CHROMOSOME NUMBERS OF THE FAMILY CRUCIFERAE. III[1]

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Abstract

Chromosome numbers are given for a number of North American species in the genera *Draba*, *Erophila*, and *Erysimum*. New basic chromosome numbers are suggested for North American species of *Draba* and *Erysimum* and it is suggested that *Erysimum inconspicuum* reproduces by agamospermy.

Introduction

This is the third of a series of papers reporting chromosome numbers of the Cruciferae of Canada and adjacent areas. The first two papers (Mulligan 1964, 1965) included chromosome numbers for species in the genera *Alyssum*, *Arabidopsis*, *Arabis*, *Barbarea*, *Braya*, *Cakile*, *Cardamine*, *Eutrema*, *Halimolobos*, *Nasturtium*, *Rorippa*, *Thellungiella*, and *Turritis*.

Materials and Methods

Chromosome counts were made from root tips or flower buds of wild plants. Voucher specimens are deposited in the herbarium of the Department of Agriculture, Plant Research Institute, Ottawa. Root tips were placed in water and exposed to a temperature of 2–4 °C for 2 to 3 hours. They were then fixed in Nawaschin solution, embedded in paraffin, sectioned, and stained in crystal violet. Meiotic material was squashed in alcoholic hydrochloric acid – carmine as outlined by Snow (1963). Permanent slides of meiotic squashes were prepared by using CO_2 gas and an apparatus described by Johnson and Janick (1962). Permanent slides for all of the chromosome counts reported here are available for examination. Chromosome counts and collection data of plants studied are listed below.

Chromosome Counts

Draba aurea M. Vahl.

n = 37 (Fig. 1): Riv. Caniapiscau, Baie d'Ungava, 56°44′ N., 69°01′ W., Quebec, bas de la falaise de sable, près de la chute Shale, A. Dutilly & E. Lepage 39,413. n = ca. 36 or 37: 2 mi SW. of Fremont Pass along road to Leadville, Colorado, disturbed, low, gravelly flats along highway, T. & L. Mosquin 4642.

Draba crassifolia Graham

n = 20 (Fig. 2): Between Dolomite and Cirque Peaks, 51°40′ N., 116°23′ W., Banff National Park, Alberta, occasional in fine shale in sparsely vegetated col well above tree line, J. A. Calder & K. T. MacKay 32714. $2n$ = 40: 1 mi NW. of Ferro Pass, 50°56′ N., 115°44′ W., British Columbia, common on shale banks of Surprise Creek at 6500 ft, R. L. Taylor & D. H. Ferguson 3760.

[1]Contribution No. 481 from the Plant Research Institute.


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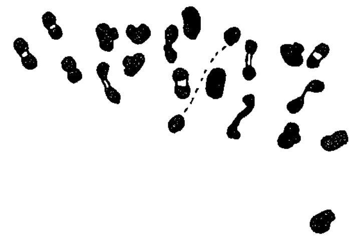
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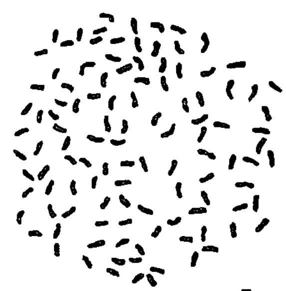
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Draba hyperborea (L.) Desv.

n = 18 (Fig. 3): Guise Bay area, Cape Scott, 50°47′ N., 128°25′ W., Vancouver Island, British Columbia, only one fertile and one sterile clump on rock ledge of cliff by sea, although common on offshore islands this is only record from mainland, Calder & MacKay 31393.

n = 19 (Fig. 4): Tree Islets off Pine Island at northwest end of Queen Charlotte Strait, B.C., R. Emrich in July 1963. *n* = 19: Small rocky inlet on south side of entrance to Gowgaia Bay, Moresby Island, B.C., Calder & Taylor 36570.

