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Biosystematic Studies of Three Sympatric Elephantopus Species (Compositae)

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BIOSYSTEMATIC STUDIES OF THREE SYMPATRIC *ELEPHANTOPUS* SPECIES (COMPOSITAE)

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ABSTRACT

The three sympatric species and two forms of Elephantopus found in Virginia show overlapping patterns of variation and have often been considered a taxonomic problem. Attempts to clarify the morphology and to better understand the causes of variation included both field and laboratory work.

Artificial hybridization was attempted in the greenhouse and several natural populations were analyzed with a hybrid index method. Additional field observations concerned the ecology and method of pollination. Both the culture plants and natural populations were tested for pollen fertility.

Cytological information, high pollen fertility and immature progeny from greenhouse crosses suggest that hybridization is possible between all combinations of the five taxa. Histograms and other diagrams constructed from hybrid index data show variation patterns corresponding to introgressants and only the occasional presence of forms exactly intermediate between two species. This may be due to genetic barriers, rapid ecological succession or lack of hybrid habitats which consequently preserves the species as recognizable units. Perhaps further intervention by man will provide more suitable niches for the establishment of interspecific hybrids which could lead to new intermediate groups or to one polymorphic species.

BIOSYSTEMATIC STUDIES OF THREE SYMPATRIC *ELEPHANTOPUS* SPECIES (COMPOSITAE)

INTRODUCTION

The genus Elephantopus is composed of about forty species of perennial herbs, primarily of tropical regions. Together with the more familiar "Ironweeds" of the genus Vernonia, and several related genera, Elephantopus is included in the Tribe Vernonieae of the sub-family Tubuliflorae of the family Compositae.

The classification proposed by Baker (1902) is slightly different. Baker considers Elephantopus as one of several closely related genera making up a separate Tribe Elephantopeae. A synonymic list of genera in this tribe includes:

1. Elephantopus L. 1753.
   = Euelephantopus Endl. 1836.
2. Spirochaeta Turcz. 1851.
3. Elephantosis Less. 1829.
4. Pseudelephantopus Rohr. 1792.
   = Distrepus Cass. 1817.
   = Matamoria La Llave. 1824.
5. Elephantopsis Sch. Bip. 1847.
6. Micropappus Sch. Bip. 1847.

Only four species of the genus Elephantopus occur in the United States. Of these, E. elatus Bertol. is restricted to the southeast from South Carolina south, while the other three range northward into Virginia and beyond. These are E. carolinianus Willd. and its forma vestitus Fern., the latter known only from southeastern Virginia, E. tomentosus and its forma rotundatus Fern. and E. nudatus Gray. Not only are these three rather similar species sympatric over much of their range, but in

eastern Virginia at least, they occupy similar habitats, have similar blooming periods, and share the same chromosome number of 2n=22 (Baldwin and Speese, 1955). This study will attempt to bring together what is known about the genus Elephantopus to date and more particularly to investigate the relationships of the three species and their forms, native to Virginia.

TAXONOMY OF THE GENUS

The genus Elephantopus may be described as follows (Gleason, 1922; Fernald, 1950; Gleason and Cronquist, 1963):

Elephantopus L.

> Herbs with leafy or scapiform stems. Leaves alternate or basal, entire or toothed, pinnately veined. Inflorescence of corymbed pedunculate glomerules of 1-several heads. Glomerules of heads terminating the branches, each glomerule subtended by 1-3 sessile cordate bracts. Heads 1-5 flowered. Involucre of 4 decussate pairs of scales, the two outer pairs shorter, the alternate pairs conduplicate; flowers all perfect and fertile; receptacle flat or nearly so. Corolla-tube slender, the limb unequally 5-cleft with a much deeper fissure on the inside. Anthers sagittate, obtuse at base. Style-branches slender. Achenes truncate, mostly 10-ribbed. Pappus of 5-8 short, rigid, flattened scales, usually prolonged into terminal bristles. Perennials of trop. and warm reg., with purplish flowers. (Name composed of the Greek elephus, elephant, and pous, foot, translation of aboriginal name.)
>
> Type species, Elephantopus scaber L.

A major treatment of the genus as a whole is C. F. Baker's "A revision of the Elephantopeae" published in 1902. The species occuring in North America (i.e., north of the Isthmus of Panama) have been studied and keys and descriptions furnished by Gleason (1922), for the North American Flora. From these and more recent publications plus Index Kewensis, 1895 and supplements through 1955, the known species of Elephantopus

are enumerated in the appendix.

DESCRIPTION OF VIRGINIA SPECIES

The three species of Elephantopus found in Virginia are described by Fernald (1950), Gleason and Cronquist (1963), and Gleason (1919, 1922). Basic characteristics are mentioned by all of these authors; however, more detailed observations are included in the following key to the three species and in the description of the five taxa.

The morphological terms are used according to Lawrence (1951). The term glomerule refers to an aggregation of several heads. The glomerule is subtended by three foliaceous bracts, and each head is composed of four complete flowers or florets. The chaffy involucral bracts surrounding each head are referred to as phyllaries.

Elephantopus L. - Elephant's foot

KEY TO SPECIES

A. Stem extensively branched, the branches spreading; leaves cauline, the first 4-7 of similar size, rhombic-ovate, abruptly and highly tapered to the base....1. E. carolinianus.

AA. Stem slightly branched, erect; leaves in a basal rosette, round-ovate to oblong -ovate, evenly tapered to the base.....B

B. Leaves densely to moderately pilose along midrib of lower side; bracts triangular to round-ovate; pappus 6-7.5mm. long.....2. E. tomentosus.

BB. Leaves slightly to moderately strigose along midrib of lower side; bracts oblong-ovate; pappus 5-5.5mm.....3. E. nudatus.

1. Elephantopus carolinianus Willd.

Elephantopus violaceus Schultz-Bip.

Plants up to 6 dm. tall. Fibrous roots extensive; upper three-fourths of plant with numerous, dichotomous and spreading branches. Leaves cauline, 10-75 per plant, arranged alternately. Stem with resinous granules, densely hirsute, becoming moderately hirsute in upper branches and strigose in ultimate branches. Leaves sessile, their sheath-like bases encompassing stem. Upper leaves ovate, 5-10 x 2-5 cm., at axil of each pair of dichotomous branches. Lower leaves longer, rhombic to round-ovate, abruptly and strongly tapered, 12-15 x 4-6 cm. Leaf thin with crenate margin. Leaf midrib on lower side moderately to densely hirsute, the surface slightly pilose.

Glomerules numerous, terminal or axillary to each pair of dichotomous branches. Bracts, three, unequal, the largest ovate with acute apex; midrib on lower side moderately hirsute. Heads 1 cm. tall, numerous, 8-20 per glomerule, with four complete florets. Phyllaries thin, acuminate, in two rows; the inner ones 8 cm. tall, the outer ones 5 cm. tall, short-strigose. Lobes of corolla 5, light pink to white. Pappus 3.5-5.0 mm., lance-subulate at base attenuating into an awn. Open dry woods and thickets, Fla. to Tex., n. to s. N. J., Pa. W. Va., O., Ind., Ill., Mo., and Kansas; Cuba and Puerto Rico.

Elephantopus carolinianus Willd. forma vestitus Fern.

Similar to E. carolinianus proper with stouter stem and reduced branching. Leaves usually large, up to 30 cm. x 12 cm., ovate-oblong and tapering gradually, thick and highly rugose. Leaves and stem dark green. Midrib dark green or purple. Wooded swamps, se. Va.

2. Elephantopus tomentosus L.-Devil's Grandmother, Tobaccoweed.

Elephantopus nudicaulis Poir.

