

3.3.2 Tribe Erysiphaceae

3.3.2.1 Subtribe Erysiphinae

3.3.2.1.1 *Erysiphe*

Erysiphe DC., Fl. Fr. II, p. 272 (1805)
(:Fr., Syst. myc. 3, p. 234, 1829)
emend. Léveillé (1851)

*Synonyms: *Alphitomorpha* auct. p.p. *Tigra* Trev., Spighe e Fagii, Scr. Bot. varj. 1, p. 22 (1853). *Erysiphella* Peck, 28th Rep. N.Y. Stat. Mus. 2, p. 63 (1874). *Erysiphopsis* Halst., Bull. Torrey bot. Club 26, p. 594 (1899). *Ortochaeta* Sawada, Taiwan Agr. Exp. Stat. 85, p. 22 (1943). *Linkomyces* Golovin (1958, p. 127) nom. nud. *Salmonomyces* Chidd., Sydowia 13, p. 55 (1959). *Ischnochaeta* Sawada, Descr. Cat. Taiwan Fungi XI, p. 16 (1959). *Golovinomyces* (U. Braun) Geljuta, Biol. Ž. Arm. 41(5), p. 357 (1988). *Uncinula* auct. p.p.
*Type species: *Erysiphe polygoni* DC. (selected by Clements & Shear 1931).

Mycelium external, superficial, haustoria in the epidermal cells, appressoria present, unlobed, \pm nipple-shaped to lobed, hyphae ca. 2-12 μ m wide, branched, septate, anamorphic states belonging to *Oidium*, conidiophores arising from the superficial mycelium, erect, conidia in chains or formed singly, shape and size variable, fibrosin bodies absent. Erysiphacean cleistothecia globose to depressed globose, non-dorsiventral, peridium multilayered, coloured, dark, not transparent, appendages usually mycelioid, simple to irregularly branched, rarely setiform, mostly arising from the lower half of the ascocarp, sometimes from base to top, asci numerous, 2-8-spored, spores developed in the current season or after overwintering.

*Notes: *Erysiphe* is usually considered as the most ancient genus of the Erysiphaceae. There are some well-established morphological groups within this genus. Braun (1978, 1981) dealt with this problem, and the following classification was proposed:

(1) *Erysiphe* sect. *Erysiphe*
(type species - *E. polygoni*)

Conidia formed singly (*Pseudoidium* type), appressoria mostly \pm lobed, asci (2-) 3-8-spored.

(a) subsect. *Erysiphe*

Asci (2-) 3-6-spored.

(b) subsect. *Polysporae* U. Braun (1981, p. 693)

Asci 5-8-spored, rarely 5-spored, often 8-spored (type species - *E. ulmariae*).

(2) *Erysiphe* sect. *Golovinomyces* U. Braun (1978, p. 659)

(type species - *E. cichoracearum*)

Conidia in chains (*Euoidium* type), appressoria \pm nipple-shaped, sometimes indistinct, asci 2 (-4)-spored.

(a) subsect. *Golovinomyces*

Foot-cells of the conidiophores cylindrical, straight to curved, mostly shorter than 100 μ m, conidia ellipsoid-ovoid to doliform, without constricted areas.

(b) subsect. *Depressa* U. Braun (1981, p. 695)

Foot-cells of the conidiophores long, often longer than 100 μ m, width increasing from base to top, conidia broad, often with constricted areas at the ends (type species - *E. depressa*).

(3) *Erysiphe* sect. *Galeopsidis* U. Braun (1981, p. 690)

(type species - *E. galeopsidis*)

Conidia in chains (*Euoidium* type), but appressoria lobed, ascospores not developed before overwintering, asci always immature in the current season.