Draba incerta Payson

2*n* = ca. 112 (Fig. 5): ENE. of Saskatchewan Glacier near Sunwapta Pass, 52°11′ N., 117°05′ W., Banff National Park, Alberta, occasional on dry, shale slopes above 7000 ft, Calder & MacKay 32710. 2*n* = ca. 112: Starvation Peak area adjacent to Waterton, 49°02′ N., 114°12′ W., British Columbia, common but scattered on SW.-facing coarse talus with rock outcrops at 6800 to 8000 ft, Taylor, Calder & Ferguson 3324.

Draba lanceolata Royle

n = 16: Redstone River Region, Mackenzie Mountains, 62°55′ N., 126°38′ W., Mackenzie District, Northwest Territories, limestone cliffs at 4000 ft, E. Kvale & K. Haggard 52. 2*n* = 32: Mile 1090 Alaska Highway near Burwash Landing, 61°19′ N., 138°57′ W., occasional on dry, open, prairie slope above pond at 2900 ft, Calder & I. Kukkonen 28213. 2*n* = 32. 0.9 mi S. of junction of Kananaskis Road and Hwy. 1, Alberta, L. C. Sherk & Taylor (G.A.M. 2918). *n* = 16 (Fig. 6), 2*n* = 32: NW. of Azousetta Lake, Pine Pass area, 55°27′ N., 122°46′ W., British Columbia, rare on ledges of limestone cliffs at base of mountain, 2700 ft, Calder & Kukkonen 26906.

n = 24 (Fig. 7): Campbell Lake, 10 mi SE. of Inuvik, 68°14′ N., 133°28′ W., Mackenzie District, Northwest Territories, shallow soil crevices of limestone talus, W. J. Cody & F. Kehoe 12676.

Draba lonchocarpa Rydb.

2*n* = 16: ENE. of Saskatchewan Glacier near Sunwapta Pass, 52°11′ N., 117°05′ W., Banff National Park, Alberta, occasional on dry, shale slopes above 7000 ft, Calder & MacKay 32710A. 2*n* = 16: Below Stanley Peak, Kootenay National Park, 51°11′ N., 116°05′ W., British Columbia, occasional on sparsely vegetated limestone talus slopes well above tree line, Calder & MacKay 32771. *n* = 8 (Fig. 8), 2*n* = 16: Fairy Lake, SSW. of Fort Nelson, 57°20′ N., 123°55′ W., British Columbia, common on talus slopes and rock slides and occasional along east facing cliffs at 4500 to 5000 ft, Calder and Kukkonen 27216. *n* = 8: about 3 mi W. of head of Cumshewa Inlet below north face of Mount Moresby, Moresby Island, Queen Charlotte Islands, British Columbia, Calder & Taylor 36382.

Draba McCallae Rydb.

n = 41 (Fig. 9): Highwood Summit on Kananaskis Road about 37½ mi S. of Kananaskis, Alberta, occasional in disturbed soil by roadside in late-snow

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FIGS. 1–8. ×2000. Fig. 1. *Draba aurea*, 2*n* = 37. Fig. 2. *D. crassifolia*, *n* = 20. Fig. 3. *D. hyperborea*, *n* = 18. Fig. 4. *D. hyperborea*, *n* = 19. Fig. 5. *D. incerta*, 2*n* = ca. 112. Fig. 6. *D. lanceolata*, *n* = 16. Fig. 7. *D. lanceolata*, *n* = 24. Fig. 8. *D. lonchocarpa*, *n* = 8.