Elephantopus carolinianus simplex Nutt.

Plants 2-7 dm. tall. Fibrous roots extensive; upper stem with a few vertical branches. Leaves sessile, 4-7 in basal rosette round-ovate, tapering gradually to base, apex round to obtuse, 12-15 cm. x 5-8 cm. Occasional cauline leaves in middle of stem and at axis of branches, smaller, ovate, 3-5 cm. x 5-8 cm. Leaf surface moderately velutinous, velvety to touch, midrib moderately to densely velutinous on lower side. Stem densely to moderately velutinous near base becoming slightly strigose in upper branches. Stem and leaves have resinous granules. Bracts unequal and overlapping at base, largest 9mm. x 4mm., triangular with acute apex, densely velutinous along midrib or lower surface. Glomerules terminal and axillary, 8-12 per plant, extending beyond bracts. Two rows of 5 phyllaries each, the inner ones 12 mm. tall, the outer ones 7 mm. tall, thin and acuminate. Heads 1.5 cm. tall. Lobes of corolla 5, light purple to pink. Pappus 6.0-7.0 mm., triangular-subulate at base, tapering into an awn. Open, sandy woods; coastal plain from se. Va. to Fla. and Tex., n. to Md., W. Va. and Ky.

Elephantopus tomentosus L. forma rotundatus Fern.

Rosette leaves round-ovate with slightly tapered or rounded base. Leaves dark green; surface and midrib of lower side densely velutinous. Woodlands, Va.

3. Elephantopus nudatus A. Gray

Plants 0.5-2.5 dm. tall. Fibrous roots in a limited network, branches of stem few, unequal, erect, Leaves sessile, 5 or more in basal rosette, narrowly oblong-ovate or oblanceolate, evenly tapered to the base, 6-12 cm. x 1-2 cm., apex obtuse or rounded. Occasional small cauline leaf at middle of stem and at axis of each pair of dichotomous branches. 2.5-4.0 cm. x 1-2 cm. Leaf veins and midrib on lower surface reddish-brown, densely strigose. Both leaf surfaces slightly strigose and hirsute. Stem slightly to moderately strigose. Stem and leaves medium green with resinous granules. Bracts three per glomerule, longer than inflorescence, two long and one short, oblong-oval with acuminate apex, 1 cm. x 0.5 cm., strigose along midrib of lower side. Glomerules mostly terminal, some axial, 1-6 per plant. Heads numerous, 9-15 per glomerule, 1 cm. tall. Florets 4 per head, less than 1 cm. tall. Phyllaries in two rows of 4, inside ones 7 mm., the outside ones 4 mm. tall., thin with long acute apex. Lobes of corolla 5, dark pink to rose. Pappus 5.0-6.0 mm., deltoid at base, abruptly terminating in an awn. Woods and sandy openings on the coastal plain, Fla. to La., n. to Del. and Ark.

NOMENCLATURAL HISTORY OF VIRGINIA SPECIES

In "A Revision of Elephantopeae", Baker (1902) explains that the type species of the genus Elephantopus is scaber. The locality listed with many early specimens is Jamaica; however, in the Linnaean description of 1753, the habitat is noted as "in Indies". Willdenow records the location as "Indea orientali". More recent specimens have been collected from India, the Philippines and Formosa. E. scaber has also been introduced into Costa Rica and Guatemala and is now widely disseminated in both the Old and New World tropics.

E. scaber and E. tomentosus have similar glomeruli; however, in the 18th and early 19th centuries they were recognized as distinct species. Later

taxonomists such as De Candolle in 1836, and Dietrich in 1847 do not mention E. tomentosus. About the same time a third taxonomist, Schultz Bipontinus recognized E. scaber as the Old World form and lumped all the American forms under E. tomentosus.

For a short period of time many authors included several of the North American and South American species under E. scaber. According to Baker (1902) both E. mollis and E. tomentosus were placed under E. scaber in Flora Brasiliensis by Baker. Hemsley presented an extremely artificial view by combining E. tomentosus, E. Martii, E. mollis and E. Carolinianus under E. scaber (Baker, 1902).

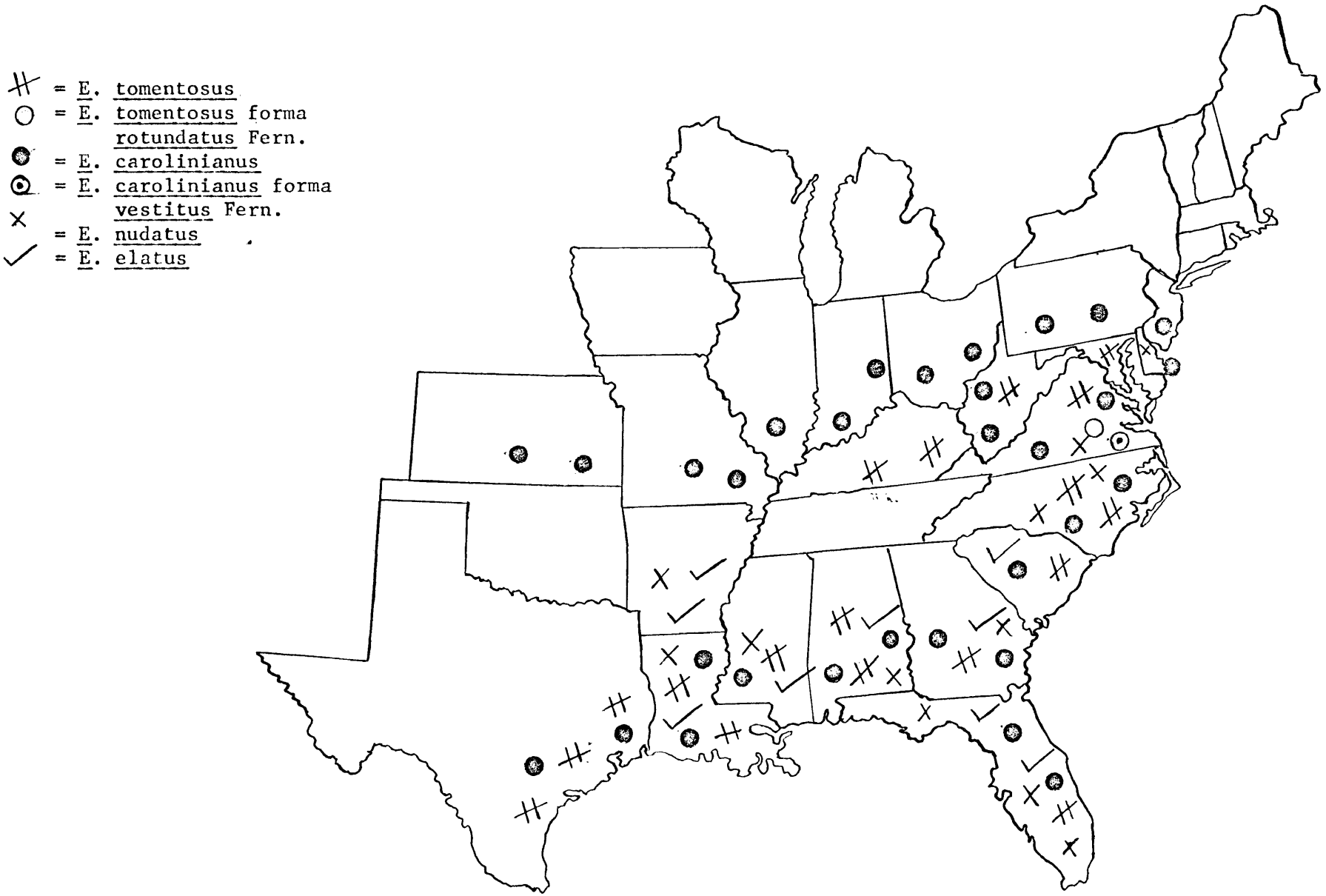
In 1879, Gray presented a more critical separation of the forms by describing E. nudatus and soon several other forms in the United States, West Indies, Mexico, Central and South America, Africa and the Far East were accepted (Baker, 1902).