The three sections are well-characterized. Sect. *Galeopsidis* takes an intermediate position between sect. *Erysiphe* and sect. *Golovinomyces*. The asci are (2-) 3-6 (-8)-spored and the appressoria are lobed (agreeing with sect. *Erysiphe*), but the conidia are produced in chains (as in sect. *Golovinomyces*). There are also some additional intermediate species (e.g. *E. galii* var. *galii* in sect. *Golovinomyces* - ascospores only developed after overwintering; some forms of *E. cichoracearum* with moderately lobed appressoria or with

2-4-spored asci; some species in sect. *Erysiphe* with unlobed appressoria). Sawada (1949, 1951, 1959) was the first author to propose the separation between sect. *Erysiphe* and sect. *Golovinomyces* on generic level. He established the genus *Ischnochaeta* for the species with *Pseudoidium* anamorphs. Golovin (1958) introduced a similar proposal. He established the new genus *Linkomyces*. Geljuta (1988) raised *Erysiphe* sect. *Golovinomyces* to generic rank. However, the separation of *Erysiphe* into two distinct genera is not tenable because of the mentioned intermediate species as well as the existence of sect. *Galeopsidis*.

Key to the species

1. Conidia in chains (*Euoidium* type), appressoria usually nipple-shaped, asci 2-spored, very rarely with 3 or 4 spores, ascospores developed before overwintering (sect. *Golovinomyces*). 30

1. Conidia formed singly (*Pseudoidium* type), appressoria usually \pm lobed, asci (2-) 3-8-spored, spores developed before overwintering (sect. *Erysiphe*), or conidia in chains, but appressoria lobed and asci without spores in the current season, spores only developed after overwintering (sect. *Galeopsidis*). 2

2. Conidia formed singly, appressoria lobed, asci with spores before overwintering (sect. *Erysiphe*). 4

2. Conidia in chains, appressoria \pm lobed, asci always without spores before overwintering. 3

3. Appressoria nipple-shaped to slightly lobed, asci of overwintered ascocarps 2-4-spored, mostly 2-spored, on *Galium aparine* and related taxa. (59) *E. galii* var. *galii*

3. Appressoria usually lobed, asci of overwintered ascocarps 2-8-spored, mostly 3-6-spored, on host species of the Lamiaceae. (58) *E. galeopsidis* 4(2). Asci usually 6-8-, frequently 8-spored (subsect. *Polysporae*). 5

4. Asci 2-7-, usually 3-6-spored, occasionally 5-7-spored, but never 8-spored (subsect. *Erysiphe*). 7

5. Cleistothecia large, ca. 120-160 μm diam., appendages 2-5 times as long as the cleistothecial diam., asci 8-15, on *Alnus*. (37) *E. vernalis*

5. Cleistothecia smaller, ca. 75-140 μm diam., on other hosts. 6

6. Appendages very short, mostly shorter than the cleistothecial diam., frequently irregularly branched, peridium dark, on *Cirsium*. (34) *E. mayorii* var. *mayorii*

6. Appendages long and narrow, 0.5-6 times as long as the cleistothecial diam., the asci are easily to be seen within the intact ascocarps, peridium not very dark, on *Filipendula*. (35) *E. ulmariae*

7(4). Infections often confined to stems, cleistothecia large, (100-) 110-185 (-210) μm diam., appendages fairly thick-walled throughout, strongly flexuous, undulate-geniculate, on *Astragalus*. (36) *E. caulicola*

(if ascocarps ca. 110-180 μm diam., appendages narrow, ca. 3.5-8.5 μm wide, \pm thick-walled, strongly undulate-geniculate, on *Hedysarum Anthyllis*, cf. immature samples of *Microsphaera hedysari*)

7. Cleistothecia either smaller and/or appendages thin-walled, not confined to stems. 8

8. Appendages frequently irregularly branched. 9

8. Appendages simple (or only a few appendages rarely irregularly branched). 16

(if appendages attached to the equatorial zone or somewhat in the upper half, septate or aseptate, horizontally spread or with a tendency to turn towards one direction, often somewhat thick-walled at the base, cf. immature samples of *Microsphaera* species - on *Astragalus*, cf. *M. astragali*; on *Vicia*, cf. *M. baeumleri*; on various other legumes, cf. *M. trifolii*; on *Hypericum*, cf. *M. hypericacearum*; on *Cornus*, cf. *M. tortilis*)

9. Ascocarps with 6-16 asci, frequently more than 10, appendages constantly short, mostly about as long as the cleistothecial diam. or shorter, on *Cicerbita*. (34) *E. mayorii* var. *cicerbitae*

