

CHROMOSOMAL RACES IN
EASTERN NORTH AMERICAN SPECIES
OF HEDYOTIS (HOUSTONIA)¹

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In a phylogenetic study of the North American species of *Hedyotis* (including *Houstonia*) (Rubiaceae), Lewis (1962 b) reported diploid and tetraploid races in populations of *H. caerulea*, *H. polypremoides* (Gray) Shinnery, and *H. purpurea*. Reference was made to a more extensive study of the occurrence of infraspecific polyploidy. The purpose of this paper is to report these findings.

Chromosome numbers of 116 collections of species in the *H. caerulea* and *H. purpurea* groups were determined. P. M. C. meiosis or somewhat less frequently mitosis was studied in immature flower buds fixed in the field. The methods used to prepare slides were identical to those described for *Hedyotis* (Lewis, 1962b). In addition, representative permanent slides were mounted in euparal. Voucher specimens for each collection are filed in the herbaria of the U. S. National Museum (US), the Southern Methodist University (SMU), or Indiana University (IND; one collection).

The nomenclature of the *H. purpurea* complex follows the revision by Terrell (1959) except that the taxa are treated under *Hedyotis* rather than *Houstonia* (Lewis, 1961). This does not imply acceptance of *Hedyotis* by Terrell.

RESULTS

The chromosome numbers of *Hedyotis purpurea*, *H. longifolia*, *H. canadensis*, *H. nuttalliana* (= *Houstonia tenuifolia* Nutt.), *H. caerulea*, and *H. michauxii* (= *Houstonia serpyllifolia* Michx.), are listed with voucher data and, in parentheses, the number of plants examined. Although the chromosome numbers of several collections were published by Lewis (1962b), as indicated by an asterisk, they are included for completeness and as a basis for mapping.

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1. *H. purpurea* (L.) T. & G.1a. *H. purpurea* var. *purpurea*

n = 6. SOUTH CAROLINA: Edgefield Co., 4 miles WSW of Owdoms, *Terrell & Barclay* 3430 (3). TEXAS: Newton Co., 2.8 miles S of Newton, *Lewis* 5620 (5)*.

n = 6, n = 12. TENNESSEE: Polk Co., 0.5 mile N of Hwys. 64 & 30 junction, *Lewis* 5638 (4 2n, 2 4n).

n = 12. GEORGIA: Gilmer Co., 3.9 miles NE of Ellijay, *Lewis* 5645 (3). MARYLAND: Montgomery Co., Wheaton, *Terrell* 3525 (4). NORTH CAROLINA: Guilford Co., Guilford College, *Terrell* 3244 (1)*; Jackson Co., summit of Whitesides Mountain, *Terrell & Barclay* 3472 (3); Macon Co., SE of Highlands, *Terrell & Barclay* 3463 (2); Standing Indian Wildlife Management Area, *Terrell & Barclay* 3478 (2). TENNESSEE: Cheatham Co., near Kingston Springs, *Terrell & Barclay* 3360; Cumberland Co., 1.5 miles W of Ozone, *Terrell & Barclay* 3516 (3); Polk Co., 2.5 miles E of Hwys. 64 & 30 junction, *Lewis* 5643 (atypical) (4); Sullivan Co., near Sullivan-Carter Co. line & Hwy. 19E, *Terrell & Barclay* 3524 (3). VIRGINIA: Sussex Co., along Nottoway River W of Homeville, *Terrell* 3636 (2).

1b. *H. purpurea* var. *calycosa* (Gray) Fosberg

n = 6. TENNESSEE: Wilson Co., Cedars of Lebanon State Park, *Terrell & Barclay* 3339 (5); W border of Lebanon, *Terrell & Barclay* 3340 (6).

n = 12. ALABAMA: Franklin Co., 7 miles E of Russellville, *Terrell & Barclay* 3499 (3); just E of Russellville, *Terrell & Barclay* 3361 (2); Jackson Co., 3 miles W of Scottsboro, *Terrell & Barclay* 3485 (3). MISSISSIPPI: Carroll Co., 1.5 miles E of Carrollton, *Lewis* 5634 (atypical) (3). TENNESSEE: Maury Co., 16 miles NW of Lewisburg, *Terrell & Barclay* 3351 (4)*; Meigs Co., 7 miles S of Decatur, *Terrell & De Selm* 3246 (1).

