSP 71640 and 71641.

Verbena bonariensis, a South American plant, is planted in gardens in North America, often escapes into moist habitats, and apparently is expanding in range (DiTomaso and Healy 2007). Powdery mildews on various *Verbena* species are documented in Farr et al. (n.d.), including records of *Erysiphe cichoracearum* auct. on *V. bonariensis* in Australia, and "*Oidium* sp." on numerous *Verbena* spp., including *V. bonariensis* from Argentina, Australia, Brazil and Japan. *Erysiphe cichoracearum* D.C. sensu stricto is presently considered confined to Asteraceae (Braun 1987). Specimens of *E. cichoracearum* on *Verbena* are considered under *Golovinomyces orontii* (Castagne) V.P. Heluta (= *Erysiphe orontii* Castagne) in Braun (1987). Other powdery mildews commonly reported on *Verbena* spp. are now in the genera *Erysiphe* (lacking true conidial chains) or *Podosphaera* (conidia with fibrosin bodies), and hence do not apply to our specimen.

An excellent photograph of symptoms of powdery mildew on *V. bonariensis* is published on line (Pscheidt and Ocamb n.d.), with the suggestion that the fungus is likely *Golovinomyces orontii* or *G. verbenae* (Schwein.) V.P. Heluta, but neither the geographic origin of the specimen nor characters of the powdery mildew were provided.

The dimensions of conidia in our specimen are more congruent with those of *G. verbenae* than with those of *G. orontii* in Braun (1987), wherein both species have *Verbena* listed as a host. GenBank has numerous sequence records for *G. orontii*, but none for *G. verbenae*, and descriptions of the latter that might complement Braun (1987) were not located. We therefore refrain from applying a specific epithet for our specimen, but note that this appears to be the first formal report of any *Golovinomyces* sp. on *Verbena bonariensis* in Washington State.

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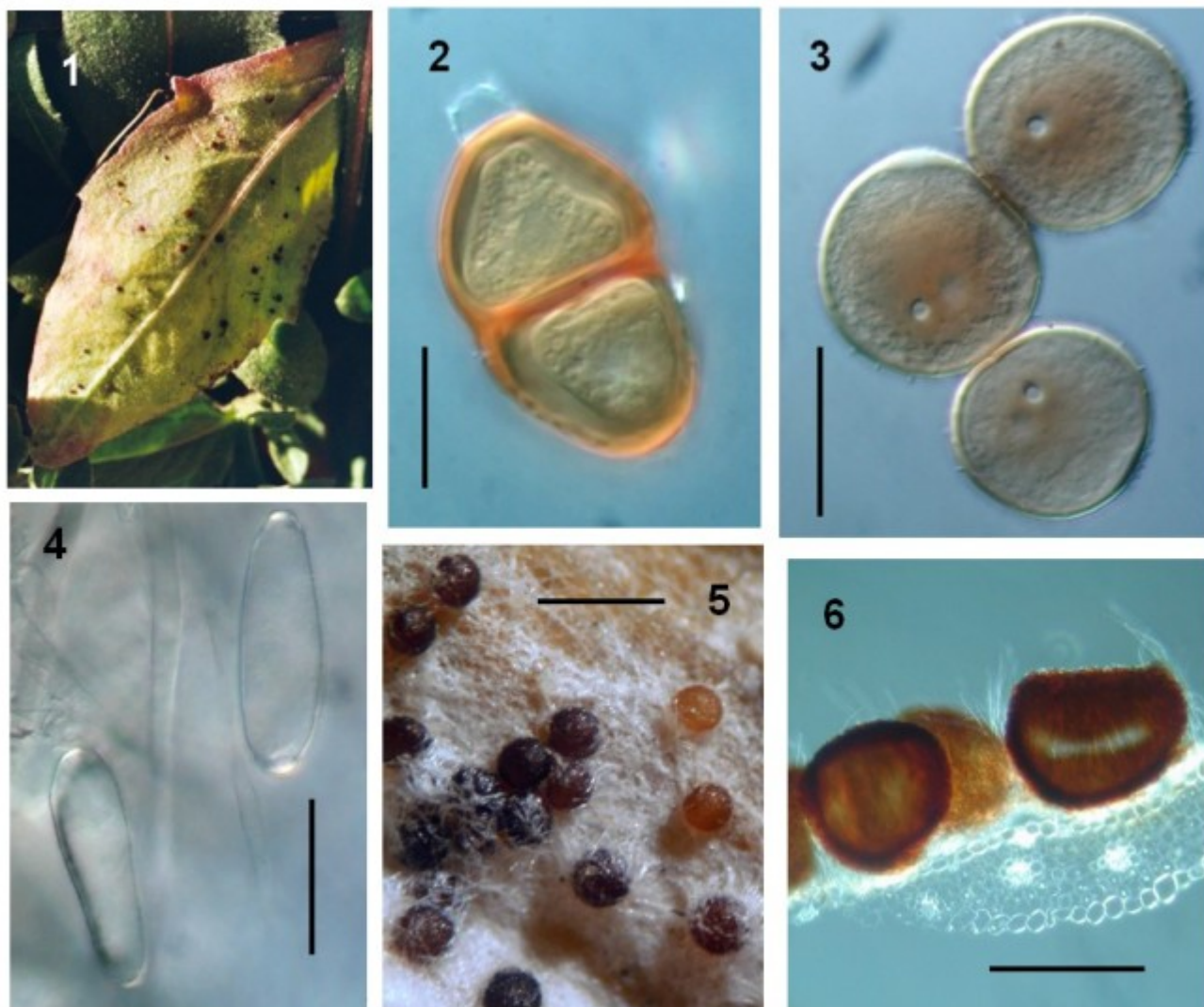
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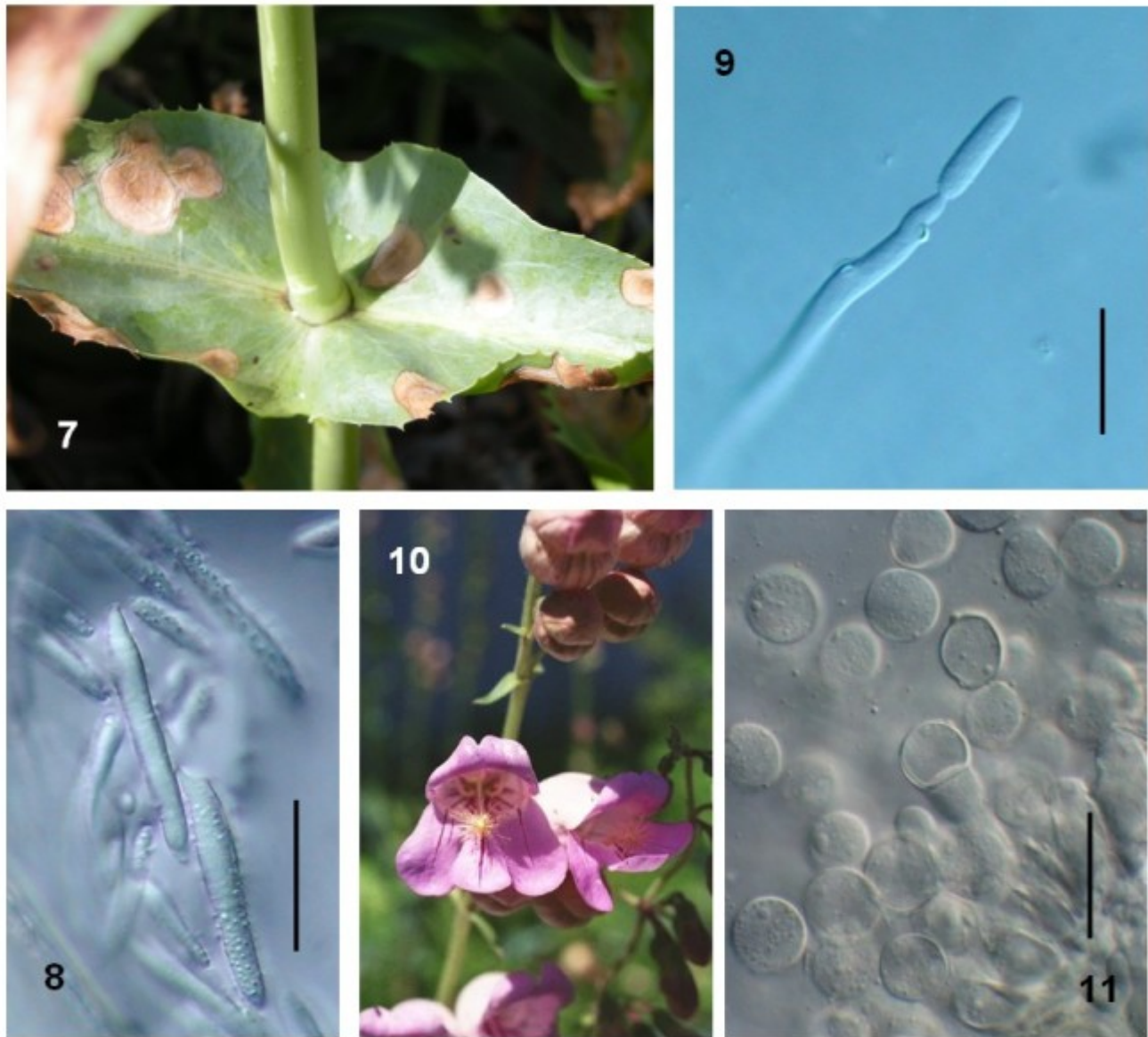