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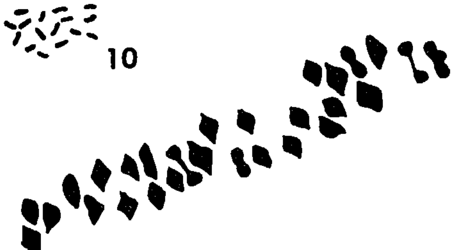

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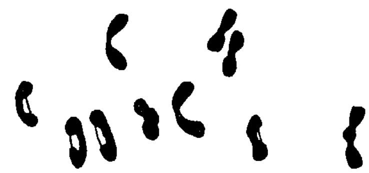

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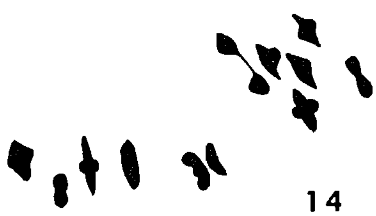

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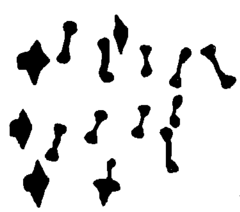

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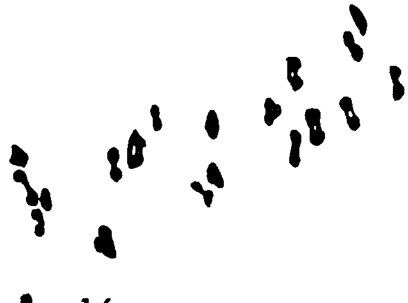

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area just below summit on heathy slope, Calder 37270. $2n = 40_{II} + 1_{I}$: Sunwapta Pass near Banff–Jasper Park boundary, dry gravelly slope at edge of valley, 6700 ft, Calder 23936.

Draba nemorosa L.

$2n = 16$ (Fig. 10): 6 mi S. of Elkwater, Sask., roadside slope, Sherk & Taylor 134. $n = 8$: 5 mi SE. of Athabaska Falls, Alberta, disturbed gravelly area along road, T. & L. Mosquin 4685.

Draba praealta Greene

$n = 28$: Highwood Summit on Kananaskis Road about 37½ mi S. of Kananaskis, Alberta, occasional in disturbed soil by roadside in late-snow area just below summit. Calder 37269. $n = 28$ (Fig. 11): Line Creek Cabin, approximately 49°58′ N., 114°44′ W., British Columbia, occasional on grassy–willow margin of small spring fed creek at 5200 ft, Taylor & Ferguson 3187.

Draba reptans (Lam.) Fernald

$n = 15$, $2n = 30$ (Fig. 12): 3 mi au sud-ouest de Móntmarte, District de Weyburn, Saskatchewan, coulée de la Montagne d'Original, B. Boivin 13494. $n = 15$: 2 mi NNW. of Savoy, Lawrence Co., Black Hills, South Dakota, Mulligan & Mosquin 2804.

Draba spectabilis Greene

$n = 10$ (Fig. 13): 10 mi SW. of Silverton, San Juan Co., Colorado, on steep rock faces and in crevices at 10,400 ft, Mulligan & C. Crompton 3065.

Draba stenoloba Ledeb.

$n = 12$ (Fig. 14): 9.4 mi W. of the Snowy Range Pass, Medicine Bow Mountains, Carbon Co., Wyoming, T. & L. Mosquin 4659.

Erophila verna L.

$n = 15$ (Fig. 15): 0.3 mi S. of junction of Hwys. 41 and 53, north of Rathdrum, Kootenai Co., Idaho, Taylor (no voucher specimen).

$2n = 19_{II} + 1_{I}$ (Fig. 16): about 4 mi W. of Grand Forks on highway to Greenwood, British Columbia, occasional on open, south-facing, grassy slopes on north side of valley, Calder & K. W. Spicer 33089.

Erysimum amoenum (Greene) Rydb.

$n = 18$ (Fig. 17): 16½ mi SSW. of Ouray, Ouray Co., Colorado, fairly common on rocky slopes of mountains at 10,700 ft, dark purple flowers, Mulligan & Mosquin 2748.

Erysimum amophilum Heller

$n = 18$: ½ mi N. of the Naval Post-graduate School, Monterey, Monterey Co., California, scattered plants on partially stabilized sand dunes above the shore of Monterey Bay, T. C. Fuller 11702.

