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EVIDENCE FOR THE HYBRID ORIGIN OF DROSER A ANGLICA

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AMPHIPLOIDY as a mechanism whereby new species of plants come suddenly into being has been demonstrated in a number of groups of plants and new examples continue to come to light. These include both artificial species unknown in nature and an increasing number of wild and cultivated species for which an origin in the past by hybridization followed by polyploidy has been either proved or postulated. (See Stebbins, 1950, Chap. 8.) That this process continues to operate in nature has been shown by three wild species which are known to have originated by amphiploidy within historic time (*Spartina Townsendii*, *Tragopogon mirus* and *T. miscellus*). From the nature of amphiploidy it would be expected that such species might spring into existence more or less simultaneously at two or more different points, thus being polytopic in origin. This indeed appears to be the situation with *Tragopogon mirus*, for which Ownbey (1950) and Ownbey & McCollum (1954) have presented evidence of independent origin at three separate localities. Similarly, an independent origin presumably is true for each of five colonies of *T. miscellus* reported by the same authors. It may also be expected that a widespread and successful species of amphiploid origin might be synthesized again and again in the course of time as long as the diploid ancestors continue in existence and hybrids between them are genetically and ecologically possible. Ordinarily, it would be difficult to detect such an event occurring under natural conditions unless the diploids and the original amphiploid occupy different areas

at the time of resynthesis, thus making it possible to distinguish the new amphiploid from the old. It is with such an event, however, that this report is concerned: the finding of sterile hybrids between two diploid sundews, *Drosera linearis* and *D. rotundifolia*, and the chance finding of a small colony of a fertile hybrid of the same parentage which, from all of the evidence available, appears to be a spontaneous resynthesis of the circumpolar *Drosera anglica*, the only known tetraploid of this genus in the northern hemisphere.

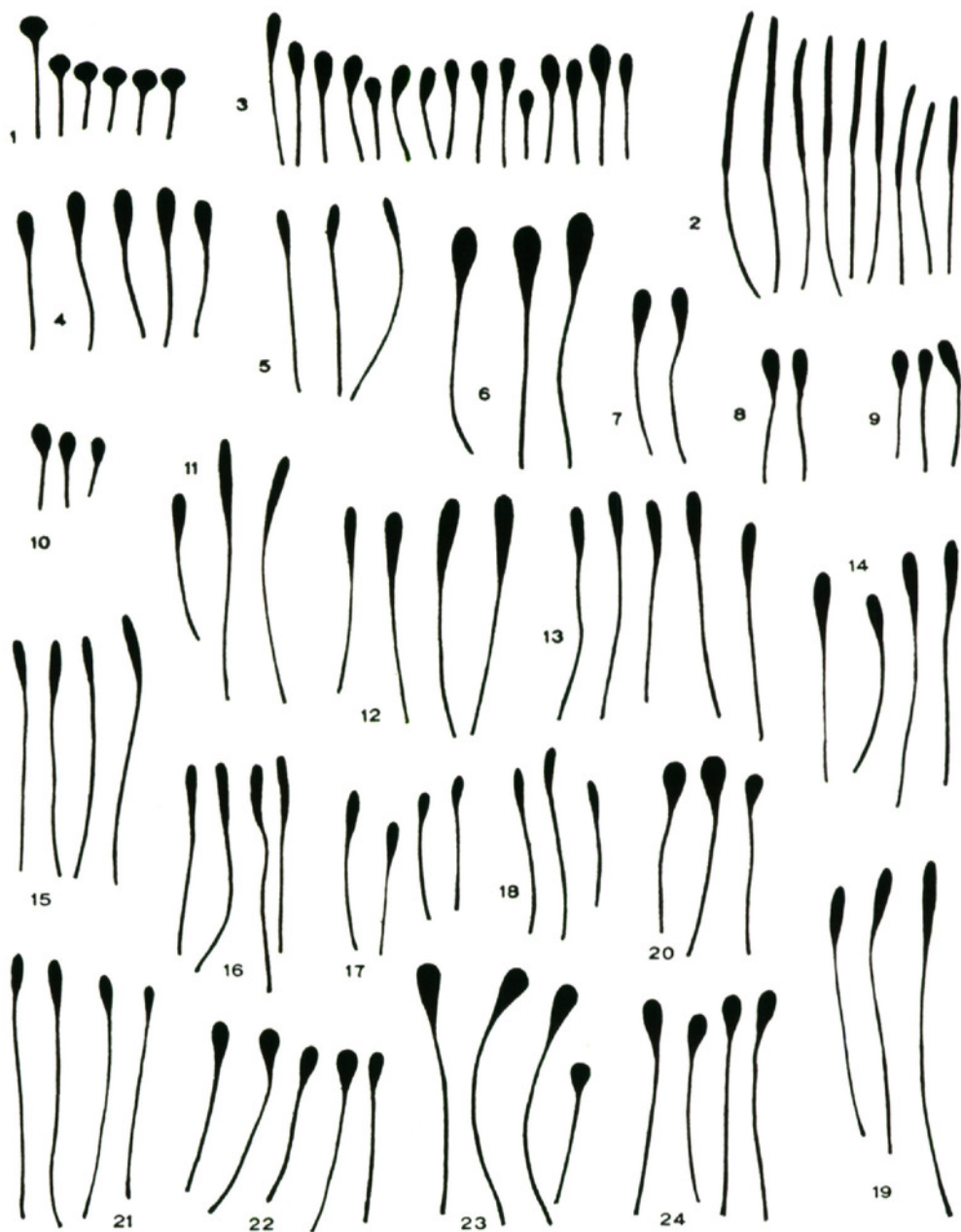
It may be remarked both for the historical interest attached and for its bearing upon the origin of *Drosera anglica* that a hybrid origin for this species was suggested by Winge (1917) in the classical paper in which he proposed the origin of polyploid series of species by hybridization followed by chromosomal doubling. As Stebbins (1950) has pointed out, he apparently was at the time unaware of Digby's work (1912) on *Primula kewensis*, the only concrete supporting example. Winge cited, however, the equally classical work of Rosenberg (1904, 1909) on a triploid hybrid in *Drosera* which had focused attention on polyploidy and on chromosomal behavior in hybrids.

Rosenberg reported that in *Drosera rotundifolia*, with 10 pairs of chromosomes, and *Drosera anglica*, with 20 pairs of chromosomes, meiosis is normal with the chromosomes pairing and disjoining regularly. However, in *D. × obovata*, the hybrid between them, he found that the 30 chromosomes formed 10 bivalents which disjoined normally while the remaining 10 chromosomes remained unpaired and were distributed irregularly. The interpretation suggested was that the 10 chromosomes from *D. rotundifolia* paired with 10 of those from *D. anglica*, the other 10 having no homologues and remaining unpaired. (Shimamura later [1941] reported identical behavior in Japanese material of these three plants.) Recounting these and other observations of Rosenberg, Winge wrote (p. 244): "I could therefore imagine that *D. longifolia* [*D. anglica*] was produced by hybridization between two species or forms with $x = 10$, the chromosomes of which had become added together in the zygote, and then suffered division. On further crossing with *D. rotundifolia* only half would then be capable of conjugation with those of the latter."

Although it now appears that *Drosera anglica* is indeed an amphiploid of which *D. rotundifolia* is one of the progenitors, it has been pointed out by various authors (e.g., Sharp, 1934; Darlington, 1937; Dobzhansky, 1941) that in this particular example Rosenberg's interpretation of chromosomal behavior is open to doubt, it being impossible to determine whether this is a case of allosyndesis, as suggested, with pairing only between "rotundifolia" and "anglica" chromosomes or whether the 20 "anglica" chromosomes are forming 10 pairs with each other or whether some intermediate degree of autosyndesis is present with some "rotundifolia" chromosomes and some "anglica" chromosomes pairing with other members of their own sets. On the basis of the behavior of the chromosomes in the sterile *D. linearis* \times *D. rotundifolia* I should also wish to re-examine this interpretation, as well as to question the regular formation of 20 bivalents in *D. anglica*. It is to be noted, however, that Winge's suggestion based on Rosenberg's interpretation fits in with all of the other evidence which suggests a hybrid origin for *Drosera anglica*.