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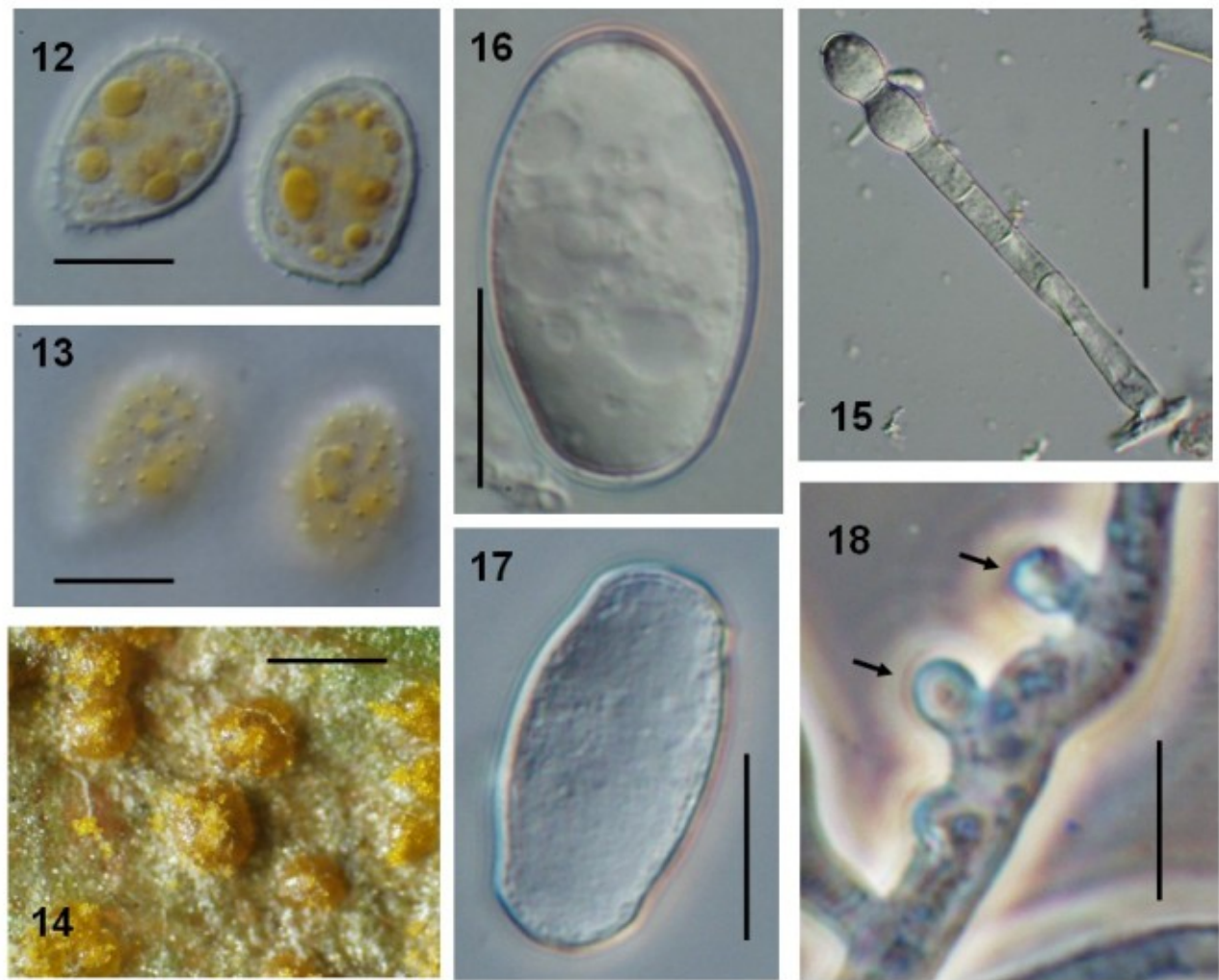
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Figs. 1-6. Fungi on *Centaurea stoebe* or *Poa bulbosa*. Fig. 1. Telia of *Puccinia jaceae* on *Centaurea stoebe*. Fig. 2. Teliospore of *Puccinia jaceae*. Bar = 15 μ m. Fig. 3. Urediniospores of *Puccinia jaceae*. Bar = 25 μ m. Fig. 4. Conidia of *Blumeria graminis*. Bar = 20 μ m. Fig. 5. Chasmothecia of *Blumeria graminis* in varying stages of maturation on *Poa bulbosa* subsp. *vivipara*. Bar = 450 μ m. Fig. 6. Transverse section of chasmothecia of *Blumeria graminis*, including surrounding mycelium and thick-walled setae. Bar = 200 μ m.



Figs. 7-11. Fungi on *Penstemon palmeri* or *Lunaria annua*, and flowers of *P. palmeri*. Fig. 7. Leaf spots induced by *Ramularia nivosa* on *Penstemon palmeri*. Fig. 8. Conidia of *Ramularia nivosa*. Bar = 20 μ m. Fig. 9. Conidiogenesis in *Ramaria nivosa*. Bar = 15 μ m. Fig. 