1c. *H. purpurea* var. *montana* (Small) Fosberg

n = 6. TENNESSEE-NORTH CAROLINA: Carter Co.-Mitchell Co., summit of Roan Mountain, *Terrell & Barclay* 3615 (2).

2. *H. longifolia* (Gaertn.) Hook.2a. *H. longifolia* var. *longifolia*

n = 6. MASSACHUSETTS: Middlesex Co., Horn Pond, Woburn, *E & B Terrell* 3595 (3).

n = 6, n = 12. MINNESOTA: Chisago Co., St. Croix River at Taylors Falls, *Likhite*, July 1961 (2 2n, 5 4n).

n = 12. ONTARIO: Norfolk Co., Turkey Point, *C & M Heimbürger*, 15 July 1961 (1).

2b. *H. longifolia* var. *compacta* (Terrell) Lewis

n = 6. GEORGIA: Meriwether Co., 5 miles W of Greenville, *Terrell & Barclay* 3410 (2). NORTH CAROLINA: Alexander Co., base of Rocky Face Mountain, *Terrell* 3257 (1)*. SOUTH CAROLINA: Abbeville Co., E side of Savannah River, *Terrell & Barclay* 3424 (atypical) (1); Anderson Co., ca. 11 miles NNE of Anderson, *Terrell & Barclay*

3451 (2); Lexington Co., ca. 10 miles S of Columbia, *Terrell & Barclay* 3444 (atypical) (3). VIRGINIA: Augusta Co., 11 miles NE of Hwys. 42 & 250 junction, *E & B Terrell* 3569 (3); Frederick Co., 2 miles WNW of Gore, *E & B Terrell* 3539 (2); Page Co.-Madison Co. line, Milepost 47, Skyline Drive, Shenandoah Natl. Pk., *E & B Terrell* 3577 (3); Rappahannock Co., Hazel Mountain Overlook, Shenandoah Natl. Pk., *Terrell* 60-11 (2) (no voucher); Shenandoah Co., 4.5 miles SW of Jerome, *E & B Terrell* 3567 (3). Another collection is quite atypical: GEORGIA: Dade Co., Lookout Mountain, *Terrell & De Selm* 3254 (1).

n = 12. MARYLAND: Frederick Co., Boonesboro Mountain Rd. & Hwy. 40 junction, *E & B Terrell* 3533 (4). SOUTH CAROLINA: Edgefield Co., near Hwy. 378 & 67 junction, *Terrell & Barclay* 3429 (3). VIRGINIA: Augusta Co.-Albemarle Co., 0.4 miles S of Milepost 97, Skyline Drive, Shenandoah Natl. Pk., *E & B Terrell* 3570 (3); Bedford Co., Milepost 90, Blue Ridge Parkway, *Terrell* 3250 (2); Rockingham Co.-Greene Co., Sandy Bottom Overlook, Skyline Drive, Shenandoah Natl. Pk., *E & B Terrell* 3573 (2). WEST VIRGINIA: Pendleton Co., 5 miles N of Hwy. 33 & Spruce Knob rd. junction, *E & B Terrell* 3545 (3).

2c. *H. longifolia* var. *glabra* (Terrell) Lewis

n = 6. NORTH CAROLINA: Jackson Co., summit of Whitesides Mountain (type locality), *Terrell & Barclay* 3473 (3); Macon Co., near Highlands, *Terrell* 3255 (1)*; Slick Rock, SE of Highlands, *Terrell & Barclay* 3464 (2).

3. *H. canadensis* (Willd. ex R. & S.) Fosberg

n = 6. TENNESSEE: Cheatham Co., near Kingston Springs, *Terrell & Barclay* 3358 (4).

n = 12. INDIANA: Clark Co., 4 miles NW of Henryville, *Terrell* 3251 (1)*. TENNESSEE: Marion Co., below Hales Bar Dam, *Terrell & Barclay* 3480 (3). ONTARIO: Bruce Co., Bruce Peninsula, Red Bay, *Heimburger & Price*, 17 June 1961 (2).