9. Ascocarps with fewer asci, usually less than 10, and/or appendages longer. 10

10. Appendages long, 0.5-5 times the cleistothecial diam., conidia \pm cylindric, (25-) 40-55 (-65) \times 14-22 μm , asci (2-) 3-4 (-6)-spored, on *Convolvulus* (= var. *convolvuli*) or asci (3-) 5-6-spored, on *Calystegia* (= var. *calystegiae*). (56) *E. convolvuli*

10. Appendages shorter (and/or conidia smaller). 11

11. Appendages very frequently branched, branchings coral-like, hyaline or only faintly coloured, yellowish, aseptate or few inconspicuous septa, verrucose throughout, on *Paeonia*. (57) *E. paeoniae*

11. Branchings moderate, appendages brown when mature, at least below, with many conspicuous septa. 12

12. Foot-cells of the conidiophores long, sometimes slightly flexuous, (35-) 40-75 (-100) \times 6.5-8.5 (-10) μm , on Caryophyllaceae. (55) *E. buhrlii*

12. Conidiophores shorter, straight, on other hosts. 13

13. Conidia \pm ellipsoid, on hosts of the Fabaceae, especially *Ononis* and *Lathyrus*.
(38) *E. pisi* var. *cruchetiana*
13. Conidia cylindrical, on other hosts. 14
14. Foot-cells of the conidiophores usually followed by 1-2 shorter cells or cells of about the same length, on Polygonaceae. (41) *E. polygoni*
14. Foot-cells frequently followed by a longer second cell and a shorter third cell (dominant arrangement), on other hosts. 15
15. On *Beta* and *Chenopodium* (Chenopodiaceae), branches moderately developed. (52) *E. betae*
15. On Apiaceae, branches strongly developed. (51) *E. heraclei*
- 16(8). Ascocarps small, ca. 60-115 μ m diam., mostly 80-105 μ m in diam., average mostly below 100 μ m. 17
16. Ascocarps larger, ca. 80-150 μ m diam., average larger than 100 μ m. 21
17. Appendages very long, often setiform, ca. 3-12 times as long as the cleistothecial diam., on Ranunculaceae. (47) *E. aquilegiae* var. *aquilegiae*
17. Appendages shorter, ca. 0.25-4 times the cleistothecial diam., mycelioid. 18
18. Appendages brown throughout when mature, on *Circaea* or host species of the Ranunculaceae. 19
18. Appendages coloured in the lower half, yellowish to brown, paler or hyaline in the upper part, on other hosts. 20
19. Foot-cells of the conidiophores frequently curved or flexuous, on *Circaea*. (46) *E. circaeae*
19. Foot-cells straight, erect, not curved, not flexuous, on Ranunculaceae hosts. (47) *E. aquilegiae* var. *ranunculi*
- 20(18). Conidia 32-46 x (13-) 15-20 (-25) μ m, ascospores (18-) 20-30.5 x (8.5-) 11-17 μ m, on Dipsacaceae hosts. (45) *E. knautiae*
20. Conidia and ascospores smaller, on *Geranium*. (49) *E. geraniacearum*
- 21(16). Appendages not very numerous, setiform, stiff and straight, 0.5-1.5 times as long as the cleistothecial diam., aseptate or with few septa, on *Catalpa*. (48) *E. catalpae*
