

dular or nonglandular and \pm as long as indusial width.

Spores brown or dark brown. $2n = 80$.

Moist woods, thickets, swamps; 10–2000 m; Ala.,

Ark., Conn., Del., Fla., Ga., Ill., Ind., Kans., Ky., La.,
Md., Mass., Miss., Mo., N.J., N.Y., N.C., Okla., Pa.,
R.I., S.C., Tenn., Tex., Va., W.Va.

6. GYMNOCARPIUM Newman, Phytologist 4: 371. 1851 · Oak fern [Greek *gymnos*, naked, and *karpos*, fruit, referring to the absence of indusia]

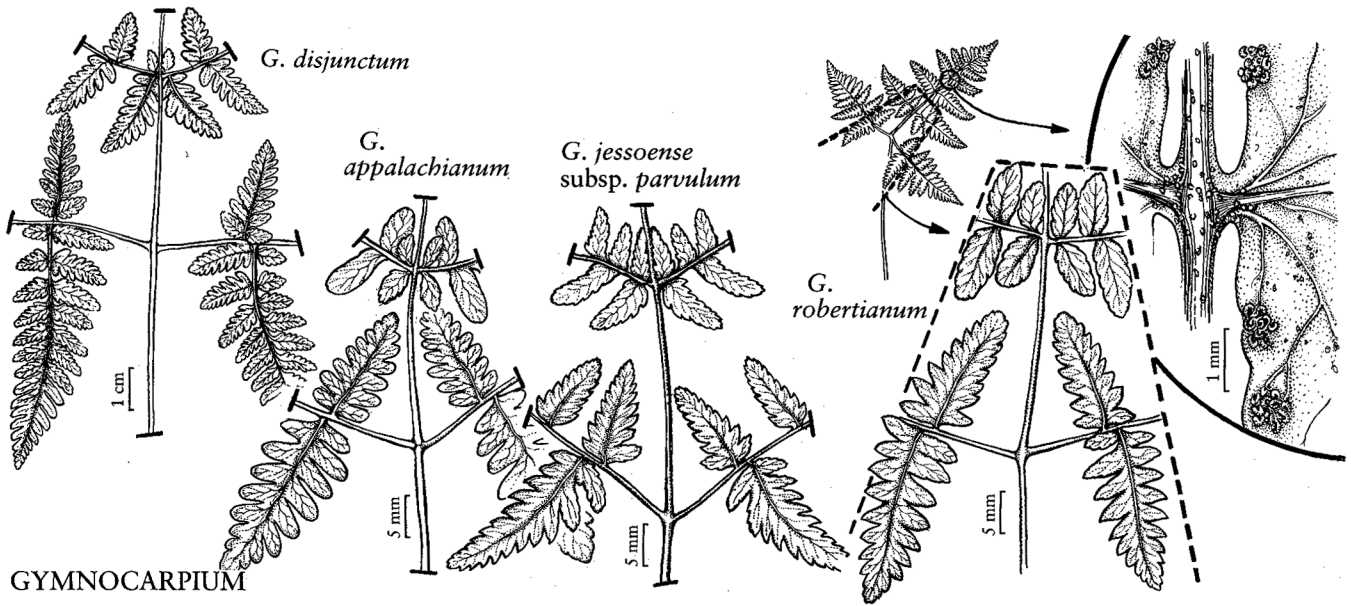
Kathleen M. Pryer

Plants terrestrial. Stems long-creeping, stolons absent. Leaves monomorphic, dying back in winter. Petiole ca. 1.5–3 times length of blade, base not swollen; vascular bundles 2, lateral, \pm oblong in cross section. Blade broadly deltate, ternate, or ovate, 2–3-pinnate-pinnatifid, reduced distally to pinnatifid apex, herbaceous. Pinnae weakly articulate to rachis but persistent, segment margins entire to crenate; proximal pinnae longest, petiolulate, usually \pm inequilateral with pinnules on basisopic side longer than those on acroscopic side; costae adaxially grooved, grooves not continuous from rachis to costae; indument lacking or of minute (0.1 mm) glands abaxially and sometimes along costae adaxially. Veins free, simple or forked. Sori in 1 row between midrib and margin, \pm round; indusia absent. Spores brownish, rugose. $x = 40$.