4. *H. nuttalliana* Fosberg

n = 6. ALABAMA: Randolph Co., ca. 5 miles W of Wedowee, *Terrell & Barclay* 3397 (4); Saint Clair Co., 0.5 mile W of Hwys. 35 & 53 junction, *Terrell & Barclay* 3391 (3). ARKANSAS: Montgomery Co., 11.5 miles WSW of Norman, *Lewis* 5169 (2)*. GEORGIA: Heard Co., 3 miles SW of Franklin, *Terrell & Barclay* 3401 (5). NORTH CAROLINA: Stokes Co., Hanging Rock State Park, *Terrell* 3243 (1)*. OKLAHOMA: LeFlore Co., Lake Wister State Park, *Lewis* 5161 (2)*. SOUTH CAROLINA: Lexington Co., ca. 4 miles E of Lexington Co.-Saluda Co. line, *Terrell & Barclay* 3445 (3). VIRGINIA: Shenandoah Co., 2.6 miles E of Liberty Furnace, *E & B Terrell* 3560 (3).

5. *H. caerulea* (L.) Hook.

5a. *H. caerulea* var. *caerulea*

n = 8. ALABAMA: Blount Co., ca. 3 miles E of Cullman, *Terrell*

& *Barclay* 3387 (3); Randolph Co., ca. 5 miles W of Wedowee, *Terrell & Barclay* 3398 (3); Saint Clair Co., 0.5 mile W of Hwys. 35 & 53 junction, *Terrell & Barclay* 3392 (3); Talladega Co., 2-3 miles W of Talladega Co.-Clay Co. line & Hwy. 77, *Terrell & Barclay* 3396 (2). ARKANSAS: Clark Co., 2.4 miles SE of Alpine, *Lewis* 5171 (3)*; Dallas Co., 1.9 miles S of Ouachita, *Lewis* 5172 (3)*; Hot Spring Co., 1.5 miles NE of Donaldson, *Lewis* 5613 (1). GEORGIA: Gilmer Co., 3.9 miles NE of Ellijay, *Lewis* 5646 (1). INDIANA: Brown Co., near Trevlac, *Heiser & Ellis* 4763 (IND) (3). KENTUCKY: Logan Co., 1.3 miles SW of Auburn, *Lewis* 5602 (2); Metcalf Co., 3.1 miles E of Wisdom, *Lewis* 5605 (4). NORTH CAROLINA: Alleghany Co., 2 miles NE of Blue Ridge Parkway & Hwy. 21 junction, *Terrell* 3242 (2); Jackson Co., ca. 4 miles E of Cashiers, *Terrell & Barclay* 3455 (3); Macon Co., Nantahala River & Hwy. 64, *Terrell & Barclay* 3479 (3). SOUTH CAROLINA: Lexington Co., ca. 4 miles E of Lexington Co.-Saluda Co. line, *Terrell & Barclay* 3446 (3). TENNESSEE: Cheatham Co., near Kingston Springs, *Terrell & Barclay* 3359 (3); Stewart Co., 12.9 miles WSW of Dover, *Lewis* 5601 (2); Kentucky Lake & Hwy. 79, *Lewis* 5610 (2).

n = 9. ARKANSAS: Hot Spring Co., 3.6 miles NNE of Hwys. 67 & 210 junction, *Lewis* 5612 (2).