A STERILE DIPLOID HYBRID

In August, 1951, during the course of a field trip from the University of Michigan Biological Station to beach pools along the shore of Lake Huron at Hammond Bay, Presque Isle County, near the tip of the southern peninsula of Michigan, a clump of a *Drosera* with obovate-spatulate leaves was collected by Mr. Clare B. Kenaga from the midst of a large colony of *Drosera linearis*. In leaf-shape this plant resembled *Drosera intermedia*, a widespread species of wet and very acid habitats, but the leaves were much larger, the color a yellowish green with bright red tentacles, in contrast to the rather dull, dark red of *D. intermedia* in northern Michigan, and the plants were quite sterile, the ovaries containing only aborted ovules. The sterility of the plants, the leaf shape, and the occurrence of *D. linearis* in the pools and *D. rotundifolia* on hummocks nearby suggested, instead, a hybrid between these two species. Two summers later when I was again at the Biological Station, I had the opportunity of revisiting Hammond Bay and of studying other areas along the northern shores of the southern peninsula of



FIGURES 1-24. Leaves of *Drosera*. Tracings from herbarium specimens, tentacles and leaf-bases omitted. $\times \frac{1}{3}$. 1. *Drosera rotundifolia*, Hammond Bay, Mich., Wood 8236, et al. (GH). 2. *D. linearis*, Hammond Bay, Mich., Wood 8075, 8316 (GH). 3. Sterile hybrid (*D. linearis* \times *D. rotundifolia*), Hammond Bay, Mich., Wood 8315, Wood 8327, et al. (GH). 4. Sterile hybrid, Lake Orion, Mich., Sutton 440 (MICH). 5. Sterile hybrid, Raspberry Island, Isle Royale, Mich., McFarlin 2238 (MICH). 6. Sterile hybrid, Lake Orion, Mich., Billington 66 (MICH). 7. Sterile hybrid, Lake Orion, Mich., Billington 66 (NY). 8. Sterile hybrid, Emmet Co., Mich., Wood 8122 (GH). 9. Sterile hybrid, Presque Isle, Mich., Wood 8307 & McVaugh (GH). 10. Fertile hybrid (*D. linearis* \times *D. rotundifolia* Amphiploid), Presque Isle, Mich., Wood 8308 & McVaugh (GH). 11. *D. anglica*, Keeweenaw Co., Mich., Hermann 8208 (NY). 12. *D. anglica*, Ireland, Prager, 1896 (GH). 13. *D. anglica*, Gaspé Co., Quebec, Collins, Fernald & Pease (*Pl. Exsic. Gray*, 218) (NY). 14. *D. anglica*, Sweden, H. Svenonius, 1932 (NY). 15. *D. anglica*, Japan, Uno 21043 (GH). 16. *D. anglica*, Marquette Co., Mich., Dachnowski, 1906 (MICH). 17. *D. anglica*, Glacier Park,

Michigan. The sterile plants are of sporadic occurrence around the northern Great Lakes in company with *Drosera linearis* and *D. rotundifolia* and are indeed hybrids between these two species.

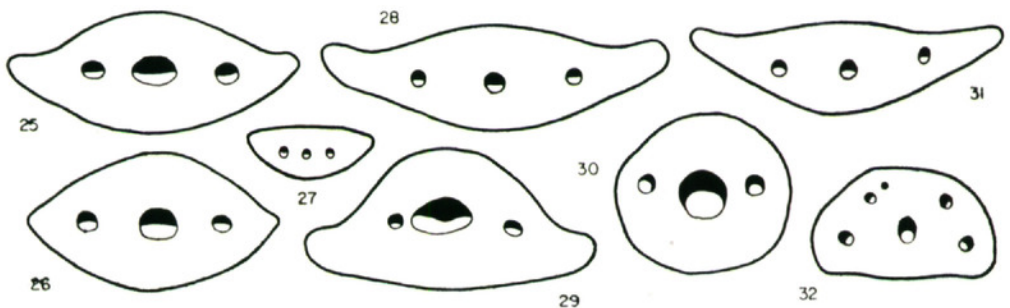
MORPHOLOGY. The parental species, the common and widespread *Drosera rotundifolia*¹ and the sometimes abundant but very much more local *Drosera linearis*, differ from one another

D. ROTUNDIFOLIA	STERILE HYBRID	D. LINEARIS
Leaves spreading or horizontal.	Leaves ascending or spreading.	Leaves ascending or erect.
Petioles compressed and winged, moderately to densely hairy with flat, twisted hairs.	Petioles somewhat compressed (intermediate), sparsely to moderately hairy.	Petioles terete, glabrous or with a few scattered hairs.
Leaf blades suborbicular to orbicular-reniform, broader than long, (4-)6-10 mm. long, (5-)7-11 mm. wide, bright yellowish green, the tentacles bright red.	Leaf blades obovate-spatulate to elongate-spatulate, longer than broad, 11-17(-20) mm. long, 4-6(-7) mm. wide, bright yellowish green, the tentacles bright red.	Leaf blades exactly linear, the tip rounded, 20-50 mm. long, 2-2.5 mm. wide, dull green or reddish, the tentacles dull red.
Leaf base slightly winged, the stipules adnate 2-3 mm. above the base, of fimbriate segments.	Leaf base with a narrow wing-like margin and numerous fimbriate, crinkled segments.	Leaf base dilate-winged, the stipules adnate 2-4 mm. above the base, of numerous crinkled, fimbriate, setaceous segments.
Inflorescences (4-)7-16 (-21) cm. long, the peduncle (3.2-)6-15 cm. long.	Inflorescences (2.5-)6-14(-19) cm. long, the peduncle (2.3-)4-13.5 cm. long.	Inflorescences (3-)5-11(-12) cm. long, the peduncle (2.7-)4-8(-8.7) cm. long.
Flowers per inflorescence (3-)4-13(-15).	Flowers (2-)4-8(-11).	Flowers (1-)4-6(-7).
Calyx green; petals white; pollen white.	Calyx blackish; petals white, pink tinged without; pollen orange.	Calyx blackish; petals white, tinged pink at tips without; pollen orange.
Capsules oblanceolate-elliptic in outline, 4.5-5.5 mm. long, 2.5 mm. diameter.	Ovaries fail to develop into fruit.	Capsules elliptic in outline, 5-5.5 mm. long, 2.5-3.5 mm. wide.
Seeds light brown, shiny with a metallic luster, sigmoid-fusiform, finely longitudinally striate, 1-1.5 mm. long.	Seeds fail to develop. Ovules aborting.	Seeds shining black, oblong-obovate in outline or rhomboidal, minutely and densely pebbled, 0.5-0.8 mm. long.

¹ See Wynne (1944) for range-maps of the North American species of *Drosera*.

Montana, *Mains 6053* (MICH). 18. *D. anglica*, Kauai, Hawaiian Ids., *Rock*, 1909 (NY). 19. *D. anglica*, Alaska, *Anderson 764* (NY). 20. *D. × obovata* (*D. anglica × D. rotundifolia*), Sweden, *Bergström*, 1915 (GH). 21. *D. × obovata*, Ozegahara, Japan, *Suzuki 45* (GH). 22. *D. × obovata*, Finland, *Hallström 1202* (NY). 23. *D. × obovata*, Sweden, *Asplund*, 1923 (NY). 24. *D. × obovata*, Newfoundland, *Fernald, Long & Fogg 1759* (GH).

in a number of conspicuous features, including habitat and habit, leaf-shape, cross-sectional shape and pubescence of petioles, stipules, the number of flowers per inflorescence, color of anthers and color, shape and surface-markings of seeds. There are also other less conspicuous differences. In most respects the sterile, spatulate-leaved plants from Hammond Bay are morphologically intermediate between the two species, but in a few characteristics resemble one or the other species more strongly. In pollen color and color of the calyx the



FIGURES 25-32. Cross-sections of petioles of *Drosera*. $\times 20$. Cross-sectional shape of petioles offers interesting possibilities as an additional distinguishing characteristic in fresh material of *Drosera*, as will be noted from the five species and one hybrid shown here. Fresh specimens or material preserved in liquid must be used, however, for the tissues shrink so badly in drying that it is difficult to re-expand petioles from herbarium specimens. Vascular bundles are shown diagrammatically, the xylem in black, the phloem in white.