10. *Penstemon palmeri* var. *palmeri* in flower, Moscow, ID. Fig. 11. Sporangia of *Albugo candida* on leaf of *Lunaria annua*. Differential interference contrast. Bar = 30 μ m.



Figs. 12-18. Fungi on *Epilobium brachycarpum* or *Verbena bonariensis*. Figs. 12,13. Urediniospores of *Pucciniastrum pustulatum* from *E. brachycarpum*. Differential interference contrast. Fig. 12. Optical section. Bar = 10 μ m. Fig. 13. Surface view. Bar = 10 μ m. Fig. 14. Uredinia of *Pucciniastrum pustulatum*, showing release of urediniospores from apical pores. Bar = 230 μ m. Fig. 15. Conidia, conidiophore and foot cell of *Golovinomyces* sp. on *Verbena bonariensis*. Differential interference contrast. Bar = 45 μ m. Figs. 16, 17. Conidia of *Golovinomyces* sp. on *Verbena bonariensis*. Differential interference contrast. Fig. 16. Terminal conidium. Bar = 12 μ m. Fig. 17. Intercalary conidium. Bar = 15 μ m. Fig. 18. Appressoria (arrows) of *Golovinomyces* sp. on *Verbena bonariensis*. Phase contrast. Bar = 13 μ m.