A total of four species is now recognized in the United States (Gleason, 1922) (Fig. 1), however, varieties and intergradations have produced several problems and synonyms in the taxonomy.

E. carolinianus is the most common species, having a wide distribution. The variety violaceus Sch. Bip. refers to plants with a purple pappus found from Missouri to Louisiana and Alabama, but is no longer recognized. More recently Fernald (1936) named the forma vestitus which is cinereous with short and close pubescence to the summit.

E. tomentosus shows a great amount of variation in the vestiture and in the form of the floral and radical leaves. The nomenclature involves

Fig. 1. Geographic distribution of Elephantopus in the United States.



a list of three synonyms: E. nudicaulis Poir., E. nudicaulis Ell. and E. carolinianus simplex Nutt. The forma rotundatus Fern. is recognized today and can be distinguished by round-tipped short rosette-leaves and broad and numerous cauline leaves.

E. nudatus also has many puzzling forms. The most typical plants occur in the Northeast, while extremely variable plants were collected in the Southwest. Baker, (1902) believes that this may be due to the amount of variability within the species or to hybridization.

The fourth species, E. elatus was collected in Florida and throughout the Southern States east of the Mississippi. Variability was also noted in this species which has some characters resembling both E. nudatus and E. tomentosus (Baker, 1902). The same author suggested that much of the material of E. elatus under study could be hybrids but that only actual experimentation involving the production and study of authentic hybrids could give direct evidence.

Another study by James (1959) states that E. elatus and E. tomentosus can be distinguished by direction of pubescence and glomerule size and pappus; however, several intermediates or varieties of E. tomentosus have been found in Florida. James (1959) suggests that these plants may be introgressants or hybrids of E. tomentosus with E. elatus or with E. nudatus but no evidence has been obtained.

A species known as Elephantopus spicatus is now thought to be generically distinct from Elephantopus and has been named Pseudelephantopus spicatus (Juss.) Rohr. According to Gleason (1922), the genus Pseudelephantopus Rohr. is similar to Elephantopus in leaf arrangement and

inflorescence structure including number of heads and flowers. However, the involucre is markedly different. It consists of four pairs of decussate scales, the first and third pairs conduplicate, the outer two pairs shorter than the inner. The achenes are also distinctive, 10-striate flattened, and the pappus has 10-15 bristles, with two long stout lateral ones plicate at the tip, two straight ones almost as long, and several short scarious bristles, all gradually dilated and fimbriate-ciliate at the base (Gleason, 1922).

The type species is Elephantopus spicatus Juss. (Gleason, 1922). Its synonomy and description are as follows:

Pseudelephantopus spicatus (Juss.) Rohr.

Elephantopus spicatus Juss.
Distreptus spicatus Cass.
Matamoria spicata Llave & Lex.
Distreptus spiralis Less.
Elephantopus crispus D. Dietr.

Pseudelephantopus spicatus has a simple or branched stem, thinly pubescent or glabrate; leaf-blades ascending, oblong linear to broadly elliptic or ovate, thinly papillose-pilose or glabrous on the veins; spikes numerous and terminal, with bracteal leaves; involucre narrowly companulate or cylindric; achenes 7-8 mm. long; pappus 5-6 mm. long, the plicate bristles exserted from the involucre (Gleason, 1922).

The type locality is French Guiana but Pseudelephantopus spicatus is known to range from Cuba and Mexico to tropical South America and has also been found in the tropics of the Old World (Gleason, 1922).

Blake (1948) describes P. spicatus as a weed of potential importance in Florida. It is especially similar to Elephantopus mollis but differs markedly in pappus.

DISTRIBUTION WITHIN VIRGINIA

The distribution of Elephantopus in Virginia has been described by M. L. Fernald in a series of three papers. In 1936, Fernald compiled "Plants from the Outer Coastal Plain in Virginia" in which he recorded E. carolinianus in Princess Anne Co. and in Nansemond Co. Both locations were in dry sandy woods. E. tomentosus was also found in Princess Anne Co., in a rich woods and in Northhampton Co. where the species was growing in a dry sandy pine woods on the border of a gum swamp.

Fernald (1936) found that E. nudatus, E. tomentosus, and E. tomentosus forma rotundatus Fern. were abundant both east and west of the Dismal Swamp, two sharply distinguished areas having different surface soils and often reflecting a different flora. East of the Dismal Swamp and south of the entrance to the Chesapeake Bay, the Tertiary beds are buried under Quaternary sands and clays, while west of the Swamp the Tertiary regions consist of deposits with beds of Miocene fossil shells underlying the superficial sands, clays and peats. However, the different soil surfaces seem to have little effect on the continuous distribution of the three taxa.

"Plants of the Inner Coastal Plain of Virginia" was published by Fernald in 1937. Here Fernald mentions that E. nudatus and E. tomentosus are two of the ubiquitous plants having a uniform occurrence throughout the southeastern part of Virginia.

In a third paper, "Additions to the Flora of Virginia", Fernald (1942) recorded E. carolinianus in Adams Swamp, south of Baines Hill School in

Nansemond Co. He also named E. carolinianus forma vestitus Fern. from the same location.

The Virginia Flora presents the county distribution of Elephantopus as currently known (Massey, 1961). Most counties which include all three species are found bordering the James River and in the two counties of the Eastern Shore. E. carolinianus is also recorded in three northern counties and in one county of the Alleghany region. All three species and two forms have been found growing within a few yards of one another along the side of the road in the Mariner's Museum Park in Newport News. The county distribution of Elephantopus is illustrated in Fig. 2.

The present treatment of the North American Elephantopus species, based primarily upon herbarium materials, is inadequate. The objective of this study is a better understanding of the variation pattern within each species, and the ecological and genetic relationships between species. Their broadly sympatric ranges as exemplified in Virginia pose special problems concerning isolating mechanisms and hybridization. Methods of study used include further morphological study, field observations, cytological study, and attempts at synthesis of artificial hybrids.