25. *Drosera rotundifolia*, middle of petiole; Emmet Co., Mich., Wood 8076 (GH). 26. *D. linearis* \times *D. rotundifolia*, middle of petiole; Hammond Bay, Mich., Wood 8237 *et al.* (GH). 27. *D. brevifolia*, middle of petiole; Carteret Co., N. C., Wood 8237 (GH). 28. *D. capillaris*, middle of petiole; Pender Co., N. C., Wood 8236 (GH). 29. *D. rotundifolia*, petiole near the base of the blade. 30. *D. linearis*, middle of petiole; Emmet Co., Mich., Wood 8120 (GH). 31. *D. capillaris*, petiole near base of the blade; compare with fig. 29. 32. *D. intermedia*, middle of petiole; Cheboygan Co., Mich., Wood 8130 (GH).

plants are similar to *D. linearis* but in the yellow-green of the leaf blades and the bright red of the tentacles and in the elongate shape of the aborted ovules they approach *D. rotundifolia*. A comparison of all three plants is given in the accompanying table² from which the intermediacy of the sterile plants is, I believe, evident. (See also fig. 1-9, 25, 26, 30.)

The only other species which could be involved as a parent of the hybrid is *Drosera intermedia* Hayne, which it superficially

² Since there is abundant evidence of ecological variation in *Drosera*, the comparisons drawn in the table are based upon material from northern Michigan, rather than upon specimens from throughout the range of the parental species, so that a more uniform sample is obtained for this purpose.

resembles in leaf-shape. This species in northern Michigan, however, is a plant of very acid and wet habitats, particularly *Sphagnum* bogs where it occupies the wettest depressions in the *Sphagnum* mat. It occasionally crosses with *D. rotundifolia*, which grows on the drier *Sphagnum*, producing a sterile hybrid with much more rotund leaves than the sterile plant of the beach pools. I have never found *Drosera intermedia* growing anywhere in the vicinity of *D. linearis*. *Drosera intermedia* is also ruled out by its completely glabrous petioles, D-shaped in cross-section (compare figs. 25, 26, 30 & 32), small, spatulate leaf blades, free stipules and inflorescences which emerge horizontally before curving upward.

On morphological grounds the sterile plant of the Hammond Bay beach pools is certainly a hybrid between *Drosera linearis* and *D. rotundifolia*. It is now known from a number of other localities and the description given below is drawn from all of these collections. Since I believe that the amphiploid of this hybrid is *Drosera anglica*, nothing but confusion would result from a "specific" name for this putative hybrid. It is accordingly designated only by formula.

***Drosera linearis* Goldie × *D. rotundifolia* L.**

Very short-stemmed rosette plant intermediate between the parental species and occurring with them. Principal leaves ascending or spreading, (2-)2.5-6(-8) cm. long, the petioles (1.3-)2-4(-5.5) cm. long, slightly compressed and winged, sparsely to moderately hairy with crinkled or twisted white hairs to 2 mm. long; base of petiole flattened, with a narrow wing-like margin, the stipules pink, adnate 2-4 mm. above the base, with several flat fimbriate segments and few to many twisted flat hairs to 5 mm. long. Leaf blades obovate-spatulate to oblanceolate-spatulate, the apex rounded, 11-23(-30) mm. long, 4-6(-8) mm. wide, bright yellowish-green, the tentacles bright red (as in *D. rotundifolia*), to 5 mm. long. Inflorescences 1-3(-4), scapose, including the peduncle (2.5-)6-14(-20) cm. tall, the first usually the largest; peduncle (2.3-)4-13(-15) cm. long, glabrous or with scattered hairs near the base. Flowers (2-)4-8(-11) per inflorescence, the pedicels 1-2.5 mm. long. Calyx dark blackish-green (as in *D. linearis*), 4-5 mm. long, the lobes oblong, obtuse to acute, 3-3.5 mm. long, 1-1.5 mm. wide, the margins glandular-denticulate. Petals white, obovate-cuneate or narrowly obovate, 4-4.5 mm. long, 2.5 mm. wide. Stamens 3.5-4 mm. long, the pollen orange (as in *D. linearis*). Ovary failing to develop into a fruit; ovules fusiform, aborting; styles slender, clavate, bifurcate to the base, the branches 1.5-2 mm. long. Somatic chromosomes 20; meiosis irregular.

SPECIMENS EXAMINED.³ Canada. Ontario. Bruce Co.: edges of pools in marly bog-marsh area near Lake Huron, Oliphant, Annabel Twp., *Cain, Hagenah & Thompson*, 6 July 1947 (BLH); grassy bog, Sauble Beach, *Krotkov 9099* (US).

United States. Michigan. [Charlevoix Co.:] border of a (marl) lake near Charlevoix, *C. F. Wheeler*, 26 Aug. 1894 (GH). Emmet Co.: marly flats with scattered *Thuja* and *Larix* behind dunes along Sturgeon Bay, Sec. 5, R5W, T38N, Bliss Twp., *Wood 8122* (GH). Keeweenaw Co.: transition zone between sedges and sphagnum, Raspberry Island bog, Isle Royale, *R. M. Linn*, 9 & 15 Aug. 1954 (GH); bog on Raspberry Island, Rock Harbor, Isle Royale, *J. B. McFarlin 2238*, 22 July 1930 (MICH); Isle Royale, *University Party*, 1868 (MICH) (probably this plant—one plant with a plant of *D. intermedia*). Oakland Co.: [all of the following are from the same locality]: marsh, edge of Lake Orion, *B. F. Chandler*, 30 July 1914 (BLH, US); boggy ground, Marl Lake, near Orion, *Chandler*, 19 Sept. 1915 (MICH); wet open ground (boggy ground) on the margin of Marl Lake, Orion Twp., *Billington*, 9 & 13 July 1916 (NY), 9 July & 13 Aug. 1916 (MICH), 9 July 1916 (MICH); borders of Marl Lake near Orion, *O. A. Farwell 4289*, 9 July 1916 (BLH, GH), *4289½* (GH), *4371*, 13 Aug. 1916 (GH); Marl Lake, north of Orion, *Sutton 440*, 30 July 1914 (MICH); Marl Lake, near Rochester, *Ballard*, July 1897 (GH). Presque Isle Co.: on edge of open beach pool at Hammond Bay, Sec. 22, R3E, T36N, *Kenaga 14*, 6 Aug. 1951 (UMBS); boggy beach pool, Evans property, Hammond Bay near old Coast Guard Station, *F. K. & A. G. Sparrow*, 19 July 1952 (UMBS); open sand and small hummocks along seeping edges of shore and sandy, marly beach pools in front of *Thujas* along low shore of Hammond Bay, Lake Huron, w. of Coast Guard Station, Sec. 22-23, R3E, T36N, Ocqueoc Twp., *Wood 8077*, 23 June 1953, *8315*, 22 Aug. 1953, *Wood 8237*, *E. Clover & M. Fulford*, 24 July 1953 (GH, MICH, NY, UMBS, US); rare, with *D. rotundifolia* and *D. linearis*, both of which are abundant, marly flats back of Lake Huron beach, small bay, ca. 3 mi. n. of Presque Isle P. O., between Sec. 21 & 27, R8E, T34N, *McVaugh 10892*, 11 July 1949 (MICH), *Wood 8307 & McVaugh*, 22 Aug. 1953 (GH).