n = 16. CONNECTICUT: Litchfield Co., 1-1/2 miles S of junction 112 & 7, Salisbury Twp., *Terrell* 3662 (1); Tolland Co., 3 miles S of Rockville, *Terrell* 3663 (2); near State Line Pond, *Terrell* 3664 (3). MAINE: York Co., North Berwick, *E & B Terrell* 3591 (1). MARYLAND: Frederick Co., Catoctin Creek & Hwy. 17, *E & B Terrell* 3538 (1); Montgomery Co., Wheaton Regional Park, *Terrell* 3526 (2). MASSACHUSETTS: Franklin Co., 3 miles S of Northfield, *Terrell* 3667 (3); Worcester Co., 1/2 mile N of Hardwick, *Terrell* 3665 (3). NEW HAMPSHIRE: Cheshire Co., 3 miles E of Winchester, *Terrell* 3666 (1); Coos Co., lower slopes of Mount Washington (alt. 2500 ft.), *E & B Terrell* 3589 (2); Grafton Co., Hanover, *Fosberg* 39838 (2). NORTH CAROLINA: Guilford Co., Guilford College, *Terrell* 3231 (5)*; Stokes Co., NW of Francisco, *Terrell* 3239 (1)*. PENNSYLVANIA: Franklin Co., 0.5 mile N of Richmond Furnace, *Terrell* 3629 (2); Juniata Co., 5 miles NE of East Waterford, *Terrell* 3628 (4); Perry Co., 1 mile SE of Sherman-dale, *Terrell* 3627 (3). SOUTH CAROLINA: Edgefield Co., ca. 4 miles WSW of Owdoms, *Terrell & Barclay* 3431 (2). TENNESSEE: Cumberland Co., 7 miles SE of Mayland, *Terrell & Barclay* 3514 (3); Knox Co., Knoxville, *De Selm*, 1 May 1962 (1). VERMONT: Windham Co., 2 miles W of Brattleboro, *Terrell* 3668 (2). VIRGINIA: Hanover Co., 2 miles NW of Doswell, *Terrell* 3631 (2); Page Co.-Madison Co., Big Meadows, Shenandoah Natl. Pk., *E & B Terrell* 3575 (2). WEST VIRGINIA: Tucker Co., 8 miles S of Davis, *E & B Terrell* 3544 (2); 1-2 miles N of Thomas, *E & B Terrell* 3540 (1). ONTARIO: Toronto (introduced), *Heimbürger*, 5 May 1961 (4) (omitted from map in Fig. 2).

n = 24. VIRGINIA: Sussex Co., along Nottoway River W of Homeville, *Terrell* 3634 (1).

5b. *H. caerulea* var. *faxonorum* (Pease & Moore) Fosberg

n = 16. NEW HAMPSHIRE: Coos Co., below summit of Mount Washington (alt. 6000 ft.), *E & B Terrell* 3586 (4).

6. *H. michauxii* Fosberg

n = 16. NORTH CAROLINA: Macon Co., Standing Indian Wildlife Area, *Terrell & Barclay* 3477 (3); Transylvania Co., 0.5 mile N of Davidson River & Hwy 64 junction, *Terrell & Barclay* 3460 (4). TENNESSEE: Monroe Co., Cherokee National Forest, *De Selm*, 1 May 1962 (3). TENNESSEE-NORTH CAROLINA: Carter Co.-Mitchell Co., summit of Roan Mountain, *Terrell & Barclay* 3520 (5).

n = 24. NORTH CAROLINA: Alleghany Co., 2 miles NE of Blue Ridge Parkway & Hwy. 21 junction, *Terrell* 3241 (1)*.

7. Putative hybrids or intergrading collections

7a. *H. longifolia*—*H. purpurea*

n = 6. SOUTH CAROLINA: McCormick Co., 2.5 miles NW of Mount Carmel, *Terrell & Barclay* 3425 (1) (< *longifolia*).

n = 12. GEORGIA: Elbert Co., 2 miles W of Hwys. 72 & 79 junction, *Terrell & Barclay* 3423 (2) (< *longifolia*); Rabun Co., ca. 7 miles S of North Carolina-Georgia line & Hwy. 28, *Terrell* 3147 (1); Walton Co., 4 miles NE of Monroe, *Terrell & Barclay* 3420 (2) (< *longifolia*). TENNESSEE: Cumberland Co., 2 miles NW of Mayland, *Terrell & Barclay* 3513 (3) (< *purpurea*).

7b. *H. canadensis* > — *H. purpurea*

n = 12. INDIANA: Clark Co., 4 miles NW of Henryville, *Terrell* 3252 (1).

7c. *H. caerulea*—*H. michauxii*

n = 16. WEST VIRGINIA: Tucker Co., just above Blackwater Falls, *E & B Terrell* 3542 (5).

DISCUSSION

The basic chromosome number of *Hedyotis purpurea*, *H. longifolia*, *H. canadensis*, and *H. nuttalliana* is $x = 6$. The basic chromosome number of *H. caerulea* and *H. michauxii* is $x = 8$. These data agree with the morphological evidence: the first four species are closely related and were included by Terrell (1959) in the *H. purpurea* group; the last two species are so alike that herbarium material sometimes is difficult to distinguish.