Species 8 (5 in the flora): north temperate regions, North America, Eurasia.

SELECTED REFERENCES Pryer, K. M. 1992. The status of *Gymnocarpium heterosporum* and *G. robertianum* in Pennsylvania. Amer. Fern J. 82: 34–39. Pryer, K. M. and D. M. Britton. 1983. Spore studies in the genus *Gymnocarpium*. Canad. J. Bot. 61: 377–388. Pryer, K. M., D. M. Britton, and J. McNeill. 1983. A numerical analysis of chromatographic profiles in North American taxa of the fern genus *Gymnocarpium*. Canad. J. Bot. 61: 2592–2602. Pryer, K. M. and C. H. Haufler. 1993. Isozymic and chromosomal evidence for the allotetraploid origin of *Gymnocarpium dryopteris* (Dryopteridaceae). Syst. Bot. 18: 150–172. Sarvela, J. 1978. A synopsis of the fern genus *Gymnocarpium*. Ann. Bot. Fenn. 15: 101–106. Sarvela, J., D. M. Britton, and K. M. Pryer. 1981. Studies on the *Gymnocarpium robertianum* complex in North America. Rhodora 83: 421–431. Wagner, W. H. Jr. 1966b. New data on North American oak ferns, *Gymnocarpium*. Rhodora 68: 121–138.

1. Adaxial blade surface glabrous or moderately glandular, abaxial blade surface and rachis moderately or densely glandular.
 2. Blades glabrous on adaxial surface; proximal pinnae and basisopic pinnules of proximal pinnae curving toward apex of leaf and apex of pinna, respectively; pinnae of 2d pair almost always sessile with basal pinnules \pm equal in length to adjacent pinnules. 4a. *Gymnocarpium jessoense* subsp. *parvulum*
 2. Blades moderately glandular on adaxial surface; proximal pinnae and basisopic pinnules of proximal pinnae \pm perpendicular to rachis and costa, respectively; pinnae of 2d pair usually stalked, or if sessile with basal pinnules shorter than adjacent pinnules. 5. *Gymnocarpium robertianum*
1. Adaxial and abaxial blade surfaces and rachis essentially glabrous.
 3. Pinnae of 2d pair and basal basisopic pinnule of proximal pinnae stalked. 1. *Gymnocarpium appalachianum*
 3. Pinnae of 2d pair sessile or rarely stalked; basal basisopic pinnule of proximal pinnae sessile.
 4. Pinnae of 2d pair sessile with basal pinnules unequal in length (basisopic markedly longer); ultimate segments of proximal pinnae slightly lobed to crenate, apex often crenulate, acute; blades 8–24 cm. 2. *Gymnocarpium disjunctum*
 4. Pinnae of 2d pair rarely stalked, if sessile with basal pinnules \pm equal in length (basisopic = acroscopic); ultimate segments of proximal pinnae crenate to entire, apex entire, rounded; blades 3–14 cm.



- 5. Sessile basal basiscopic pinnule of proximal pinnae with basal basiscopic pinnulet (division of pinnule) \pm equal in length to adjacent pinnulet; pinnae of 2d pair usually sessile, with basal pinnules \pm equal in length to adjacent basal pinnule; spores 34–39 μm 3. *Gymnocarpium dryopteris*
- 5. Sessile basal basiscopic pinnule of proximal pinnae with basal basiscopic pinnulet shorter than adjacent pinnule; pinnae of 2d pair sessile, with basal pinnules shorter than adjacent pinnule, or 2d basal pinnae rarely stalked; spores 27–31 μm 1. *Gymnocarpium appalachianum*

1. *Gymnocarpium appalachianum* Pryer & Haufler,
Syst. Bot. 18: 161. 1993 · Appalachian oak fern



Stems 0.5–1.5 mm diam.; scales 1.5–3 mm. **Fertile leaves** usually 10–32 cm. **Petiole** 6–20 cm, with sparse glandular hairs distally; scales 2–5 mm. **Blade** broadly deltate, 2–3-pinnate-pinnatifid, 4–12 cm, lax and delicate, abaxial surface and rachis glabrous or with occasional glandular hairs, adaxial surface glabrous. **Pinna apex** entire, rounded. **Proximal pinnae** 3–10 cm, \pm perpendicular to rachis, with basiscopic pinnules \pm perpendicular to costa; basal basiscopic pinnules stalked or sessile, pinnate-pinnatifid or pinnatifid, if sessile then with basal basiscopic pinnulet (division of pinnule) always shorter than adjacent pinnulet; 2d basal basiscopic pinnule infrequently stalked, if sessile then with basal basiscopic pinnulet shorter than adjacent pinnulet; basal acroscopic pin-