21. Appendages not setiform, but flexuous, mycelioid, usually richly and conspicuously septate. 22
22. Appendages short, 0.5-1.5 times as long as the cleistothecial diam., hyaline or only faintly coloured, on *Limonium* or *Urtica*. 23
22. Appendages longer, 0.5-4 times as long as the cleistothecial diam., often brown, on other hosts. 24
23. Conidia ellipsoid-cylindric, wide, ca. (25-) 30-40 x (12-) 15-20 μ m, on *Urtica*. (50) *E. urticae*
23. Conidia \pm cylindric, narrow, ca. 25-47 x 11-16 (-19) μ m, on *Limonium*. (54) *E. limonii*
- 24(22). Conidia large, \pm cylindric, ca. 35-45 x 13-19 μ m (appendages often irregularly branched), on Polygonaceae. (41) *E. polygoni*
24. Conidia \pm ellipsoid (- ovoid or doliform), and/or appendages simple, on other hosts. 25
25. Ascospores broadly ovoid to subglobose, (18-) 20-26 (-30) x (11-) 12.5-18 (-20) μ m, on *Sedum*. (40) *E. sedi*
25. Ascospores narrower, not subglobose, on other hosts. 26
26. Conidia cylindric (- doliform), (27-) 30-48 (-55) x 12-21 μ m, on hosts of the Capparales (Capparidaceae, Cleomaceae, Brassicaceae, Resedaceae) and Papaverales (Fumariaceae, Papaveraceae). (43) *E. cruciferarum*
26. Conidia \pm ellipsoid (- ovoid, doliform), on other hosts. 27
27. Appendages not very numerous, often only 5-15, fairly long, ca. 1-4 times the cleistothecial diam., asci 3-6-spored, on *Thesium*. (39) *E. thesii*
27. Appendages numerous, and/or appendages shorter, on other hosts. 28
28. Foot-cells of the conidiophores subcylindric or often somewhat decreasing in width from base to top, (15-) 20-50 (-70) x 6-10 μ m, on Fabaceae. (33) *E. pisi* var. *pisi*
28. Foot-cells cylindric, on other hosts. 29
29. Conidia (20-) 30-40 (-45) x (12.5-) 16-22.5 (-25) μ m, on *Anchusa*. (53) *E. lycopsidis*
29. Conidia narrower, ca. 13-17.5 μ m wide, on *Lysitrum*. (42) *E. lythri*
- 30(1). Conidiophores very long, foot-cells or sometimes secondary cells very long, ca. 80-250 μ m, width conspicuously increasing from base to top, conidia large, especially wide, 25-50 (-70) x 18-30 μ m, mostly wider than 20 μ m, lw ratio below 2, broadly ellipsoid-ovoid to doliform, often with somewhat constricted ends, on *Verbascum* or hosts of the Asteraceae (subject. *Depressa*). 31
30. Conidiophores shorter, foot-cells about 40-140 μ m long, mostly 40-80 μ m, cylindric, conidia narrower, ca. 14-22 μ m, rarely wider (subject. *Golovinomyces*). 34
31. Ascocarps ca. 95-150 μ m diam., appendages very short, shorter than the cleistothecial diam., often rudimentary, 3.5-9 μ m wide, hyaline to faintly coloured, on *Verbascum*. (72) *E. verbasci*
31. Cleistothecia often larger, more than 150 μ m diam., or appendages well-developed, wider, brown when mature. 32
32. Cleistothecia 80-145 μ m diam., appendages