ECOLOGY. In northern Michigan *Drosera rotundifolia* and *D. linearis* usually occupy very different habitats. *Drosera rotundifolia* is characteristically a plant of *Sphagnum* bogs but it also occurs on other mosses, on wet, rotting logs, or on moist or wet sands, usually in acid habitats with a pH in the neighborhood of 4 or 5. The very different *D. linearis*, in contrast, is always (insofar as I can determine) a plant of constantly wet, open, circumneutral (pH 6.5-7.5) or slightly alkaline habitats, such as marl bogs and the seeping beach flats of the northern Great Lakes, especially Lake Huron. In these areas the plant often occurs by the thousands, literally covering the ground. Although the respective habitats of the two species are, for the

³ The abbreviations used to designate herbaria are those of *Lanjouw and Stafleu in Index Herbariorum*, Pt. I., *The Herbaria of the World*, ed. 2, Utrecht, 1954, with the exception of the University of Michigan Biological Station, Cheboygan, Michigan (UMBS).

most part, quite separate, at some points they come together and it is in these areas that hybrids have been found.

A description of one such area, that at Hammond Bay, Presque Isle County, Michigan, is given below. At this locality, back from the gently curving shore of Hammond Bay south of the Ocqueoc River, the land drops abruptly from the level of the fossil beaches of glacial Lake Algonquin to a *Thuja* bog which stretches toward Lake Huron. At the edge of the bog, some 40–50 yards from the lake shore, is a low, stabilized dune with a dirt road running along the top to several summer cottages. On the shoreward side of the road the sand slopes gently to a wet depression, the inner edge of a beach pool, a distance of some 25 feet. Characteristic plants of the stabilized upper portion of the slope are *Pinus Strobus*, *Larix laricina*, *Thuja occidentalis*, *Juniperus horizontalis*, *Shepherdia canadensis*, *Andropogon scoparius*, *Calamovilfa longifolia*, *Arctostaphylos Uva-ursi*, *Linnaea borealis* var. *americana*, and *Campanula rotundifolia*. The lower portion of the slope, some 10 feet in width, is more open and is quite moist or even wet with constant seepage from the *Thuja* bog. Here are found scattered shrubs of *Myrica Gale* with *Sarracenia purpurea*, *Primula intercedens*, *Lobelia Kalmii* and numerous plants of *Drosera rotundifolia*. In the very shallow water of the wet depression, 8 feet wide at the foot of the slope, occur *Rhynchospora capillacea*, *Pogonia ophioglossoides*, *Sarracenia purpurea*, *Utricularia cornuta*, *U. intermedia*, many plants of *Drosera linearis* and scattered individuals of the obovate-spatulate-leaved hybrids. A low, somewhat irregular ridge, from 6 inches to a foot high and from two to five feet wide, rises from the wet depression paralleling the shore. Beyond this the shallow beach pool, broken by hummocks, reaches about 30 feet to end abruptly at a wide, sandy beach which slopes gradually into Lake Huron. The low, irregular ridge provides conditions suitable for the growth of both *Drosera linearis* and *D. rotundifolia* and it is here that the greatest numbers of hybrid plants (75 or more individual plants or clumps of various sizes) were found. Also on this ridge were a few small *Thujas* and an occasional plant of *Myrica Gale*, along with *Cladium mariscoides*, *Scirpus hudsonianus*, *Lilium philadelphicum*, *Pogonia ophioglossoides*, *Sarracenia purpurea*,

Gentiana procera, *Lobelia Kalmii* and *Solidago ohionis*. The beach pool proper is dotted with scattered plants of *Sarracenia purpurea*, but none of the sundews grows there. The conspicuous plants of the beach pool are *Cladium*, *Rhynchospora* and the two species of *Utricularia*. The sandy beach is occupied by the common shore plants of the region, including *Equisetum variegatum*, *Calamagrostis inexpansa*, *Scirpus americanus*, *Juncus balticus* var. *littoralis*, *Triglochin palustris*, *Salix interior*, *Cakile edentula* var. *lacustris*, *Parnassia glauca*, *Hypericum Kalmianum* and *Lobelia Kalmii*, the distribution of these seemingly dependent upon the varying wetnesses of the beach.

The principal area in which the hybrid sundews are found parallels the shore for about 250 feet. Beyond this on either side conditions change and the two parental species are separated again, although at another area a quarter of a mile away similar conditions obtain and here again hybrids are found.

In each locality in northern Michigan where I have collected the hybrids ecological conditions similar to those described above occur. A seeping shore with open, marly flats and scattered Thujas or larches with hummocks at their bases are indications that hybrids may be looked for (but not always found, of course). *Drosera linearis* will be confined to the constantly wet soils or very shallow water, while *D. rotundifolia* may occur on the drier hummocks or at the bases of the trees. Hybrids have been found growing with either parent; at one locality (Emmet Co.), after a great deal of search I found only two hybrids, one in the midst of a colony of *D. rotundifolia*, the other among plants of *D. linearis* some distance away. I assume that the cross has occurred in both directions. Generally, however, the hybrid seems to be best developed in the wetter locations which favor *Drosera linearis*.

The hybrid was formerly abundant at Lake Orion, in southern Michigan, where both *Drosera rotundifolia* and *D. linearis* (the latter here near its southern limit) occurred. Conditions there seem to have been very favorable for its growth, for many of the specimens from this locality are large and vigorous, including one, the largest I have seen, with leaves 8 cm. long and an 11-flowered inflorescence 20 cm. tall. Accompanied by Dr. Rogers McVaugh and Dr. W. H. Wagner, Jr., I visited Lake Orion in

August of 1953 in search of the plant, only to find that the lake level has been raised several feet artificially, apparently eliminating *Drosera linearis* and the hybrid quite effectively. *Drosera rotundifolia* still survives on sphagnum hummocks along the shrubby border at several places.

CYTOLOGY. While, on the basis of occurrence and morphology alone, the spatulate-leaved plants may be presumed to be hybrids, high sterility is an additional indication of their hybrid nature. In an attempt to determine possible cytological causes for this sterility meiosis was studied in both parental species and in the hybrid from material collected at Hammond Bay on June 23, 1953. Mr. Robert Linn has also sent buds from plants which prove to be this hybrid growing in a bog on Raspberry Island, Isle Royale, Michigan. Various other collections of *Drosera rotundifolia* and *D. linearis*, as well as of *D. intermedia*, from northern Michigan have been studied. In the course of this investigation it has subsequently been possible to examine meiotic material of *Drosera brevifolia*, *D. capillaris*, *D. filiformis* and *D. filiformis* var. *Tracyi* from the southeastern United States, so that I have had the opportunity of studying all of the species occurring in North America, with the exception of one of the most crucial, the tetraploid *Drosera anglica*. The chromosome numbers now known in the genus are given in the accompanying table.

Cytological material from northern Michigan was fixed in a modified Carnoy's fixative (4 chloroform: 3 alcohol: 1 acetic acid) and that from the Southeast in Newcomer's fixative (1953). Both gave excellent results. Anthers were squashed in propriono-carmin, drawings made with the aid of a camera lucida, and the slides made permanent by Bradley's vapor transfer technique (Bradley, 1948).