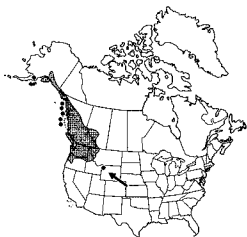
nule occasionally stalked, if sessile then with basal basiscopic pinnulet shorter than adjacent pinnule. **Pinnae of 2d pair** usually stalked, if sessile then with basal basiscopic pinnule shorter than adjacent pinnule and equaling basal acroscopic pinnule; basal acroscopic pinnule shorter than adjacent pinnule, often with entire, rounded apex. **Pinnae of 3d pair** usually sessile with basal basiscopic pinnule shorter than adjacent pinnule and equaling or shorter than basal acroscopic pinnule; basal acroscopic pinnule equaling or shorter than adjacent pinnule. **Ultimate segments** of proximal pinnae oblong, entire to crenate, apex entire, rounded. Spores 27–31 μm . $2n = 80$.

Maple-birch-hemlock (*Acer-Betula-Tsuga*) woods on mountain slopes and summits, on moist sandstone or talus slopes with cold air seepage (algific); of conservation concern; 200–1400 m; N.C., Ohio, Pa., Va., W.Va.

Gymnocarpium appalachianum, restricted to the Appalachian region, is a very local endemic.

2. *Gymnocarpium disjunctum* (Ruprecht) Ching, Acta Phytotax. Sin. 10: 304. 1965 · Western oak fern

Polypodium dryopteris Linnaeus var. *disjunctum* Ruprecht, Distr. Crypt. Vasc. Ross., 52. 1845; *Dryopteris disjuncta* (Ruprecht) C. V. Morton; *Gymnocarpium dryopteris* (Linnaeus) Newman subsp. *disjunctum* (Ruprecht) Sarvela; *G. dryopteris* var. *disjunctum* (Ruprecht) Ching



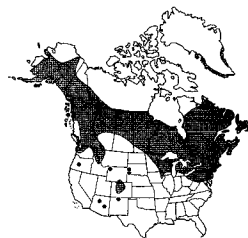
Stems 1–3 mm diam.; scales 2–4 mm. Fertile leaves usually 20–68 cm. Petiole 12–44 cm with sparse glandular hairs distally; scales 2–6 mm. Blade broadly deltate, 3-pinnate-pinnatifid, 8–24 cm, lax and delicate, abaxial surface and rachis glabrous or with sparse glandular hairs, adaxial surface glabrous. Pinna apex acuminate. Proximal pinnae 5–18 cm, ± perpendicular to rachis, with basiscopic pinnules ± perpendicular to costa; basal basiscopic pinnule sessile, pinnate-pinnatifid (with basal pinnulets, and sometimes 2 adjacent pinnulets, separate), basal basiscopic pinnule usually longer (sometimes equaling or shorter) than adjacent pinnule; 2d basal basiscopic pinnule sessile with basal basiscopic pinnule usually longer than or equaling adjacent pinnule; basal acroscopic pinnule sessile, with basal basiscopic pinnule usually longer than or equaling adjacent pinnule. Pinnae of 2d pair usually sessile with basal basiscopic pinnule longer than or equaling adjacent pinnule and markedly longer than basal acroscopic pinnule; basal acroscopic pinnule distinctly shorter than adjacent pinnule or rarely absent, apex often crenulate, obtuse. Pinnae of 3d pair usually sessile with basal basiscopic pinnule longer than or equaling adjacent pinnule and longer than basal acroscopic pinnule; basal acroscopic pinnule shorter than adjacent pinnule. Ultimate segments of proximal pinnae oblong, crenate to slightly lobed, apex crenulate, acute. Spores 27–31 μm . $2n = 80$.