FIGS. 9–17. ×2000. Fig. 9. *Draba McCallae*, $n = 41$. Fig. 10. *D. nemorosa*, $2n = 16$. Fig. 11. *D. praealta*, $n = 28$. Fig. 12. *D. reptans*, $2n = 30$. Fig. 13. *D. spectabilis*, $n = 10$. Fig. 14. *D. stenoloba*, $n = 12$. Fig. 15. *Erophila verna*, $n = 15$. Fig. 16. *E. verna*, $2n = 19_{II} + 1_{I}$. Fig. 17. *Erysimum amoenum*, $n = 18$.

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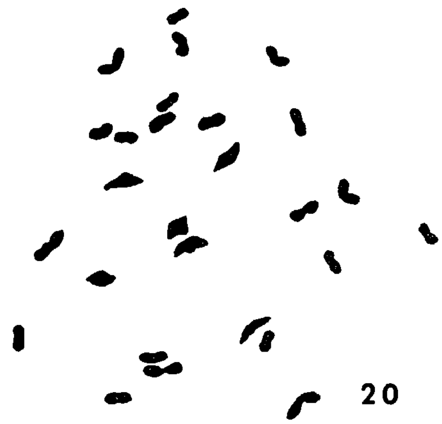

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Erysimum asperum (Nutt.) DC.

$n = 18$: 2 mi E. of Sidney on Hwy. 1, approximately 40 mi E. of Brandon, Manitoba, Taylor & Sherk 4782. $2n = 36$ (Fig. 18): Mortlach, Saskatchewan, very sandy prairie, J. H. Hudson 2057. $2n = 36$: 27 mi S. of junction of State Hwy. 23 and U.S. Hwy. 85, North Dakota, arid slope, J. M. Gillett & Taylor 11690. $n = 18$: 71 mi SSW. of Lead, Lawrence Co., Black Hills, South Dakota, common on steep rocky slope at 5150 ft, Mulligan & Mosquin 2803. $n = 18$: 68 mi N. of Rawlins, along Hwy. 220, Natrona Co., Wyoming, Mulligan & Mosquin 2789.

Erysimum capitatum (Dougl.) Greene

$2n = 36$: Mountain near Kennedy River on Tofino–Alberni road, 49°13′ N., 125°23′ W., Vancouver Island, British Columbia, locally common on boulder–gravel talus slopes from 2500 to 3000 ft, Calder & MacKay 32024. $2n = 36$ (Fig. 19): Mount Albert Edward, Forbidden Plateau, 49°41′ N., 125°26′ W., V.I., B.C., common and scattered everywhere on open rocky slopes from 6000 ft up, Calder & MacKay 32184. $2n = 36$: Salmon River, between Somes bar and forks of Salmon, Siskiyou Co., California, H. G. Baker (no voucher specimen).

Erysimum inconspicuum (S. Wats.) MacM.

$n = 27$ (only bivalents were formed at metaphase I, Fig. 20; lagging occurred at anaphase I and II; 5, 6, or 7 microspores were usually formed): Rampart House on Yukon–Alaska border, Yukon Territory, sand and gravel creek bed, J. E. H. Martin 40. $n = 27$ (only bivalents were formed at metaphase I, no observations were made on later stages): Rampart House on the Alaska–Yukon border, Yukon Territory, sand–gravel piled up by stream, Martin 24. $2n = 54$ (Fig. 21): Mile 13 on road to Dawson from Alaska Highway, Yukon Territory, 60°59′ N., 135°10′ W., common on open, SSW.-facing, prairie slopes and benches at 2100 ft, Calder & Kukkonen 28014. $2n = 54$: Tantalus Butte at Carmacks on Dawson–Whitehorse road, Yukon Territory, approx. 62°07′ N., 136°16′ W., occasional on open, steep, west-facing prairie slope above river at 2450 ft, Calder & Kukkonen 27983. $2n = 54$: $1\frac{1}{2}$ mi from Alaska Highway on road to Tagish, Yukon Territory, 60°20′ N., 134°00′ W., occasional in grassy openings in dwarf birch thickets at edge of woods at 2600 ft, Calder 28352. $2n = 26_{II} + 2_{I}$ to $25_{II} + 4_{I}$ at metaphase I (very irregular meiosis; lagging occurred at anaphase I and II; 5, 6, or 7 microspores were usually formed): Kugaluk River, Mackenzie District, Northwest Territories, 69°07′ N., 130°52′ W., among grass on slipping bank, Cody 12564. $2n =$ ca. 54: Cap à l'Original, Bic, Quebec, slaty field, H. J. Scoggan s.n. $2n = 22_{II} + 10_{I}$ at metaphase I, Fig. 22 (lagging at anaphase I and II; 5, 6, or 7 microspores were usually formed): 20 mi N. of Matapedia, Matapedia Co., Quebec, along river, Crompton & I. J. Bassett 27.