In all material of *Drosera linearis*, *D. rotundifolia* and *D. intermedia* examined ten bivalents are formed in the first division of meiosis. One pair of chromosomes is associated with the nucleolus in each of these species. (This is also true of *D. linearis* \times *D. rotundifolia* and the various other diploid species reported here.) Chromosomes pair and disjoin with no irregularities (fig. 33-36). In the sterile hybrid, although in many instances the 20 chromosomes seem to be at least loosely asso-

CHROMOSOME NUMBERS IN THE GENUS *DROSERA*

	Chromosomes		Source	Author
SEC. I. PSYCHOPHILA <i>D. regia</i> Stephens	2n = 34		Hamburg Bot. Gard. [S. Africa]	Behre, 1929
SEC. II. BRYASTRUM <i>D. pygmaea</i> DC.	2n = 20-22, 30? 2n = 32? (28-34)		Not given Hamburg Bot. Gard. [Australia & N. Z.]	Heitz, 1925 Behre, 1929
SEC. IV. THELOCALYX <i>D. Burmannii</i> Vahl.	n = 10, 3n = 30 (endosperm)		Bangalore, India	Narasimhachar, 1949
SEC. IX. PHYCOPSIS <i>D. binata</i> Labill.	2n = 32		Hamburg Bot. Gard. [Australia & N. Z.]	Behre, 1929
SEC. X. PTYCNOSTIGMA <i>D. cistiflora</i> L.	2n = 60		Hamburg Bot. Gard. [S. Africa]	Behre, 1929
SEC. VII. ROSSOLIS <i>D. brevifolia</i> Pursh	2n = 20, 2n = 10 _{II} 2n = 10 _{II}		Carteret Co., N. C. Durham Co., N. C.	Wood 8327 (GH)* R. B. Channell
<i>D. capillaris</i> Poir.	2n = 10 _{II} 2n = 10 _{II}		Jackson Co., Miss. Pender Co., N. C.	Wood 8458 & Demaree Wood 8326
<i>D. filiformis</i> Raf.	2n = 10 _{II} 2n = 20 2n = 10 _{II}		Lakehurst, N. J. Mashpee, Mass. Columbus Co., N. C.	Levine, 1916 Dahl, 1937 Wood 8507, Channell & Rock
<i>D. filiformis</i> var. <i>Tracyi</i> (McFarlane)	2n = 10 _{II} 2n = 10 _{II}		Jackson Co., Miss. Mobile Co., Miss.	Wood 8438 & Demaree Wood 8463 & Demaree
<i>D. intermedia</i> Hayne	2n = 20 2n = 20, n = 10 2n = 10 _{II} 2n = 10 _{II}		Germany Lakehurst, N. J. Cheboygan Co., Mich. Columbus Co., N. C.	Behre, 1929 Levine, 1916 Wood 8130 Wood 8550 & E. Anderson

<i>D. linearis</i> Goldie	2n = 10 _{II} 2n = 10 _{II}	Presque Isle Co., Mich. Emmet Co., Mich.	Wood 8075, 8235 Wood 8120
<i>D. rotundifolia</i> L.	2n = 20, n = 10 2n = 20 2n = 10 _{II} 2n = 20 2n = 20, n = 10 n = 10 2n = 10 _{II} 2n = 10 _{II} 2n = 10 _{II}	Germany, Norway, Sweden, Denmark Germany Lakehurst, N. J. North Falmouth, Mass. Japan Japan Presque Isle Co., Mich. Cheboygan Co., Mich. Emmet Co., Mich.	Rosenberg, 1903, 1904, 1909. Behre, 1929 Levine, 1916 Dahl, 1937 Shimamura, 1941 Nakajima, 1933 Wood 8076, 8236. Wood 8204, 8129 Wood 8121
<i>D. linearis</i> × <i>D. rotundifolia</i>	2n = 20 2n = 3-7 _{II} + 1-3 _{III} + 2-10 _I	Presque Isle Co., Mich.	Wood 8077, 8237.
<i>D. anglica</i> × <i>D. rotundifolia</i> (<i>D.</i> × <i>obovata</i> Mert. & Koch)	2n = 10 _{II} + 10 _I 2n = 30 2n = 30 2n = 10 _{II} + 10 _I	Norway, Sweden, Denmark Japan	Rosenberg, 1904, 1909 Shimamura, 1941
<i>D. anglica</i> Huds.	2n = 40, 2n = 20 _{II} 2n = 40 2n = 40, 2n = 20 _{II}	Norway, Sweden, Denmark Germany Japan	Rosenberg, 1903, 1904, 1909 Behre, 1929 Shimamura, 1941
<i>D. capensis</i> L.	2n = 36-38 2n = 40	Not stated [S. Africa] Hamburg Bot. Gard. [S. Africa]	Heitz, 1925 Behre, 1929
<i>D. spathulata</i> Labill.	2n = ca. 72 2n = 80	Not stated [Japan to N. Z.] Hamburg Bot. Gard.	Heitz, 1925 Behre, 1929

* Documenting specimens for all numbers reported here are in the Gray Herbarium.



ciated into 10 pairs in Prophase I, some pairs either fall apart or fail to move onto the spindle so that at Metaphase I only 3–7 bivalents are present. (fig. 37–45). One, two or three trivalents may occur (fig. 41–44) and an occasional quadrivalent is seen (fig. 45).

For example, of 28 metaphases (the largest number analyzable from any one hybrid plant), 3 pairs of chromosomes were present on the spindle in 3 cells, 4 pairs in 6 cells, 5 pairs in 11 cells, 6 in 5 cells and 7 in 3 cells. Twelve cells showed one trivalent and five had two. Only a single quadrivalent was seen in this plant (fig. 45). The number of unpaired chromosomes varied from 2 to 10 and the number of bivalents not on the spindle from one to four. Figure 41 shows a cell with three bivalents and one trivalent on the spindle, while four bivalents lie off the spindle.

Chromosomal distribution is consequently quite erratic. Some chromosomes lag and divide tardily and there is evidence of bridges and fragments (fig. 46–48). Following meiosis conjoined nuclei, micronuclei and other irregularities are often seen. It is not surprising that the hybrids of *Drosera linearis* and *D. rotundifolia* are sterile.

In the Droseraceae the four microspores from each pollen mother cell remain associated and develop into a united tetrad of pollen grains, generally tetrahedral in arrangement (fig. 49–50). It is thus possible to see the products of each pollen mother cell and the extent to which meiotic irregularities result in the formation of abnormal microspores or pollen grains. Fresh *Drosera* pollen mounted in lactophenol with a little cotton blue absorbs the stain readily making it fairly easy to determine

FIGURES 33–53. Meiosis in *Drosera*. $\times 800$. 33. *Drosera linearis*, metaphase I; Hammond Bay, Mich., Wood 8075. 34. *D. rotundifolia*, metaphase I; Hammond Bay, Mich., Wood 8076. 35. *D. capillaris*, metaphase I, Pender Co., N. C., Wood, 8236. 36. *D. brevifolia*, diakinesis; Carteret Co., N. C., Wood, 8237. 37–45. *D. linearis* \times *D. rotundifolia* (2n, sterile), metaphase I, Hammond Bay, Mich., Wood 8077, 8237. 46–47. *D. linearis* \times *D. rotundifolia* (sterile), metaphase II, showing tardily disjoining bivalents and dividing univalents, Wood 8077, 8237. 48. *D. linearis* \times *D. rotundifolia* (sterile), metaphase II, Wood 8077, 8237. 49. Three pollen tetrads from *D. rotundifolia*, Wood 8305 & McVaugh (GH). 50. Three pollen tetrads from *D. linearis*, Wood 8075 (GH). 51. Four pollen "tetrads" from *D. linearis* \times *D. rotundifolia* (sterile), Wood 8077, with 4, 5, 9 and 8 microspores, respectively. 52. Two pollen tetrads from fertile hybrid, *D. linearis* \times *D. rotundifolia* Amphiploid, Wood 8308 & McVaugh. 53. Pollen "tetrad" with 5 grains from same fertile hybrid. Fig. 49–53, $\times 250$.

the number of associated pollen grains and something of the condition of the protoplasmic contents.

In hybrids from Hammond Bay approximately half of the grains are associated in tetrads, although the four are sometimes of different sizes. The remaining "tetrads" consist of from 2 to 9 microspores or grains of various sizes, in most of these (about 40 per cent of the total) consisting of 5 or 6 (fig. 51). In no instances were any grains with evenly distributed and staining protoplasmic contents observed in the hybrids. Most grains (even those united in regular tetrads) lack contents altogether and the remainder show only deeply stained and clumped protoplasm. Apparently pollen sterility approaches 100 per cent. This is in great contrast to both of the parental species which are very nearly as fertile as the hybrid is sterile.