Shaded, rocky slopes and ravines, mixed coniferous woods, moist stream and creek banks; of conservation concern; 0–2400 m; Alta., B.C.; Alaska, Idaho, Mont., Oreg., Wash., Wyo.; Asia in ne former Soviet republics.

In addition to the west coast of North America, *Gymnocarpium disjunctum* is found on Sakhalin Island in southern Kamchatka, in the former Soviet republics.

3. *Gymnocarpium dryopteris* (Linnaeus) Newman, Phytologist 4: app. 24. 1851 · Common oak fern, fougère-du-chêne

Polypodium dryopteris Linnaeus, Sp. Pl. 2: 1093. 1753; *Dryopteris linnaeana* C. Christensen; *Lastrea dryopteris* (Linnaeus) Bory; *Phegopteris dryopteris* (Linnaeus) Fée; *Thelypteris dryopteris* (Linnaeus) Slosson



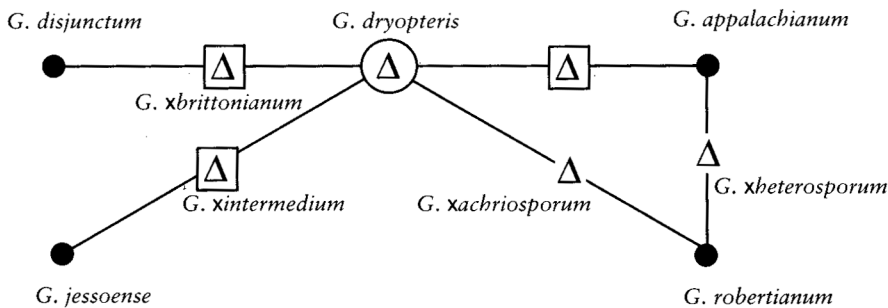
Stems 0.5–1.5 mm diam.; scales 1–4 mm. Fertile leaves usually

12–42 cm. Petiole 9–28 cm, with sparse glandular hairs distally; scales 2–6 mm. Blade broadly deltate, 2-pinnate-pinnatifid, 3–14 cm, lax and delicate, abaxial surface and rachis glabrous or with sparse glandular hairs, adaxial surface glabrous. Pinna apex entire, rounded. Proximal pinnae 2–12 cm, ± perpendicular to rachis, with basiscopic pinnules ± perpendicular to costa; basal basiscopic pinnule usually sessile, pinnatifid or rarely pinnate-pinnatifid, if sessile then with basal basiscopic pinnule often equaling or longer than adjacent pinnule; 2d basal basiscopic pinnule sessile, with basal basiscopic pinnule equaling or longer than adjacent pinnule; basal acroscopic pinnule sessile, with basal basiscopic pinnule longer than or equaling adjacent pinnule. Pinnae of 2d pair usually sessile with basal basiscopic pinnule longer than or equaling adjacent pinnule and about equal to basal acroscopic pinnule; basal acroscopic pinnule equaling or slightly shorter than adjacent pinnule, often with entire, rounded apex. Pinnae of 3d pair sessile with basal basiscopic pinnule equaling adjacent pinnule and equaling basal acroscopic pinnules; basal acroscopic pinnule equaling or slightly shorter than adjacent pinnule. Ultimate segments of proximal pinnae oblong, entire to crenate, apex entire, rounded. Spores 34–39 μm . $2n = 160$.

Cool, coniferous and mixed woods and at base of shale talus slopes; 0–3000 m; Greenland; St. Pierre and Miquelon; Alta., B.C., Man., N.B., Nfld., N.W.T., N.S., Ont., P.E.I., Que., Sask., Yukon; Alaska, Ariz., Colo., Conn., Idaho, Iowa, Maine, Mass., Mich., Minn., Mont., N.H., N.J., N.Mex., N.Y., Ohio, Oreg., Pa., R.I., S.Dak., Vt., Wash., W.Va., Wis., Wyo.; n,c Europe; n Asia to China, Japan.

Gymnocarpium dryopteris is a fertile allotetraploid species that arose following hybridization between *G. appalachianum* and *G. disjunctum* (see reticulogram). Its wide distribution over much of the north temperate zone has provided ample opportunity for secondary contact between *G. dryopteris* and each of its diploid parents, thereby resulting in a wide-ranging composite of abortive-spored triploid crosses (*G. disjunctum* ×

Gymnocarpium



Relationships in *Gymnocarpium*. Solid circles represent parental taxa; circled triangle represents an allopolyploid; boxed triangles represent hybrids presumed to be apogamous; and triangles represent other sterile hybrids.