FIGS. 18–24. ×2000. Fig. 18. *Erysimum asperum*, $2n = 36$. Fig. 19. *E. capitatum*, $2n = 36$. Fig. 20. *E. inconspicuum*, $n = 27$. Fig. 21. *E. inconspicuum*, $2n = 54$. Fig. 22. *E. inconspicuum*, $2n = 22_{II} + 10_{I}$. Fig. 23. *E. inconspicuum*, $n =$ probably $37_{II} + 7_{I}$. Fig. 24. *E. pallasii*, $n = 12$.

n = 81/2 (very irregular meiosis; for example, one metaphase I plate had $36_{II} + 2_{III} + 3_{I}$; lagging occurred at anaphase I and II; and 5, 6, or 7 microspores were usually formed): along Madawaska River below Camel Chute, Renfrew Co., Ontario, steep slope in open pasture, W. G. Dore & Gillett 17515. n = 81/2 (one metaphase plate, see Fig. 23, probably $37_{II} + 7_{I}$; very irregular meiosis; 5, 6, or 7 microspores were usually formed): west side of St. Ignace Island, $1\frac{1}{2}$ mi S. of Whitefish Point on Nipigon Straits, Thunder Bay District, Ontario, open areas around old logging camp site, C. E. Garton 6807. n = 81/2 (meiosis was very irregular; lagging at anaphase I and II; 5, 6, or 7 microspores were usually formed): Ninette, Manitoba, roadside, Bassett 3580. n = ca. 81/2 (meiosis was very irregular; lagging at anaphase I and II; 5, 6, or 7 microspores were usually formed): near Jasper, Alberta, highway between C.N.R. tracks and Miette River, L. Jenkins 7954. n = ?? (meiosis was very irregular; lagging at anaphase I and II; 5, 6, or 7 microspores were regularly formed): 1 mi W. of Belleview, Alberta, only few plants seen, Mulligan & Mosquin 2673. n = ?? (meiosis was irregular; 5, 6, or 7 microspores were usually formed): 4 mi SE. of Michel, British Columbia, disturbed roadside, Mulligan & Mosquin 2678. n = 81/2 (from $40_{II} + 1_{I}$ to $30_{II} + 6_{III} + 3_{I}$ at metaphase I; very irregular meiosis; lagging at anaphase I and II; 5, 6, or 7 microspores were usually formed): 1 mi NW. of Elko, British Columbia, roadside and dry prairie, Mulligan & Mosquin 2681. n = ?? (lagging at anaphase I and II; 5, 6, or 7 microspores were usually formed; very irregular meiosis): $17\frac{1}{2}$ mi NW. of Townsend, Broadwater Co., Montana, common at base of steep slopes at 4425 ft, Mulligan & Mosquin 2815. n = ?? (very irregular meiosis; lagging at anaphase I and II; 5, 6, or 7 microspores were usually formed): 5 mi ESE. of Lonetree, Uinta Co., Wyoming, scattered plants among sagebrush at 7725 ft, Mulligan & Mosquin 2782. n = ?? (very irregular meiosis; lagging at anaphase I and II; 5, 6, or 7 microspores were usually formed): $32\frac{1}{2}$ mi eastward along Hwy. 50 from Gunnison, Gunnison Co., Colorado, a few plants on rolling slopes at 8450 ft, Mulligan & Mosquin 2758. n = ?? (very irregular meiosis; lagging at anaphase I and II; 5, 6, or 7 microspores were usually formed): 3 mi ESE. of Bonanza, Custer Co., Idaho, scattered plants on screes at 6050 ft, Mulligan & Mosquin 2705.