A dash, —, is used here to indicate morphological intergradation. The second author prefers to use this symbol instead of X, as in this case additional knowledge about the species is needed to attribute their intermediacy to hybridization. He believes that botanists should restrict the use of X to instances in which evidence of hybridization has been thoroughly studied. The symbols > and < were used by others (cf. Li, 1957; Hardin, 1958). For example, *H. canadensis* > — *H. purpurea* denotes specimens which intergrade but are more similar to the former species.

In *H. purpurea* (Fig. 1) our sampling indicates that tetraploid populations are in the great majority. The only known $2n$ populations are in the southern part of the range. One population included both $2n$ and $4n$ individuals. The sampling is not sufficient to show any geographic separation of chromosomal races, if such exists. Var. *montana*, the only known stations for which are on Roan Mountain and Grandfather Mountain, is diploid at the former station (not shown in Fig. 1).

In contrast to *H. purpurea*, *H. longifolia* has almost twice as many $2n$ populations as $4n$. These are found in the north



Figure 1. Generalized range (enclosed by dashed line) of *H. purpurea* and locations of diploid and tetraploid collections. Var. *montana* not shown. New England distribution of *var. calycosa* not shown.

as well as in the south, and one population in Minnesota contains individuals with both chromosome numbers. Var. *glabra*, restricted to the southern Appalachians, is diploid on the basis of three collections.

Plants of *H. canadensis* from only four localities were studied but these included samples from the extremes of the species range in Tennessee and Ontario. On the basis of the small sample, the tetraploids prevail over the diploids in a proportion similar to that for *H. purpurea*. With both $2n$ and $4n$ races in Tennessee, no geographic separation of the forms is apparent. Only $2n$ individuals were found among plants of *H. nuttalliana* from 8 stations in 7 states, from Virginia to Oklahoma. This sample is sufficiently large and widespread to indicate that tetraploid individuals must be rare in *H. nuttalliana* if they exist. Intraspecific polyploidy is probably unimportant in the recent evolution of the species. On the basis of the frequency of diploidy and tetraploidy, with the high frequency of tetraploidy representing the higher stage of evolution, the species in the $x = 6$ group can be ranked from the simplest to the most specialized as: *H. nuttalliana* ($2n$ only), *H. longifolia* ($2n:4n = 2:1$), *H. purpurea* and *H. canadensis* ($2n:4n = 1:3$). Using this criterion, *H. nuttalliana* is the least evolved species of the series, a position corroborating the results of Lewis (1962b) based chiefly on morphological evidence.

Among 45 collections of *H. caerulea* var. *caerulea* sampled from a wide area of the species range, 18 were diploid ($n = 8$), 25 were tetraploid ($n = 16$), one was aneuploid ($n = 9$), and one was hexaploid ($n = 24$). Thus, this species consists predominantly of $2n$ and $4n$ populations, with the latter slightly outnumbering the former in our sample. The base number is $x = 8$. The chromosomal races appear to have partly distinct distributions: the diploid race is widely distributed in the southern United States (Fig. 2) and in our sample occurs only south of the glacial boundary. Only tetraploids are known in New England, but they do occur also in certain parts of the South. The single collection of var. *faxonorum*, a variety restricted primarily to higher altitudes in the White Mountains, was tetraploid.

On the basis of a single population of *H. michauxii*, Lewis

(1962b) reported the species as hexaploid. Additional sampling has shown, however, that $4n$ and $6n$ races exist, the former occurring much more frequently. The species is limited in distribution to the higher regions of the southern and central Appalachians, a distribution interestingly associated with the finding of two polyploid races and no diploid forms in a subgenus where "pure" polyploid species are infrequent.