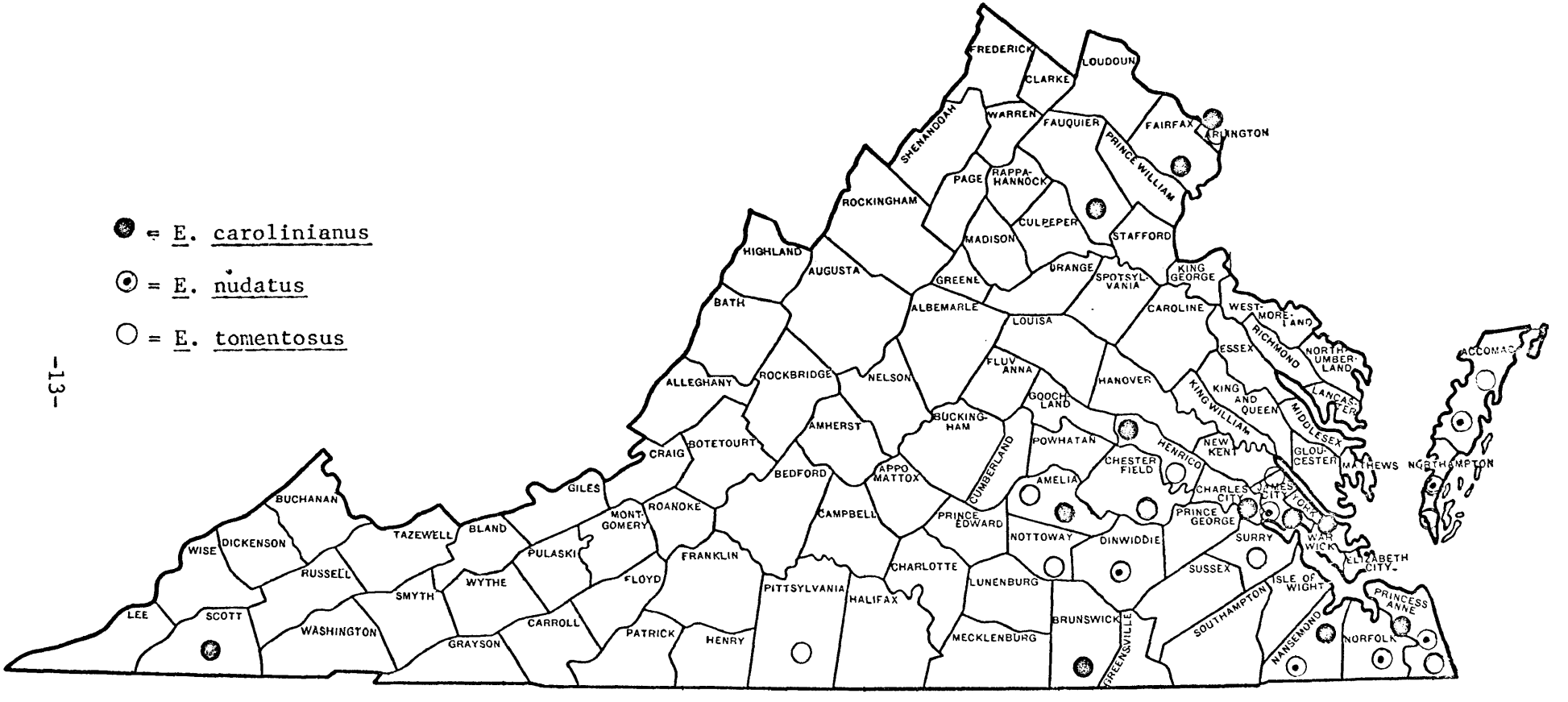


Fig. 2. County distribution of Elephantopus in Virginia (Fernald, 1936, 1937, 1942; Baldwin and Speese, 1955; Massey, 1961).

MATERIALS AND METHODS

This project included several related types of investigation. The experimental work involved ten cultures, each representing a field population. From January to August, 1966, a total of 201 plants of the three species and two forms were obtained from areas within a 25 mile radius of Williamsburg. The specimens were transplanted into individual six inch pots in the greenhouse. From January 13 to May 29, 1966, inflorescent lights were used to produce a 16 hour day. On May 29, a black-curtained structure was assembled to produce the natural 10 hour day of the September blooming season. After one week the plants began to bloom and the practice was discontinued. Data concerning the location are listed in the appendix and composition of each population is compiled in Table I.

Cultures I, V, and VI and cultures IV and X were duplicate groups from the College Woods and Mariner's Museum populations; however, each culture represents plants from a slightly different area of the population. Culture III was grown from seeds taken from the dried stalks of specimens in Culture I.

The greenhouse plants bloomed from June to October. Self-pollination tests were done by bagging immature heads. Crosspollinations were also attempted between all combinations of the three species. A mutual exchange of pollen was accomplished by rubbing the opposing heads together.

TABLE 1. DATA CONCERNING EXPERIMENTAL POPULATIONS

Population and Press Numbers	Species	Date of Transplant	Number of Transplants
I. College Woods	E. carolinianus	1/13/66	14
	E. c. forma vestitus	1/13/66	4
	E. tomentosus	1/13/66	8
	E. t. forma rotundatus	1/13/66	9
II. Colonial Parkway	E. carolinianus	2/18/66	5
	E. tomentosus	2/18/66	3
	E. t. forma rotundatus	2/18/66	7
III. College Woods	E. carolinianus	2/12/66	4
	E. c. forma vestitus	2/12/66	1
	E. tomentosus	2/12/66	1
	E. t. forma rotundatus	2/12/66	2
IV. Mariner's Museum	E. carolinianus	6/3/66	6
128-512	E. c. forma vestitus	6/3/66	0
153-171	E. tomentosus	6/3/66	8
	E. t. forma rotundatus	6/3/66	28
	E. nudatus	6/3/66	31
V. College Woods	E. carolinianus	6/26/66	5
510-545	E. c. forma vestitus	6/26/66	0
	E. tomentosus	6/26/66	8
	E. t. forma rotundatus	6/26/66	4
VI. College Woods	E. carolinianus	7/23/66	2
	E. c. forma vestitus	7/23/66	1
	E. tomentosus	7/23/66	3
VII. Eastern State "Far"	E. carolinianus	7/23/66	1
316-381	E. c. forma vestitus	7/23/66	7

TABLE 1. (continued)

Population and Press Numbers	Species	Date of Transplant	Number of Transplants
VIII. Eastern State "Near" 346-381	E. carolinianus	7/23/66	4
	E. c. forma rotundatus	7/23/66	6
IX. Population Laboratory 269-310	E. carolinianus	7/24/66	1
	E. c. forma vestitus	7/24/66	9
X. Mariner's Museum	E. tomentosus	7/27/66	5
	E. t. forma rotundatus	7/27/66	2
	E. nudatus	7/27/66	11
Kingsmill Historical Site 382-406	E. carolinianus		
Mariner's Museum Valley 172-220	E. carolinianus		
221-268	E. tomentosus		
Quonset Hut 5 109-127	E. carolinianus		
Bellfield Plantation Site 495-509	E. carolinianus		
Ringfield Picnic Area 458-484	E. carolinianus		
Naval Weapons Station 434-457	E. carolinianus		
Glebe Land Historical Site 407-433	E. carolinianus		

Distilled water was also sprayed on heads to be used as pistillate flowers. The water was applied to burst the native pollen and after evaporation, foreign pollen from the second species was introduced. All cross-pollinated heads were covered with translucent paper bags and the same cross was repeated daily until all the florets in the designated glomerules had blossomed.

The achenes were allowed to mature until December when the heads were collected and the individual achenes separated. The mature achenes were placed in petri dishes containing wet filter paper. They were stored in the refrigerator for two weeks. In some cases the seeds were placed out of doors but under all conditions the achenes were alternately frozen and thawed to weaken the seed coat and promote germination. The petri dishes were kept well moistened and placed under table lamps for one week. When green shoots of the second generation appeared, the achenes were planted in flats of vermiculite in the greenhouse. Seedlings having well established primary leaves were then transplanted to six inch pots.

Descriptive morphological data were collected and a random sample of culture specimens was pressed as were any plants showing extreme variations and plants contributing buds for cytogenetic work. The press numbers include: Sheffy # 103-108, 546-565.

Separate and group Kodachrome photographs were taken of the vegetative and reproductive habits of the three species of the original ten cultures. In January the stock plants were trimmed to ground level and new vegetative structures were produced by March 1, 1967. The second growth of the stock plants began to bloom by March 10, 1967. Additional self-pollination tests

were done on all three species.

Buds of all stages of maturity were collected from each species of each of the original cultures. They were fixed and stored in Carnoy's solution, a mixture of three parts ethanol and one part glacial acetic acid, for later cytological analysis.