Erysimum pallasii (Pursh) Fern.

n = 12 (Fig. 24): Richardson Mountains on Yukon–Mackenzie border, 67°57′ N., 136°27′ W., Mackenzie District, Northwest Territories, locally common on step, west-facing, shale slope in valley bottom, 2500 ft, Calder 34130. $2n$ = 24: Trout Lake near Babbage River, approx. 68°51′ N., 138°42′ W., edge of British Mountains, Yukon Territory, occasional on open shale slopes back from lake, Calder 34295.

Erysimum repandum L.

n = 8: Flagstaff, Coconino Co., Arizona, a few plants at northern outskirts of town, Mulligan & Mosquin 2734.

Discussion

The Genus Draba

The genus *Draba* contains a large number of mainly arctic and alpine species that are primarily found in the Northern Hemisphere. The chromosome numbers of many European species of this genus have been determined but relatively few North American species of *Draba* have been examined cytologically. It has been well documented that European species of *Draba* have chromosome numbers based on $x = 8$ (Darlington and Wylie 1955; Löve and Löve 1961; Tutin *et al.* 1964). The chromosome numbers reported in this paper now show that North American species of *Draba* have chromosome numbers based not only on $x = 8$ but also on other base numbers.

Draba incerta ($2n =$ ca. 112), *D. lanceolata* ($n = 16$ and 24), *D. lonchocarpa* ($n = 8$), *D. McCallae* ($n = 40$ and 41), and *D. nemorosa* ($n = 8$) have the $x = 8$ base number of European species. *Draba aurea* ($n =$ ca. 36 and 37), *D. crassifolia* ($n = 20$), *D. hyperborea* ($n = 18$ and 19), *D. praealta* ($n = 28$), *D. reptans* ($n = 15$), *D. spectabilis* ($n = 10$), and *D. stenoloba* ($n = 12$) obviously do not have chromosome numbers based on $x = 8$. It is impossible to determine the direction of evolution in North American species of *Draba* using the information now available. The base number of *D. crassifolia* could be either $x = 5$ or $x = 10$, of *D. praealta* either $x = 7$ or $x = 14$, of *D. reptans* either $x = 5$ or $x = 15$, of *D. spectabilis* either $x = 5$ or $x = 10$, and of *D. stenoloba* either $x = 6$ or $x = 12$. If the base numbers of North American species are $x = 8$, 7, 6, and 5, we should eventually find diploid species with these base numbers. However, evolution in North American species may have taken place through aneuploidy at the polyploid level. Duplicate genetic material may have been lost at the tetraploid level resulting in a reduction in chromosome number from $n = 16$ to 15, 14, 13?, 12, 11?, and 10. There is, of course, always the possibility that both of these processes may have operated in North American populations of *Draba*. It has often been suggested that experimental methods should be used to help clarify the confusing taxonomy of the genus *Draba*. Tutin *et al.* (1964, p. 308) in the *Flora Europaea* have stated that "the limits and particularly the rank of many described taxa are disputable, and experimental work is needed in the genus". Certainly very little experimental work has been attempted on North American species of *Draba*. This may partly be due to the fact that many of the taxonomic problems in North American *Draba* are nomenclatural not biological. Perhaps the evolutionary problems suggested in this paper will overcome the tendency of North American "experimental taxonomists" to ignore this interesting genus.