G. dryopteris and *G. appalachianum* × *G. dryopteris*. These relationships are shown on the diagram. Sterile triploid plants are not restricted only to areas where the range of the tetraploid overlaps with that of either diploid. Their broad distribution could be explained in part by their spores, which are of two types: malformed, black, and with very exaggerated perispores, or round with extensive netted perispores (K. M. Pryer and D. M. Britton 1983). The latter spore type is capable of germination and presumably permits the plants to reproduce apogamously. The name *G. ×brittonianum* (Sarvela) Pryer & Haufler has been applied to the *G. disjunctum* × *G. dryopteris* hybrid formula (K. M. Pryer and C. H. Haufler 1993). The type of *G. ×brittonianum* has aborted and round spores, and leaves that strongly resemble those of *G. disjunctum*. They are large, 3-pinnate-pinnatifid, and the second and third pairs of pinnae are sessile with basal basispic pinnules markedly longer than the basal acroscopic pinnules. Sterile triploid plants with a morphology similar to the type of *G. ×brittonianum* are frequent. The biology of both of these cryptic hybrid taxa needs further study, which should lead to detailed morphologic descriptions and distribution maps.

Gymnocarpium dryopteris also hybridizes with both *G. jessoense* subsp. *parvulum* and *G. robertianum*.

4. *Gymnocarpium jessoense* (Koidzumi) Koidzumi, Acta Phytotax. Geobot. 5: 40. 1936

Dryopteris jessoensis Koidzumi, Bot. Mag. (Tokyo) 38: 104. 1924; *Aspidium dryopteris* (Linnaeus) Baumgarten var. *longulum* H. Christ; *Gymnocarpium longulum* (H. Christ) Ki-

tagawa; *G. robertianum* (Hoffman) Newman subsp. *longulum* (H. Christ) Toyokuni
Subspecies 2 (1 in the flora): North America, Asia.

4a. *Gymnocarpium jessoense* (Koidzumi) Koidzumi subsp. *parvulum* Sarvela, Ann. Bot. Fenn. 15: 103. 1978 · Nahanni oak fern



Gymnocarpium continentale (Petrov) Pojark

Stems 0.5–1.5 mm diam.; scales 1–4 mm. Fertile leaves usually 8–39 cm. Petiole 5–25 cm, with moderately abundant glandular hairs distally; scales 2–6 mm. Blade narrowly deltate to narrowly ovate, 2-pinnate-pinnatifid, 3–14 cm, firm and robust or lax and delicate, abaxial surface moderately glandular, rachis moderately to densely glandular, adaxial surface glabrous. Pinna apex acute. Proximal pinnae 2–9 cm, strongly curved toward apex of leaf, basispic pinnules strongly curved toward apex of pinna; basal basispic pinnule usually sessile, pinnatifid or rarely pinnate-pinnatifid, if sessile then with basal basispic pinnulet often equaling adjacent pinnulet; 2d basal basispic pinnule sessile, with basal basispic pinnulet equaling adjacent pinnulet; basal acroscopic pinnule sessile with basal basispic pinnulet longer than or equaling adjacent pinnulet. Pinnae of 2d pair almost always sessile with basal basispic pinnule usually equaling or slightly shorter than adjacent pinnule and equaling basal acroscopic pinnule; basal acroscopic pinnule equaling or slightly shorter than ad-

adjacent pinnule, apex often entire, rounded. **Pinnae of 3d pair** sessile with basal basiscopic pinnule equaling adjacent pinnule and equaling basal acroscopic pinnule; basal acroscopic pinnule equaling or slightly shorter than adjacent pinnule. **Ultimate segments** of proximal pinnae oblong, entire to slightly crenate, apex entire, rounded. **Spores** 32–37 μm . $2n = 160$.

Acid or neutral substrates at summit of cool, shale talus slopes, and on granitic cliffs and outcrops; 0–2000 m; Alta., B.C., Man., N.B., N.W.T., Ont., Que., Sask., Yukon; Alaska, Conn., Iowa, Mich., Minn., Vt., Wis.; Europe in Finland; Asia in Siberia, Kazakhstan.