Work on chromosome numbers of Elephantopus species has been published by Speese and Baldwin (1955):

E. carolinianus Willd.	2n=22
E. carolinianus Willd. forma vestitus Fern.	2n=22
E. tomentosus L	2n=22
E. tomentosus L. forma rotundatus Fern.	2n=22
E. nudatus A. Gray	2n=22

The chromosome count for E. carolinianus Willd. has been verified by Lewis, Stripling and Ross (1962). Additional chromosome counts were attempted using the stored bud materials. The anthers were dissected to produce acetocarmine squash slides of the pollen mother cells. Slide preparation methods are outlined in Benson (1962). Anthers were placed in a drop of stain and a cover glass applied. The slide was heated and the anthers squashed. The method recommended by Rhoades (1950) was used to prepare permanent slides. The cover slip was removed with equal parts of glacial acetic acid and 95% ethyl alcohol and the slide then placed in a series of coplin jars for an interval of two minutes each. The first jar contained equal parts 95% ethyl alcohol and 95% tertiary butyl alcohol and the second coplin jar contained only 95% tertiary butyl alcohol. Next a drop of balsam was added to the slide and the cover slip was reunited.

Pollen fertility counts were obtained from the greenhouse cultures

throughout the summer months. Glomerules in full bloom were smeared on a slide containing a drop of cotton blue stain (Benson, 1962). After 12 hours the percent of viability could be obtained by counting the dark blue, heavily stained pollen grains compared to the inviable lightly stained pollen grains. In each case the percentage of viability was based on scoring of at least 150 grains. Pollen counts were also taken in the field.

Most Compositae have a well developed head structure; however, the heads in the genus Elephantopus are extremely reduced which would seem to indicate the possible presence of special pollination agents. Observations concerning the mode of pollination of Elephantopus were recorded from the field and greenhouse.

The Mariner's Museum population was carefully studied. This population was found along a hillside. It contained a predominance of E. carolinianus plants interspersed with two or three patches of E. tomentosus plants. Most E. tomentosus plants had achenes and only a few were still in bloom while the E. carolinianus plants were in full bloom. Small homey bees and wasps pollinated both species without a notable preference or sequence of visits and also visited other genera on the hillside. Pollen slides obtained from the field also seemed to indicate a nonspecific pollinator since three types of unidentified foreign pollen were often seen on the cotton blue slides. Black wasps were especially active around all exposed greenhouse plants. Ants and caterpillars were found on the inflorescence of all three species in the field and in the greenhouse.

Several natural populations were observed within a 25 mile radius of

Williamsburg and a random sample of twenty-five plants of each species of the population was pressed. A total of 436 specimens were collected. The populations and press numbers are listed in Table I and the location is listed in the appendix.

Pressed specimens from a total of seven populations were analyzed using a hybrid index method devised by Anderson (1936). This is a partly subjective method of analysis but it does permit the expression of qualitative data in quantitative terms. The eighteen characters selected are all macroscopic and discontinuous so that each may be subdivided into five states of equal numerical value. The five states thus are assigned 0-4 points in the total hybrid index. A plant scoring 0 in every category would represent one species and a plant scoring 4 in every category would represent the second species. The sum of the scores in the eighteen categories is calculated for each specimen and is called the hybrid index. Plants with a total score of 0 correspond to the extreme of the first species and plants with a total score of 72 correspond to the opposite extreme of the second species. Intermediate scores reflect variation of the species or the process of hybridization between the two species.

Two hybrid index values were calculated for each specimen using different keys according to the pair of species being compared. The keys for the three series of comparisons are found in the appendix and include Series I between E. tomentosus and E. carolinianus, Series II between E. tomentosus and E. nudatus and Series III between E. nudatus and E. carolinianus. Explanations concerning specific items in the keys and methods of measuring the characteristics are listed below:

1. The following leaf measurements are taken on the largest leaf of the specimen:

a. Leaf Base
b. Leaf Apex
c. Leaf Length
d. Leaf Width
e. Leaf Index
f. Leaf Width Index

2. The leaf base and apex are measured in degrees of the angle produced by two 3 cm. lines extended from the apex or base to either leaf margin.

3. The leaf index is the ratio of the maximum width to the length = W/L.

4. The leaf width index is the ratio of the length of the blade from the stem to the point of maximum width, to the total length of the leaf.

5. The number of heads is determined from the largest glomerule of the specimen or if there is little size difference a random glomerule is selected.

6. The bract length is determined from the largest outer bract of the largest or randomly selected head of the specimen.

7. The bract pubescence is determined from the above bract along the midrib as compared to a series of bract standards. The standards consist of pressed material from each species showing all the grades of pubescence density and types of pubescence corresponding to the key categories.

8. The stem pubescence is described from the first centimeter of the first internode which exceeds five centimeters. The stem pubescence is also compared to a series of standards.

9. The leaf pubescence is determined on the underside of the largest leaf, along the midrib in the area of maximum width. This is compared to a set of standards which consist of one square centimeter of leaf blade, bisected by the midrib, and taken from the area of maximum width.

10. In Series II and III some categories of characters gave almost identical scores for both species and in this case all specimens were assigned two points for the characteristic.

11. The categories concerning pubescence were divided into two or three divisions rather than five according to the range of distinct variation within the category.

In this study three hybrid index programs were constructed for the comparison of all combinations of the three species. As a result two separate hybrid indices were calculated for each specimen. The scores of the individual plants of each species were used to construct bar diagrams. Polygons and scatter diagrams were also drawn to illustrate character patterns and are presented in the following chapter.

The presence and abundance of second generation plants were recorded and listed according to the type of hybridization attempted. Only quantitative data could be obtained since the plants were not mature enough at the time of the conclusion of this study to analyze with the hybrid index method.

RESULTS

MORPHOLOGICAL STUDIES

The comparative morphology of the three species and two additional forms, as normally expressed in systematic descriptions, is presented in Table 2. After detailed comparison of the mass collections of the three species, eighteen attributes, including vegetative, floral and fruit characters were found to be most useful for quantitative study.

By using a hybrid index survey as proposed by Anderson (1936) the frequency distribution of index values for individuals within a population may be determined and populations of similar or distinct species may be compared.

Hybrid index values for two series of comparisons were determined for each of 234 specimens. These represent seven different populations. The results are illustrated in histograms showing the frequency distribution of character states in each population.