The Genus Erophila

Erophila verna is included in the genus *Draba* by most North American botanists. European botanists, including Tutin *et al.* (1964) in the *Flora Europaea*, place these small annual scapigerous herbs with basal leaf-rosettes and deeply bifid petals in the genus *Erophila* not *Draba*. Since I prefer the European treatment of this group of plants, I am using the name *Erophila verna* instead of *Draba verna* for the species being considered here.

Erophila verna is native to North America and Eurasia. Winge (1940) determined the following chromosome numbers from European material: $n = 7$, 12, 15, 16, 17, 18, 20, 26, 29, and 32. Plants from four locations in Europe had univalent chromosomes. In North America, plants from two locations were examined: one had 15 bivalents at metaphase I and the other had 19 bivalents and 1 univalent. An aneuploid series of chromosome numbers apparently also occurs in North American populations of *E. verna*.

The Genus Erysimum

Four species of *Erysimum* native to North America, *E. amoenum*, *E. amophilum*, *E. asperum*, and *E. capitatum*, have the chromosome number $n = 18$ and $2n = 36$. Pollen mother cells of these four species have 18 bivalents at diakinesis and first metaphase. All four species have large odoriferous flowers and at least the latter two species are self-incompatible outcrossers. Raven *et al.* (1965) reported $n = 18$ in plants of *E. capitatum* from California.

Another native species, *Erysimum inconspicuum*, has flowers much smaller than those of the above four species and unlike them *E. inconspicuum* almost certainly reproduces by agamospermy. Although *E. inconspicuum* produces abundant seed, all plants examined had very abnormal meiosis and pollen mother cells produced five, six, or seven microspores. Plants from Quebec, Mackenzie District, and Yukon Territory were $n = 27$ and $2n = 54$, whereas plants from Ontario, Manitoba, Alberta, and British Columbia were $n = 81/2$. Pollen mother cells of plants from one location in British Columbia (Mulligan and Mosquin 2681) had from 40 bivalents plus 1 univalent to 32 bivalents plus 3 trivalents plus 8 univalents at first metaphase. This is the first indication of agamospermy in the family Cruciferae in any genus except *Arabis*. Böcher (1951) found agamospermy in North American and Greenland material of *Arabis holboellii* and Mulligan (1964) reported agamospermy in many other North American species of *Arabis*.

Erysimum pallasii, native to arctic North America, has the chromosome number $n = 12$ and $2n = 24$ in the Richardson Mountains, Northwest Territories, and in the British Mountains, Yukon Territory. Packer (1964) reported $n =$ ca. 12 for material from the Richardson Mountains. Holmen (1952) reported $2n =$ ca. 28 for material from Greenland. *Erysimum pallasii*, like *E. inconspicuum*, has chromosomes of several different sizes and it is very difficult to determine the chromosome number of this species from mitosis. I have examined mitotic chromosomes in plants of *E. pallasii* from Hazen Camp, Ellesmere Island, and feel confident that the chromosome number was higher than $2n = 24$. Meiosis in the Ellesmere Island material was also extremely irregular. It seems likely that some populations of *E. pallasii* have a chromosome number higher than $n = 12$ and $2n = 24$.

European and Asiatic species of *Erysimum* have the basic chromosome number of $x = 7$ or $x = 8$ (Darlington and Wylie 1955; Löve and Löve 1961). The chromosome numbers of North American species ($2n = 36$, 54, and 81) suggest that evolution in *Erysimum* has proceeded along different lines on this continent as compared to the development of the genus in Europe and Asia. The base number in North American species of *Erysimum* is probably $x = 9$. It would certainly be interesting to find North American species of *Erysimum* that are diploid sexual outcrossers.

The chromosome number $n = 8$ for Arizona material of the introduced weed *E. repandum* was previously obtained on European material by Manton (1932) and Löve and Löve (1956).

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