In spite of the lack of sexual reproduction, at Hammond Bay and presumably at Lake Orion the hybrid reproduced itself vegetatively by adventitious plantlets from leaf blades, scapes, or even flowers, the carpels of which may be converted into a rosette of leaves similar to that described by Fernald as *Drosera rotundifolia* var. *comosa*. This kind of vegetative reproduction was seen at Hammond Bay in July and August and was shown by experimentally detached leaves which produced adventitious plantlets from the adaxial surfaces of the blades. Such reproductive methods are shared (at least potentially) by most species of the genus.⁴ Vegetative reproduction may thus be of considerable importance in allowing the persistence and even spread of a sterile plant over a period of years. It greatly increases the chances for the formation of restitution nuclei or other phenomena which could lead to polyploidy and the production of a fertile amphiploid such as the plant to be discussed next.

A FERTILE HYBRID

On July 11, 1949, Dr. Rogers McVaugh had collected two plants of the sterile hybrid growing with abundant *Drosera*

⁴ In his *Flore Laurentienne* (1935, p. 273), Marie-Victorin noted vegetative reproduction in *D. rotundifolia*, saying, "At the maturation of the fruits, the leaves detaching themselves are disseminated by water or wind and they are from this moment capable of giving rise to adventitious buds which develop into new plants. The process recalls the classic case of the budding of *Bryophyllum*." [Translation.] See Behre (1929) for descriptions of modes of vegetative reproduction or Lloyd (1942) for a general review in English.

linearis and *D. rotundifolia* on beach flats along the shore of Lake Huron about 3 miles north of Presque Isle Post Office, Presque Isle County, Michigan (McVaugh 10892). Since it was of considerable interest to obtain some idea of how widespread and frequent hybridization between these two species may be, Dr. McVaugh kindly showed me this locality on August 22, 1953. The ecological situation was similar to that in which hybrids have been found elsewhere, with marly flats becoming a cobble beach, a seeping shoreline along a *Thuja* bog and scattered plants of *Thuja* and *Larix* with ridges and hummocks of herbaceous vegetation. *Drosera linearis* was abundant on the wet flats and *D. rotundifolia* grew among the herbaceous plants and on mossy hummocks at the bases of *Thuja* or *Larix*. Both species of sundew were in mature fruit and at the point of shedding their seeds. Careful search produced only a single hybrid, a plant which had flowered but which was very definitely sterile. However, on the lower portion of a mossy hummock at the base of a small *Thuja* and in close proximity to both *Drosera linearis* and *D. rotundifolia*, we found a colony of ten or so plants of various sizes which were quite identical in their vegetative characteristics with both the sterile hybrid collected here and those seen elsewhere. Three of these plants, although rather small, had flowered and, unlike the other hybrids, had matured fruit and were shedding seeds. (Wood 8308 & McVaugh, GH.)

These fruiting plants are quite remarkable. The capsule is well developed, oblong in outline, 7–7.5 mm. long and 3.5 mm. wide, thus larger than that of either *Drosera linearis* or *D. rotundifolia* in this area. The scapes were 6 to 11 cm. long and bore 3 to 7 flowers. It is the seeds, however, which are most notable. These are precisely what might be expected in a fertile hybrid between *D. linearis* and *D. rotundifolia*, with the black coloration of the seeds of the former, the spindle-shape and size of those of the latter and surface markings which are quite intermediate. Most remarkable of all, they are a perfect match for the seeds of the circumpolar tetraploid *Drosera anglica*, the only species of the northern hemisphere, other than *D. rotundifolia*, with fusiform seeds. This, in a group in which seed characteristics have proved to be among the most distinctive

and stable, can not be regarded as mere coincidence. (See Wynne, 1944, text and figures, and the same illustrations in The New Britton & Brown.) Figures 60–63 show a comparison of the cells from the outer seed coats of *Drosera rotundifolia*, *D. linearis*, the fertile plants from Presque Isle and *D. anglica* from Montana.

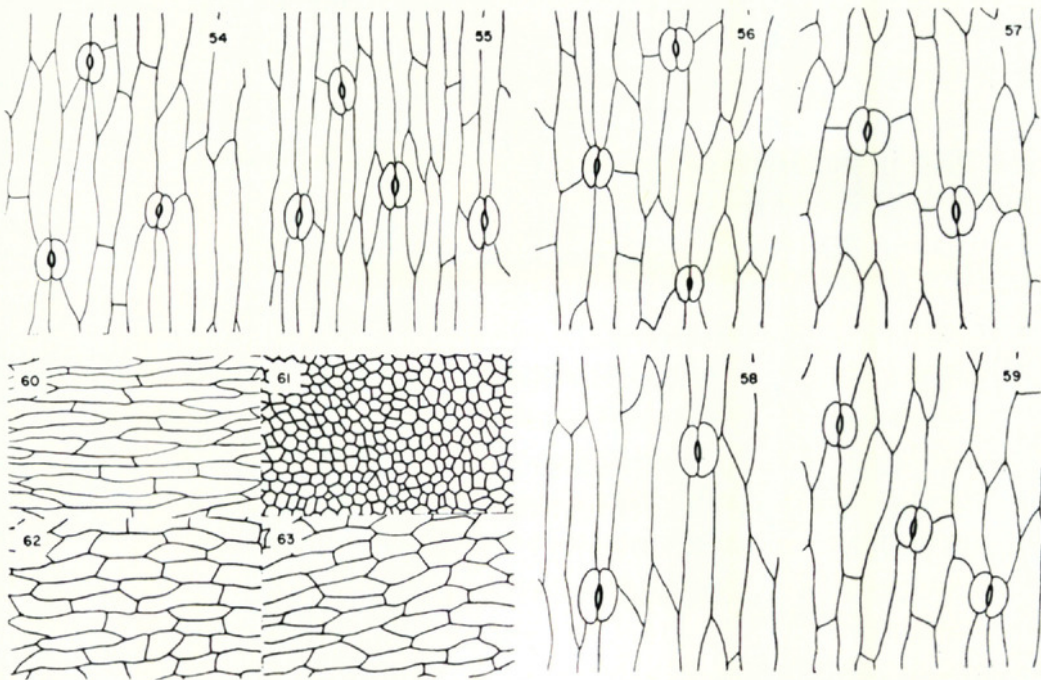
Although this small colony of exceptional fertile plants might conceivably represent a recent introduction of *Drosera anglica* from some locality to the north (the nearest in Michigan in the upper peninsula at Marquette, some 180 miles west-north-westward),⁵ the circumstances of its occurrence suggest that these are plants of *D. linearis*–*D. rotundifolia* parentage which have somehow acquired fertility. In any event, the identical vegetative characteristics of these fertile plants which produce “*anglica*” seeds and of the sterile offspring of *D. rotundifolia* and *D. linearis* need explanation, for some tie-up with *Drosera anglica* is indicated, whether this is an introduction to the area or whether it is a spontaneous development. I can see no reason to think that this is anything other than a fertile hybrid.

Assuming that these are indeed derived from *D. linearis* and *D. rotundifolia*, the very production of seeds by the fertile plants, in contrast to the sterile hybrids with their erratic chromosomal behavior and inviable pollen, suggest that these exceptional plants may be amphiploids on the same chromosomal level as *Drosera anglica*, a tetraploid with 20 pairs of chromosomes.

It was not possible to determine directly the chromosome number of the fertile plants, but this was attempted by a comparison of the areas and volumes of epidermal guard cells on the principle that the cells of a recent amphiploid, having twice the number of chromosomes of a diploid should have twice the nuclear volume and roughly twice the cellular volume. Leaves preserved in 70 per cent alcohol were available from Presque Isle plants of *Drosera rotundifolia*, *D. linearis*, the sterile hybrid and the fertile hybrid, but boiled-up herbarium material had to be used for *Drosera anglica*. Whole leaves were mounted

⁵ I have no evidence of *Drosera anglica* in the lower peninsula of Michigan, although Wynne (1944) shows two localities on her map. One of these is certainly Lake Orion and represents sterile *D. linearis* × *D. rotundifolia* and I suspect that the other, farther north in the part of the state with which I am most familiar, does also.

in water, the epidermis on the backs of the leaves studied, and pairs of guard cells (chosen at random from the central portion of the blade) drawn with camera lucida at a final magnification of 1100 diameters. The guard cells of the two diploid species and their sterile hybrid are all smaller than those of either the fertile hybrid or *D. anglica* (fig. 54–59). Areas of



FIGURES 54–59. Epidermis from lower side of leaf blades of *Drosera*. $\times 125$. 54. *Drosera rotundifolia*, Presque Isle, Mich., Wood 8305 & McVaugh. 55. *D. linearis*, Presque Isle, Mich., Wood 8306 & McVaugh. 56. *D. linearis* \times *D. rotundifolia* (sterile), Presque Isle, Mich., Wood 8307 & McVaugh. 57. *D. linearis* \times *D. rotundifolia* (fertile), Presque Isle, Mich., Wood 8308 & McVaugh. 58. *D. anglica*, Sweden, Svenonius, 1932 (NY). 59. *D. anglica*, Montana, Mains 6053 (MICH).