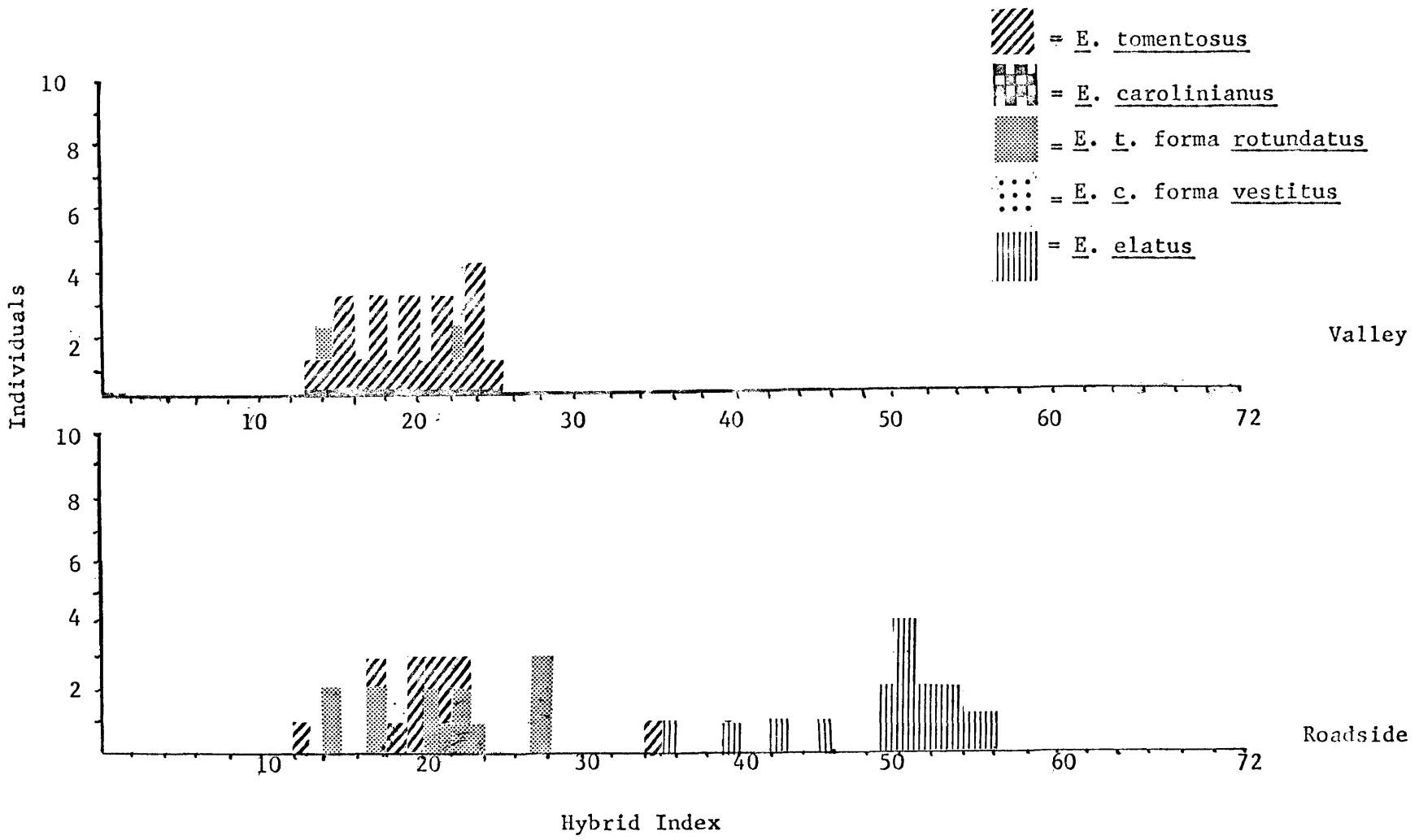
All three species were found in the Mariner's Museum Park. Approximately 25 plants each of E. tomentosus and E. nudatus were collected along the roadside. In a nearby valley an equal number of specimens were collected of E. tomentosus and E. carolinianus.

Three histograms were constructed using the above specimens. Fig. 3 shows that the character distribution of E. tomentosus from both Museum

TABLE 2. COMPARATIVE MORPHOLOGY OF VIRGINIA *ELEPHANTOPUS* TAXA

Characteristic	*E. tomentosus*	*E. t.* forma *rotundatus*	*E. carolinianus*	*E. c.* forma *vestitus*	*E. nudatus*
1. Plant Height	2-7 dm.	2-7 dm.	4-6 dm.	4-6 dm.	0.5-2.3 dm.
2. Branching	few, erect	few, vertical	numerous, spreading	numerous, spreading	few, vertical
3. Lower Stem Pubescence	densely to moderately velutinous	densely velutinous	moderately to slightly hirsute	densely to moderately hirsute	moderately to slightly strigose
4. Leaf Shape	round-ovate	round-obovate	rhombic or round-ovate	ovate or ovate-oblong	oblanceolate or oblong-ovate
5. Leaf Apex	round or obtuse	round	acute	acute	round or obtuse
6. Leaf Base	gradually tapered	slightly tapered or round	abruptly and highly tapered	gradually tapered	evenly tapered
7. Leaf Pubescence (Along Midrib)	densely to moderately velutinous	densely velutinous	moderately to densely hirsute	moderately to densely hirsute,	moderately to slightly strigose
8. No. of Heads	8-12	8-12	15 or more	15 or more	1-6
9. No. of Glomerules	8-10	8-10	8-20	8-20	9-15
10. Bract Shape	triangular	triangular	ovate	ovate	oblong-oval
11. Bract Apex	acute	acute	acute	acute	acuminate
12. Pappus Length	6.0-7.0 mm.	6.0-7.0 mm.	3.5-5.0 mm.	3.5-5.0 mm.	5.0-6.0 mm.

Fig. 3. Histogram of E. tomentosus and E. nudatus of the Mariner's Museum Population.



areas has several modes. Specimens from the roadside area growing close to E. nudatus plants have a slightly larger range, from 13-35 or 23 units and just border the E. nudatus range of 36-56 or 21 units. The E. nudatus histogram shows one mode but has four individuals with values intermediate between the two species.

Figure 4 shows that the specimens of E. tomentosus from the roadside and valley areas have similar ranges of 17-37 and 18-34 with more than one mode in the center and slight distribution in both directions. E. carolinianus shows a small range of 45-59 with a high frequency at three intervals. There seems to be a definite gap between the distribution of the two species.

Series III of the same population is depicted in Figure 5. The histograms of both species, E. nudatus and E. carolinianus are very similar with a distribution concentrated around two modes and scattering of a few individuals toward either side. Three individuals from each species are found in the intermediate area, forming an almost continuous bridge between the two species.

Figures 6 and 7 are comparative histograms of the frequency distribution of E. tomentosus in three different areas, using Series II in Figure 6 and Series I in Figure 7. All have similar hybrid index ranges of approximately 13-28 or 16 units, except for the Mariner's Museum Roadside population which has one scattered specimen with a value of 35. Each distribution has several peaks. In most cases high frequencies in categories at the end of the range seem to eliminate any intergradation toward E. nudatus.

In Figure 7 using Series I the distributions range from 17-37 or 21 units. The histograms show just two major peaks with a more scattered

Fig. 4. Histogram of E. tomentosus and E. carolinianus of the Mariner's Museum Population.