In the P. M. C.'s of all plants examined, bivalent formation and separation by and large were regular. Occasionally 1 to 3 quadrivalents were observed at metaphase I in the $4n$ plants (e.g., *H. purpurea*, Terrell & Barclay 3351; *H. caerulea*

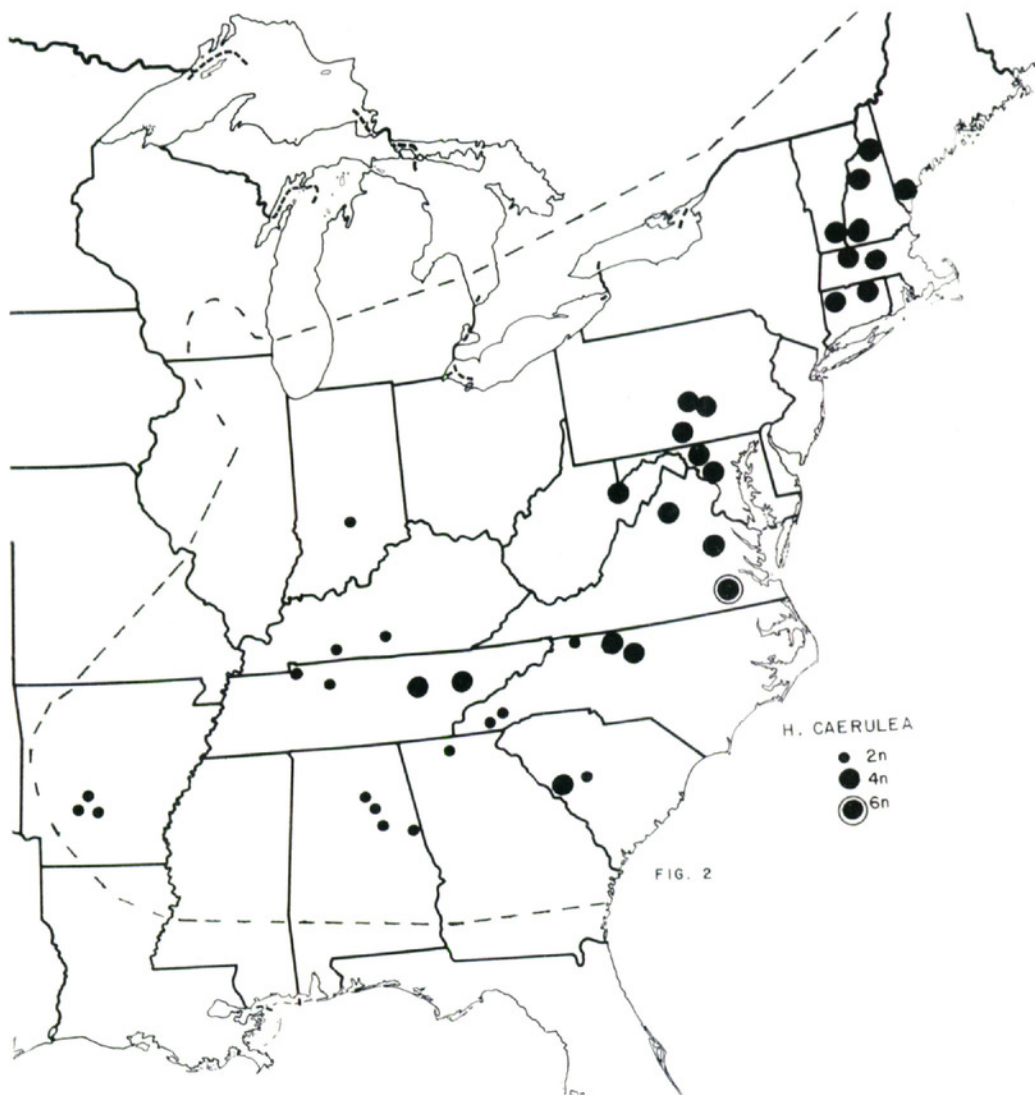


Figure 2. Generalized range (enclosed by dashed line) of *H. caerulea* and locations of diploid and polyploid collections. The single aneuploid ($n = 9$) collection not shown.

lea, Terrell 3627), but these were exceptional. Spindle disturbances were not observed. In one cell, a plant of *H. caerulea* (Lewis 5610) had $2n=15$, but all other mitotic cells had $2n=16$ and in the P. M. C.'s $n=8$. Although statistical data are not available, plump, well-stained pollen grains were noted for most diploids and tetraploids. If the fertility of the tetraploids was decreased markedly in comparison with the diploids it was not apparent from observations of pollen.