FIGURES 60–63. Portions of outer seed coats responsible for surface sculpturing of seeds of *Drosera*. $\times 75$. 60. *D. rotundifolia*, Wood 8305 & McVaugh. 61. *D. linearis*, Wood 8306 & McVaugh. 62. *D. linearis* \times *D. rotundifolia* (fertile), Wood 8308 & McVaugh. 63. *D. anglica*, Mains 6053.

the individual cells of each of the plants were determined by means of a planimeter, the average of five circumferences being used for each cell. In attempting to obtain a rough approximation of the volumes, the diameter of each guard cell was used as its depth and the volume calculated as though the guard cell were a flat-topped, straight-sided figure. Areas and volumes were calculated only for purposes of comparison; no attempt was made to convert these to the actual volumes of the cells. The results are given in the adjoining table.

A statistically significant difference exists between the mean areas of the guard cells of *D. linearis* and *D. rotundifolia*. Their sterile hybrid lies midway between, as might be expected. The mean area of the guard cells of the fertile hybrid is 1.5 times that of the sterile hybrid. There is no significant difference between the means of the fertile hybrid and those of *D. anglica* from either Montana or Sweden.

From the volume relationships it is quite evident that two distinct groups of plants, corresponding to the known diploids and tetraploids, are represented. The fertile plant from Presque Isle fits in with the latter group and the mean volume of its guard cells is 1.9 times that of the sterile plant. No statistically significant difference exists between the means of the volumes of *Drosera rotundifolia*, *D. linearis*, or their sterile hybrid, or between those of *Drosera anglica* from Europe, that from America and the fertile hybrid, but the difference between the two groups is highly significant and not due to chance.

Since in this genus the petals are persistent, shriveling together above the capsule and protecting the dried stamens and pollen grains adhering to the stigmas, it is often possible to recover pollen tetrads from plants with mature fruits. While the shape and confluence of the grains makes the determination of the volumes impossible, those of the fertile hybrid are conspicuously larger than those of either putative parental species or the sterile hybrid. (Compare fig. 52-53 with fig. 49-51.) It may be remarked in this connection that Erdtmann (1943) gives the width of a tetrad of *Drosera anglica* as 72 microns, the equatorial diameter of a single grain about 50 microns, and the width of a tetrad of *D. rotundifolia* as about 55 microns, the diameter of a single grain about 34 microns. I have not followed this line of evidence further.

Although these indications are not as precise as is desirable, it seems highly probable, on the basis of its fertility, guard cell area and volume, and pollen size, that the fertile hybrid from Presque Isle is at the tetraploid or near tetraploid level, representing a spontaneous amphiploid of *Drosera linearis* and *D. rotundifolia*.

Such a plant might be expected to be fairly fertile and could propagate itself sexually, setting seeds by self-pollination. The

COMPARISONS OF AREA AND VOLUME OF GUARD CELLS OF DROSERA

	Mean AREA \bar{x}	σ	Relative Area	Mean VOLUME \bar{x}	σ	Relative Volume	No. cells
<i>D. rotundifolia</i> (Wood & McVaugh 8305)	3.6 ± 0.08	0.51 ± 0.05	0.90	4.6 ± 0.14	0.90 ± 0.10	0.9	40
<i>D. linearis</i> (Wood & McVaugh 8306)	4.4 ± 0.09	0.67 ± 0.07	1.10	4.9 ± 0.16	1.11 ± 0.11	1.0	50
Sterile hybrid (Wood & McVaugh 8307)	4.0 ± 0.09	0.62 ± 0.07	1.00	4.9 ± 0.15	1.04 ± 0.11	1.0	42
Fertile hybrid (Wood & McVaugh 8308)	6.1 ± 0.08	0.63 ± 0.06	1.52	9.4 ± 0.18	1.43 ± 0.13	1.9	62
<i>D. anglica</i> Montana (Mains 6053, MICH)	5.9 ± 0.13	0.76 ± 0.09	1.47	8.4 ± 0.32	1.79 ± 0.22	1.7	32
<i>D. anglica</i> Sweden (Svenonius, 1932, NY)	6.0 ± 0.10	0.58 ± 0.07	1.50	8.8 ± 0.30	1.73 ± 0.21	1.8	34

flowers of *Drosera* are usually open for cross pollination only in full sunlight from morning to mid-day or early afternoon, after which the petals close bringing the anthers into contact with the stigmas, insuring pollination. A number of undeveloped ovules were noted among the seeds of the fertile Presque Isle hybrids; these might indicate either a degree of sterility or merely lack of fertilization of some ovules. Of 70 pollen "tetrads" recovered from these plants, 69 had four grains and a single one five (fig. 52, 53). It was not, of course, possible to determine whether or not the contents had been functional.

DROSERANGLICA

There is no question of the close morphological similarity of the fertile and sterile hybrids. Lacking the flowering scapes or without a compound microscope it would be quite impossible to distinguish between them. It is also quite impossible to distinguish between the distinctive seeds of the fertile plant and those of *Drosera anglica*. If the fertile plant is *Drosera anglica* at a station considerably outside of its known range, the identical features of this plant and the sterile hybrid indicate that *D. anglica* was derived from the sterile hybrid of *D. linearis* and *D. rotundifolia* by amphiploidy. If the fertile plant is regarded as a spontaneous amphiploid or near amphiploid derived from the sterile hybrid it is still tied to *D. anglica* in the same way by its seeds and other morphological features. The indications are that the latter is the case and that *D. anglica* must have first originated in this same manner at some unknown time in the past. This should be regarded, then, as an instance of the spontaneous resynthesis of a widespread and successful species.

The morphological similarities of the sterile and fertile hybrids to *Drosera anglica* are striking. Fernald and Wynne both identified the sterile hybrid as *D. anglica* and a specimen of the sterile plant from Lake Orion is illustrated as *D. anglica* in The New Britton & Brown (Gleason, 1952). In studying specimens of *D. anglica* I unhesitatingly identified a series of plants in bud from a bog on Raspberry Island, Isle Royale, Michigan, (McFarlin 2238) (fig. 5) as this species. However, when Mr. Robert Linn sent me cytological material from seemingly iden-

tical plants from the same bog the plant proved to be the sterile diploid hybrid!

In all of the characteristics which I have been able to compare, the hybrids and *Drosera anglica* match well, with the exception of the leaves of many specimens. The hybrids from the lower peninsula of Michigan tend to have obovate-spatulate leaves, (fig. 3-9), in contrast to the narrower linear-spatulate or very narrowly obovate-cuneate leaves of *Drosera anglica* over much of its range (fig. 11-19). Some leaves are a perfect match, (e.g., compare fig. 5 and the leaves at either end of fig. 3 with fig. 11-19), but most leaves of the hybrid resemble a great deal more those of *Drosera* \times *obovata*, the sterile triploid hybrid of *D. anglica* and *D. rotundifolia* (fig. 20-24). Several possibilities suggest themselves by way of explanation. Ecological differences may well be responsible, at least in part. Shimamura (1941) who studied *D. anglica*, *D. rotundifolia* and *D. \times obovata* in Japan found that, although tetraploid *D. anglica* and triploid *D. \times obovata* were separable in the field when collected, they became morphologically indistinguishable when cultivated in Tokyo. It may also be noted that the specimens of *D. \times obovata* figured by him are very narrow-leaved and would easily pass as many European or American specimens of *D. anglica*. (Compare fig. 21 with fig. 11-19.) Thus the difference between the Isle Royale hybrids and those from farther south (fig. 5 vs. fig. 3-4, 6-9) may be merely an ecological difference.