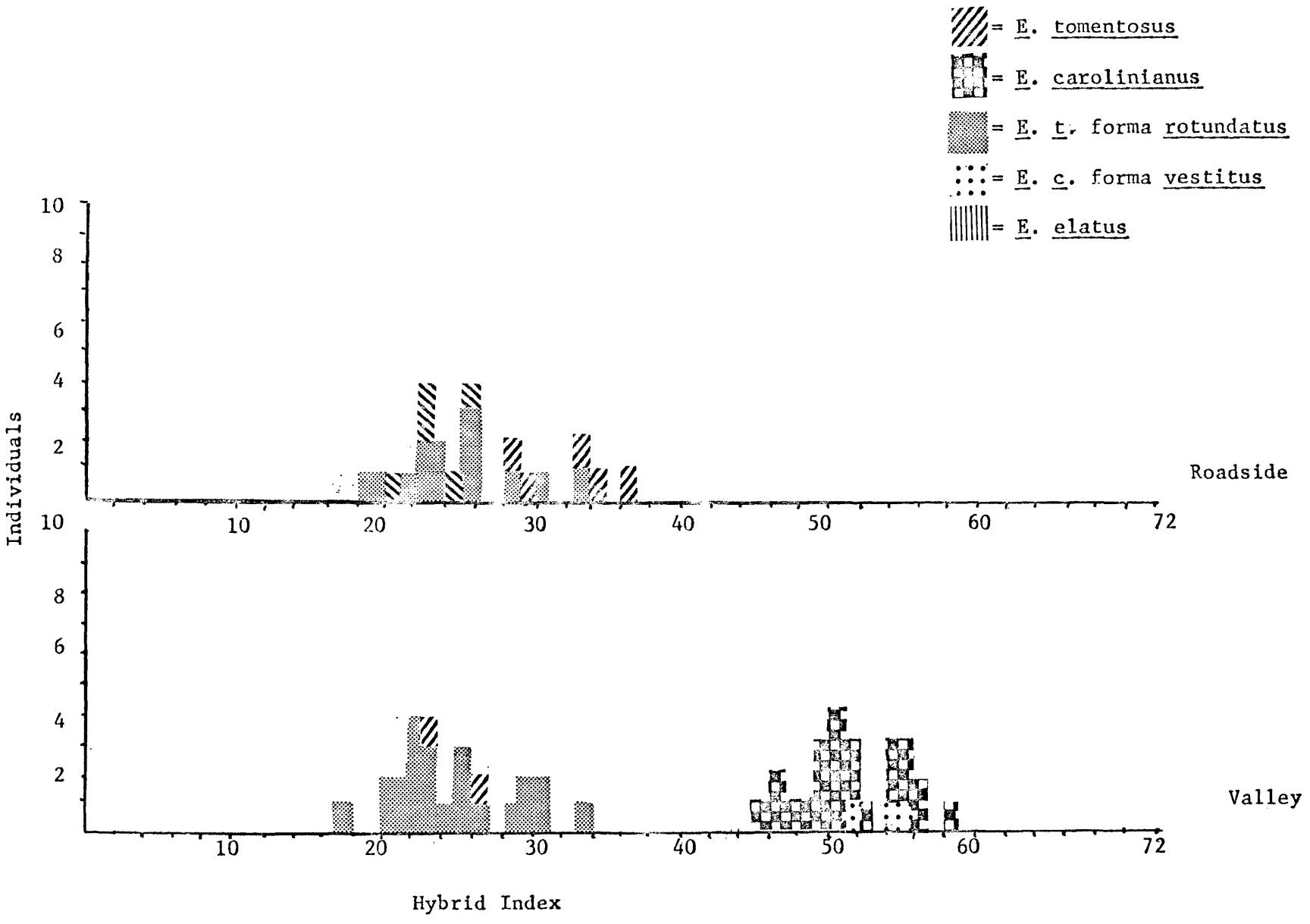


Fig. 5. Histogram of E. carolinianus and E. nudatus of the Mariner's Museum Population.

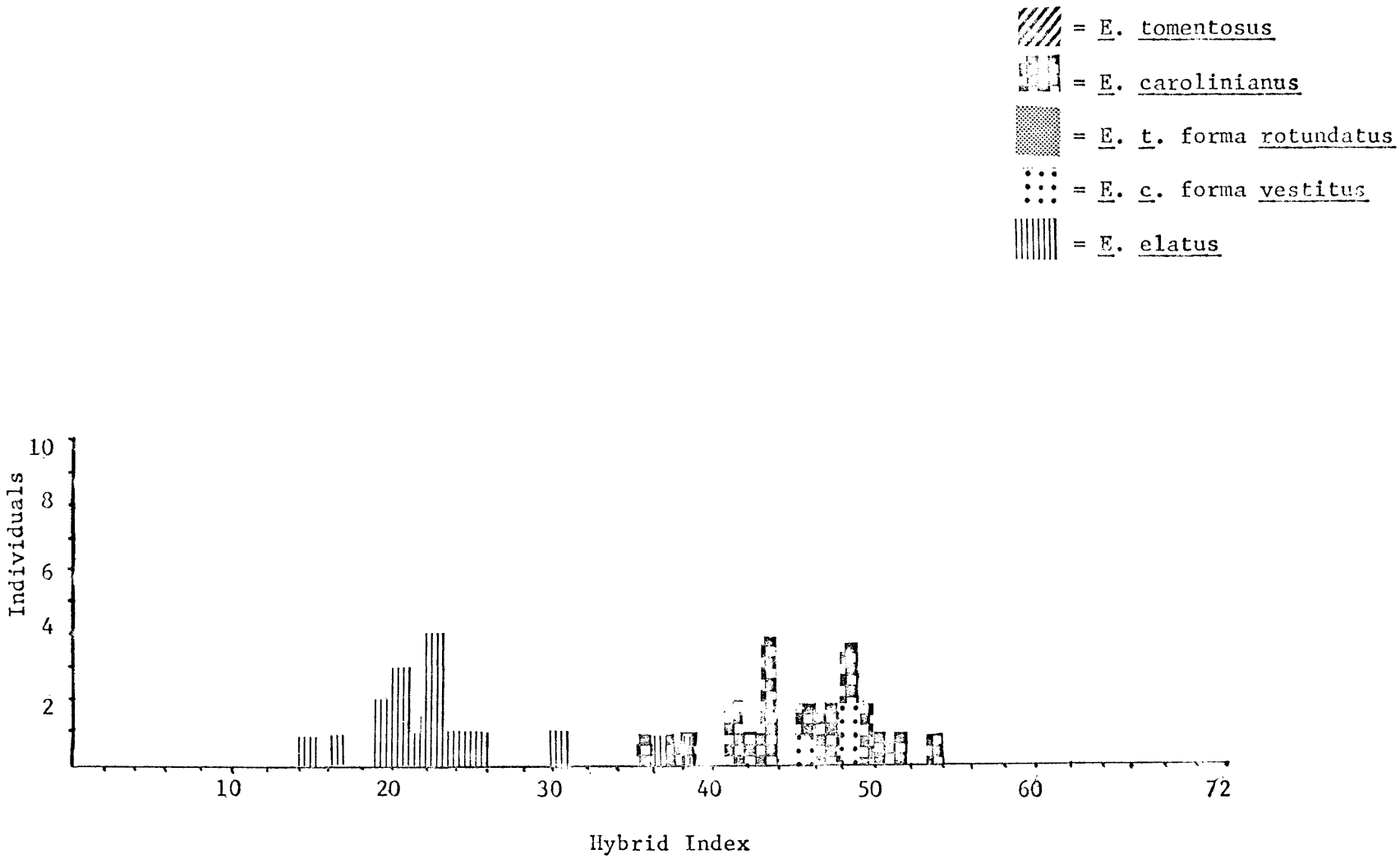


Fig. 6. Comparative histogram of E. tomentosus and E. nudatus.