Seven collections were of intermediate or intergrading morphology. Certain of these are putative hybrids. As no definite evidence of hybridization is available, we are using a dash (—) to connect the two names. This is intended to indicate intergradation without necessarily suggesting hybridization as its cause. In the seven collections diploid and tetraploid populations were found, with the latter more frequent. Of the five collections of *H. purpurea* — *H. longifolia*, a diploid (Terrell & Barclay 3425) had regular pairing at metaphase I as did all P. M. C.'s examined from the tetraploid individuals of *T. & B.* 3420 and 3513. Only mitosis was observed in the other two collections of *H. longifolia* — *H. purpurea* and in *H. canadensis* — *H. purpurea*. Meiosis in *H. caerulea* — *H. michauxii* was regular; this population is not thought to be of hybrid origin. Pollen was more or less normal in individuals of the seven collections. In general, the chromosome data indicate that chromosome number *per se* is no barrier to hybridization in these species within each ploidy level, i.e. $x=6$ and $x=8$. The chromosome numbers in the *H. purpurea* group are entirely compatible with the data from morphology expressed in the taxonomic treatment of this group by Terrell (1959) but the few admittedly preliminary chromosome counts listed in the same paper should be ignored.

As more cyto-population research is completed, it becomes apparent that varying chromosome numbers for a species are much more common than hitherto suspected. In the Rubiaceae alone, where very few cytological studies have been completed, infraspecific polyploidy has been recorded for species of 13 genera, particularly in the Rubieae (Fagerlind, 1937; Ehrendorfer, 1961), *Coffea* and *Coprosma* (cf.

Darlington & Wylie, 1956), *Bouvardia* (Lewis, 1962a), and *Hedyotis* subg. *Oldenlandia* (Lewis, 1959, 1962b).

In *Hedyotis* subg. *Edrisia*, in which the species under discussion are classified, chromosome numbers of 25 species are known (Lewis, 1962b). Of these, seventeen species are diploid, four species are diploid and tetraploid, one species is diploid, tetraploid, and hexaploid, two species are tetraploid, and one species is tetraploid and hexaploid. Twenty-three species are euploid and two have recorded aneuploid individuals. Thus six species or 24% of the North American species studied have infraspecific polyploidy, 4% exhibit infraspecific aneuploidy, and 4% exhibit both infraspecific polyploidy and aneuploidy. All of these species are heterostylous perennials and with one exception are herbaceous. No chromosomal plasticity is known among the eight annual species of the subgenus or among the species having only short-styled flowers. This suggests a certain correlation in the subgenus between the heterostylous species constructed for outbreeding and the perennial habit with the occurrence of infraspecific polyploidy and aneuploidy.

The distributions of the diploid and tetraploid races of *H. caerulea*, *H. purpurea*, and *H. longifolia* may be grouped into two categories, viz., those with different geographic distributions and those without such tendencies. As an example of the first kind, the $2n$ race of *H. caerulea* occupies a southern range while the $4n$ race has a more northern distribution. Possibly the tetraploid race colonized areas drastically altered by glaciation in the northern region of the species' present range, while the ancestral race remained predominantly south of the glacial boundary (cf. Stebbins, 1950). It also appears that the $4n$ race is now successfully competing with the $2n$ race somewhat south of the southern limits of the last glaciation. The high altitude distribution and the polyploid races of *H. michauxii* also suggest the colonization of less favorable environments by a polyploid species. That this tendency is not universal, even for species in the same subgenus, is suggested by the infraspecific distributions for *H. purpurea* and *H. longifolia*. Their diploid and tetraploid races are about equally distributed and do not appear to have

either peripheral or central concentrations although we did not sample their entire ranges.

When herbarium specimens from all of these collections were compared, tetraploid and diploid (and hexaploid) plants of each taxon looked just alike; there were no observable gross morphological differences in plants of different ploidy levels and it is clear that these are autopolyploids. Five out of the six species had polyploid populations. Autopolyploidy is an essential feature of the evolution of the *H. caerulea* and *H. purpurea* groups.

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