Hybrids between *Gymnocarpium jessoense* subsp. *parvulum* and *G. dryopteris* (*G. × intermedium* Sarvela) are usually found wherever these two taxa occur together (Finland; Manitoba, Northwest Territories, Ontario, Quebec, Saskatchewan, Yukon; Alaska, Michigan, Minnesota, Wisconsin), and they are particularly abundant in the Great Lakes region. These hybrids have sometimes been referred to as *G. × heterosporum*, a name that is, however, correctly restricted to unique hybrids between *G. robertianum* and *G. appalachianum* (see discussion under *G. robertianum*; K. M. Pryer 1992). *Gymnocarpium × intermedium* is intermediate between the two parental species in its leaf morphology and glandularity, and it can be readily distinguished by its small, blackish, malformed, abortive spores, as well as large, brown, round spores that may allow this taxon to reproduce apogamously. Of the *Gymnocarpium* sterile hybrids, *G. × intermedium* is the easiest to distinguish morphologically.

5. ***Gymnocarpium robertianum*** (Hoffmann) Newman,
Phytologist 4: app. 24. 1851 · Limestone oak fern,
gymnocarpe du Robert



Polypodium robertianum
Hoffmann, Deutschl. Fl. 2: add. et
emend. 10. 1795; *Dryopteris*
robertiana (Hoffmann)
C. Christensen; *Phegopteris*
robertianum (Hoffmann) Fée;
Thelypteris robertiana (Hoffmann)
Slosson

Stems 1–2 mm diam.; scales 2–
4 mm. **Fertile leaves** usually 10–52 cm. **Petiole** 5–33

cm, with numerous glandular hairs distally; scales 2–6 mm. **Blade** broadly deltate, 2–3-pinnate-pinnatifid, 5–19 cm, usually firm and robust, abaxial surface moderately to densely glandular, rachis densely glandular, adaxial surface moderately glandular. **Pinna apex** acute. **Proximal pinnae** 3–13 cm, \pm perpendicular to rachis, basiscopic pinnules \pm perpendicular to costa; basal basiscopic pinnules either sessile or stalked, pinnate-pinnatifid or pinnatifid, if sessile then with basal basiscopic pinnulet usually shorter than adjacent pinnulet; 2d basal basiscopic pinnule sometimes stalked, if sessile then with basal basiscopic pinnulet shorter than or equaling adjacent pinnulet; basal acroscopic pinnule sometimes stalked, if sessile then with basal basiscopic pinnulet shorter than or equaling adjacent pinnulet. **Pinnae of 2d pair** usually stalked, if sessile then with basal basiscopic pinnule usually shorter than adjacent pinnule and equaling basal acroscopic pinnule; basal acroscopic pinnule shorter than adjacent pinnule, apex often entire, rounded. **Pinnae of 3d pair** usually sessile with basal basiscopic pinnule shorter than adjacent pinnule and equaling basal acroscopic pinnule; basal acroscopic pinnule equaling or shorter than adjacent pinnule. **Ultimate segments** of proximal pinnae oblong, entire to slightly crenate, apex entire, rounded. **Spores** 34–39 μm . $2n = 160$.

Calcareous substrates; limestone pavement, outcrops, and cliffs; *Thuja* swamps; 0–1000 m; Man., N.B., Nfld., Ont., Que.; Iowa, Mich., Minn., Wis.; Europe; Asia in Caucasus Mountains.

Gymnocarpium robertianum occurs in numerous localities in eastern Canada, especially in Ontario and Quebec where it is widely distributed; populations are small. Hybrids with *G. robertianum* are extremely rare. *Gymnocarpium × heterosporum* W. H. Wagner, a putative triploid hybrid between *G. robertianum* and *G. appalachianum*, is known only from one county in Pennsylvania (plants now extirpated, K. M. Pryer 1992). *Gymnocarpium × achriosporum* Sarvela, a putative tetraploid hybrid between *G. robertianum* and *G. dryopteris*, is known only from Sweden and two localities in Quebec. Both hybrids resemble *G. robertianum* in their leaf morphology and dense glandularity but have black, malformed spores.