well-developed, brown when mature, ascospores 20-32 x 13-20 µm, on *Arctium*, *Centaurea*, *Onopordum*.

(71) *E. depressa*
32. Cleistothecia larger, often more than 150 µm diam., appendages hyaline or faintly coloured, and/or ascospores very large, 24-43 x 16-25 µm. 33

33. Cleistothecia ca. 165-210 µm diam., ascospores 20-23 x 16-18 µm, conidiophores with a long foot-cell, followed by some shorter cells, on *Helichrysum*.

(73) *E. helichrysi*
33. Cleistothecia 120-180 µm diam., ascospores 24-43 x 16-25 µm, one or two short or moderately long basal cells of the conidiophores are followed by a very long cell, on *Echinops*. (70) *E. echinopsis*

34(30). Cleistothecial appendages short, usually shorter than the cleistothecial diam., often rudimentary, narrow, ca. 2.5-8 µm wide, hyaline or only faintly coloured, conidia ellipsoid-ovoid to dolii-form, short and broad, on *Artemisia*, very rarely on *Achillea millefolium*.

(66) *E. artemisiae*
34. Appendages longer, and/or wider, brown when mature, conidia ± ellipsoid, cylindrical (- ovoid), slender. 35

35. Appendages short, 0.25-1.5 times as long as the cleistothecial diam., usually shorter than the cleistothecial diam., on *Hyoscyamus*. (60) *E. hyoscyami*

35. Appendages longer, on other hosts. 36

36. Infections characteristic, dense, white, persistent patches, often confluent, outer peridium cells of the ascocarps large, 10-40 µm diam., on *Phlox* and *Polemonium*.

(61) *E. magnicellulata* var. *magnicellulata*
36. Appearance of the infections different, and/or peridium cells smaller, on other hosts. 37

37. Appendages of mature ascocarp usually obviously verrucose, on *Valeriana*, *Centranthus*.

(69) *E. valerianae*
37. Appendages smooth to faintly rough, on other hosts. 38

38. Conidiophores frequently constricted at the basal septum, mature asci filled with numerous oil drops, on Lamiaceae.

(63) *E. biocellata*
38. Conidiophores usually not constricted at the basal septum, mature asci without numerous oil drops. 39

39. Conidia 28-45 x 18-27 µm, broadly ellipsoid-ovoid to dolii-form, l/w ratio 1.3-2, mostly 1.4-1.6, on *Ambrosia*, *Iva*, *Helianthus*, *Rudbeckia*.

(64) *E. cichoracearum* var. *latispora*
39. Conidia narrower, often slender, l/w ratio around 2 or larger. 40

40. Mycelium usually forming persistent, dense, limited patches, germ tubes of the conidia short,

often twisted, on Boraginaceae. (62) *E. cynoglossi*
40. Appearance of the mycelium different, and/or germ tubes longer, not twisted, on other hosts. 41

41. Foot-cells of the conidiophores frequently curved, on *Plantago* or *Senecio sylvaticus*, *S. viscosus*, *S. vulgaris*, occasionally on other hosts. 42

41. Foot-cells straight, cylindrical. 44

42. Ascocarps large, ca. 120-160 µm diam., on *Senecio*.

(64) *E. cichoracearum* var. *ftscheri*
42. Ascocarps smaller, on other hosts. 43

43. On *Plantago* (Plantaginaceae). (67) *E. sordida*

43. On other hosts, cf. *E. orontii*

44(41). Outer peridium cells of the ascocarps 10-30 (-40) µm diam., appendages sometimes in the upper half of the ascocarp, on *Galium*.

(59) *E. galii* var. *riedliana*
44. Peridial cells ca. 8-25 µm diam., appendages in the lower half, on other hosts. 45

45. Conidiophores erect, conidia in chains, spore units conspicuously swollen, chains often long, appressoria conspicuously nipple-shaped (occasionally slightly lobed), germ tubes moderately long, simple, ascocarps usually developed, asci mostly constantly 2-spored, on various hosts of the Asteraceae.

(64) *E. cichoracearum* var. *cichoracearum*
45. Conidiophores erect, foot-cells straight to curved, conidia in chains, chains mostly short, spore units unswollen, appressoria nipple-shaped, but often poorly developed, germ tubes short, often somewhat twisted, seldom forked, ascocarps rarely developed, asci often 3- or 4-spored, on host plants of various families (also on cultivated species of the Asteraceae, e.g. *Aster*, *Chrysanthemum*, *Dahlia*, *Helianthus*, *Solidago*).

(65) *E. orontii*

(34) *Erysiphe mayorii* Blumer, Beitr. Krypt.-Fl. Schweiz 7(1), p. 174 (1933)

var. *mayorii*

*Synonyms: *E. polygoni* auct. p.p. *E. communis* auct. p.p. *E. communis* f. *cirsii* Antipova, in Vasjagina et al. (1961, p. 231). *Golovinomyces mayorii* (Blumer) Gejjuta, Flora gribov Ukrainy, mučnistorošjanye griby, p. 135, Kiev 1989.

*Illustrations: Salmon (1900, pl. 7, fig. 134), Blumer (1933, p. 176, fig. 54; 1967, p. 211, fig. 67), Vasjagina et al. (1961, p. 233, fig. 79), Sanduville (1967, p. 203, fig. 32), Bunkina (1979, p. 130, fig. 6), Salata (1985, p. 118, fig. 49), Braun