Another possibility which warrants careful investigation but which must, for the present, await further evidence is that *Drosera anglica* is not a genomic allopolyploid but a segmental allopolyploid which resembles *D. linearis* more strongly than it does *D. rotundifolia*. In view of the partial chromosomal pairing shown by the sterile hybrid it would seem quite likely that this type of polyploidy might come about in the course of stabilization of a newly formed allopolyploid derived from it.

As was indicated in the introduction, the evidence from cytology for the origin of *Drosera anglica* is both scanty and in need of re-examination. The work of Rosenberg (1904, 1909) and Shimamura (1941) should be repeated with more modern cytological techniques. Additional evidence could come from the hybrid of *D. anglica* and *D. linearis*, if it can be found.

(This plant should occur in nature where the two species grow in close proximity, as they sometimes do. It should be difficult to distinguish from its parents in the field except by its failure to set seeds.) If *Drosera anglica* originated as suggested, some multivalent formation and other chromosomal irregularities might be expected both in this species and in its hybrids with *D. linearis* and *D. rotundifolia*. Neither Rosenberg nor Shimamura reported anything of the kind in either *D. anglica* or *D. × obovata*, perhaps because both used sectioned material in which multivalents are much more difficult to see than in smears and squashes. It is worth noting that in one paper Rosenberg (1904) illustrated a metaphase of *D. anglica* with a lagging univalent, although he later maintained that 20 pairs of chromosomes were regularly formed in *D. anglica* and 10 pairs with 10 unpaired chromosomes in *D. × obovata*.

As for this latter plant, the question of autosyndesis versus allosyndesis remains unsettled. The chromosomes of the two parental species (*D. anglica* and *D. rotundifolia*) are not morphologically distinguishable from one another and the chromosome number of the one parent is a straight multiple of the other. There is nothing to suggest, however, that *D. rotundifolia* and other species with 10 pairs of chromosomes (all of which have been referred to as diploids in this paper) are in reality polyploids with a basic chromosome number of 5, a situation which might well lead to autosyndesis in *D. × obovata*. The section Rossolis, to which all of the plants under discussion belong, seems to be a polyploid series with 10 as the base number of chromosomes. (See table of chromosome numbers.) The presence of only a single pair of chromosomes in association with the nucleolus in each of the 10-paired species points in the same direction, although this is not conclusive evidence (Stebbins, 1950, p. 464).

In spite of the equivocal nature of the cytological evidence from the pairing relationships of the chromosomes of *D. × obovata*, the hypothesis based upon it (that *D. anglica* has derived half of its chromosomes from *D. rotundifolia*) is worth considering and is highly suggestive, especially in view of the evidence from the fertile hybrid from Presque Isle County, Michigan. If it be assumed that half of the chromosomes of *D. anglica* have indeed come from *D. rotundifolia*, it becomes

necessary to find a second species with the proper combination of morphological and physiological characteristics to produce *D. anglica*. Of all of the species known from the northern hemisphere only *D. linearis* can supply these and only *D. linearis* is not ruled out by one or more conspicuous morphological features which would certainly be evident in a hybrid. (See especially Diels, 1906, for characteristics of other species.) Moreover, insofar as I can determine, both *D. linearis* and *D. anglica* are unique among northern hemisphere species in growing in marly habitats, although the latter plant appears to have a greater ecological amplitude and certainly is not confined to these.

Thus, although the question must remain unsettled for the present and many more ramifications of the problem continue to develop, the evidence from the sterile *Drosera linearis* × *D. rotundifolia*, that from the fertile hybrid with its "anglica" seeds, the close morphological correspondences, the cytological evidence and the distributional data all indicate strongly that *Drosera anglica* is an amphiploid which originated through the hybridization of *D. linearis* and *D. rotundifolia* at some time in the past and which may continue to appear from time to time in the future.

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LITERATURE CITED

- BEHRE, K. 1929. Physiologische und Zytologische Untersuchungen über *Drosera*. *Planta* **7**: 208-306.
- BRADLEY, MURIEL V. 1948. A method for making aceto-carmines squashes permanent without removal of the cover slip. *Stain Tech.* **23**: 41-44.
- DAHL, A. O. 1937. Chromosome studies in sundew (*Drosera*). *Bull. Marine Lab. Woods Hole* **73**: 368.
- DARLINGTON, C. D. 1937. Recent advances in cytology, ed. 2. Philadelphia.
- DIELS, L. 1906. *Droseraceae* in Engler, *Das Pflanzenreich* **4** (112): 1-136.
- DIGBY, L. 1912. The cytology of *Primula kewensis* and of other related *Primula* hybrids. *Ann. Bot.* **26**: 357-388.
- DOBZHANSKY, TH. 1941. Genetics and the origin of species, ed. 2. New York.
- ERDTMANN, G. 1943. An introduction to pollen analysis. Waltham, Mass.
- GLEASON, H. A. 1952. The new Britton & Brown illustrated flora of the northeastern United States and adjacent Canada. New York.
- HEITZ, E. 1926. Der Nachweis der Chromosomen: Vergleichende Studien über ihre Zahl, Grösse und Form im Pflanzenreich. I. *Zeit. für Bot.* **18**: 625-681.
- LEVINE, M. 1916. Somatic and reduction division in certain species of *Drosera*. *Mem. N. Y. Bot. Gard.* **6**: 125-147.
- LLOYD, F. E. 1942. The carnivorous plants. Waltham, Mass.
- MARIE-VICTORIN, FRÈRE. 1935. *Flore Laurentienne*. Montreal.
- NAKAJIMA. 1933. *Japanese Jour. Genetics* **9**: 1 ff. [not seen.]
- NARASIMHACHAR, S. G. 1949. A contribution to the embryology of *Drosera Burmannii* Vahl. *Proc. Ind. Acad. Sci. (Sec. B)* **29**: 98-104.
- NEWCOMER, E. H. 1953. A new cytological and histological fixing fluid. *Science* **118**: 161.
- OWNBEY, M. 1950. Natural hybridization and amphiploidy in the genus *Tragopogon*. *Amer. Jour. Bot.* **37**: 487-499.
- OWNBEY, M. and G. D. MCCOLLUM. 1954. The chromosomes of *Tragopogon*. *Rhodora* **56**: 7-21.
- ROSENBERG, O. 1903. Das Verhalten der Chromosomen in einer hybriden Pflanze. *Ber. der Deutsch. Bot. Gesellsch.* **21**: 110-119. Pl. 7.
- 1904. Über die Tetradenteilung eines *Drosera*-Bastardes. *Ber. der Deutsch. Bot. Gesellsch.* **22**: 47-53. Pl. 4.
- 1909. Cytologische und morphologische studien an *Drosera longifolia* × *rotundifolia*. *Kunl. Svenska Vetenskapsakademiens Handl.* **43** (11): 1-65, 4 pl.
- SHARP, L. W. 1934. Introduction to cytology, ed. 3. New York.
- SHIMAMURA, T. 1941. Cytological study of *Drosera obovata* Mert. & Koch with special reference to its hybridity. *Bot. Mag. (Tokyo)* **55**: 553-558.
- STEBBINS, G. L. 1950. Variation and evolution in plants. New York.
- WINGE, O. 1917. The chromosomes, their numbers and general importance. *Compt. Rend. Trav. Lab. Carlsberg.* **13**: 131-275.
- WYNNE, FRANCES E. 1944. *Drosera* in eastern North America. *Bull. Torrey Bot. Club* **71**: 166-174.



Wood, Carroll E. 1955. "Evidence for the hybrid origin of *Drosera anglica*." *Rhodora* 57, 105–130.

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