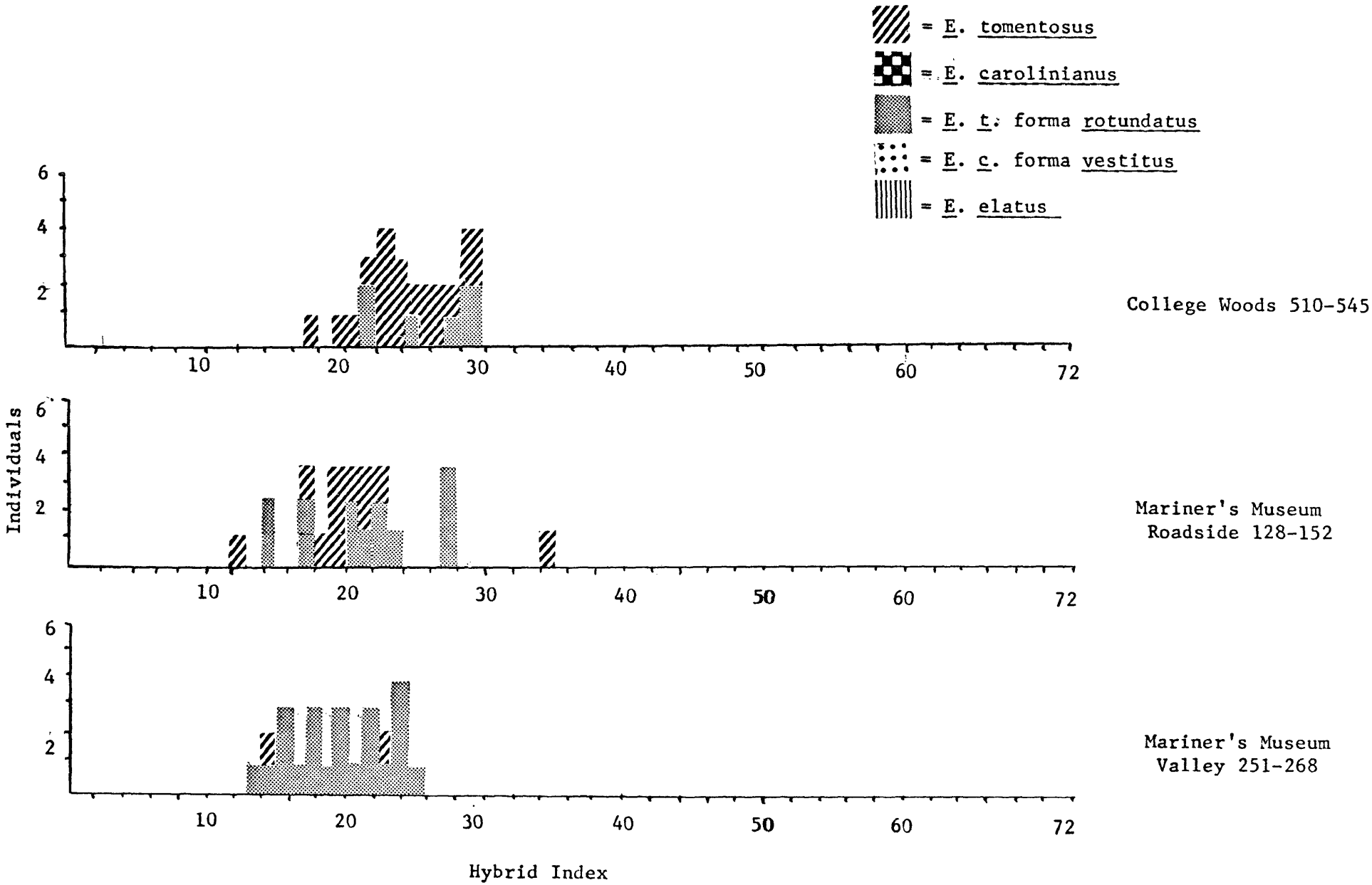
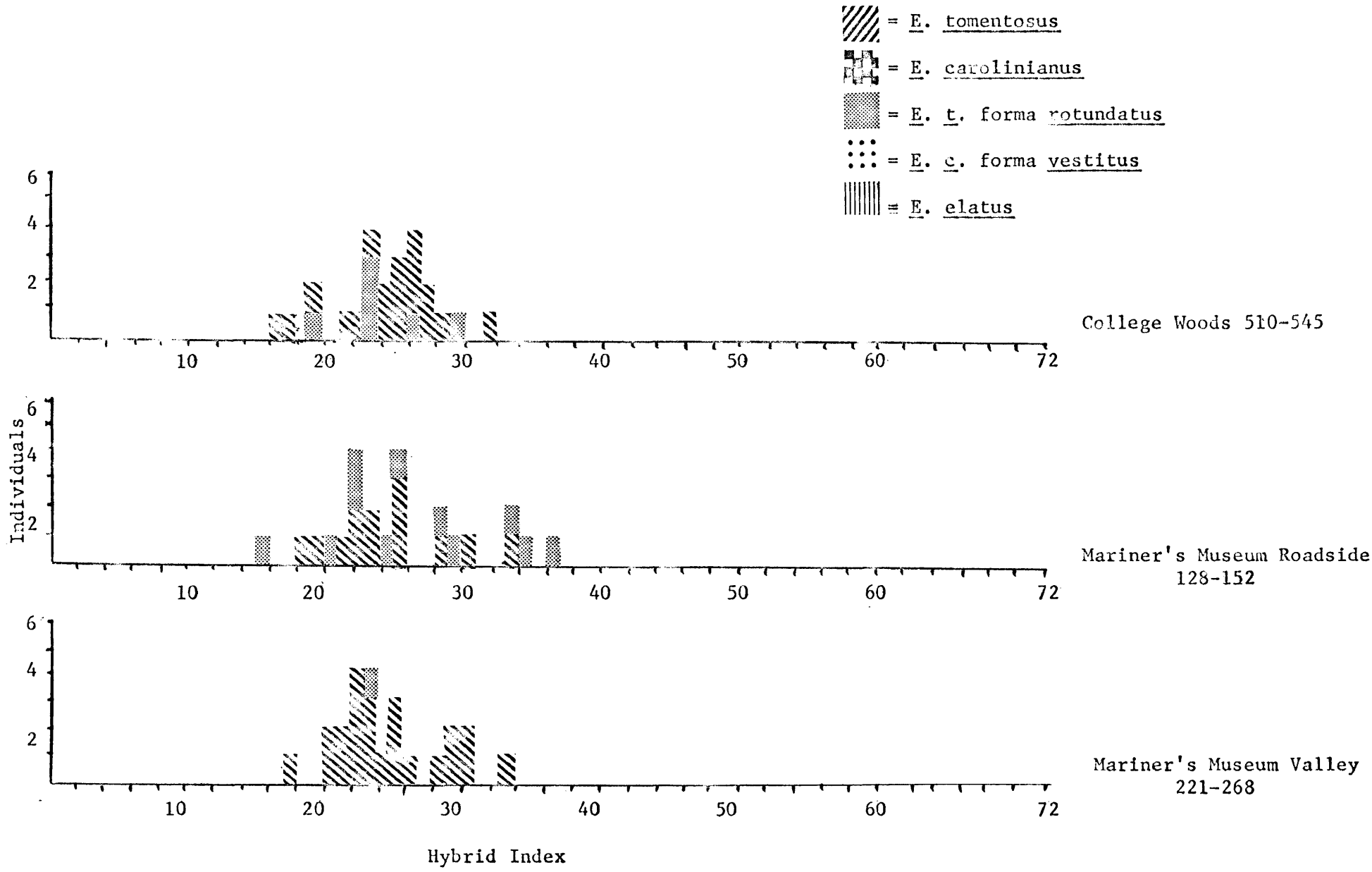


Fig. 7. Comparative histogram of E. tomentosus and E. carolinianus.



specimen scattered toward the E. tomentosus range. The Quonset Hut population showed two modes and a single isolated specimen. All ranges were between 43-65 with only the one specimen from the Kingsmill population in the intermediate area between the two species.

In Series III (Figure 9) the general range of all populations shifts to the left and extends from 33-58 or 26 units. Only the Quonset Hut population appears to have a discrete frequency distribution. Populations from Eastern State, Mariner's Museum and Kingsmill have two modes. Specimens with lower values extend on either side and between the modes. Only one mode is found in the histograms of specimens from the Population Laboratory and Naval Weapons Station areas. In the first group there is scattered distribution to the right and in the second, individuals extend toward the area between the two species.

The E. carolinianus populations in Figure 9 seem to show a wider range and more scattering of individuals toward the intermediate area with E. nudatus. The histograms in Figure 8 seem to indicate a more discrete central frequency distribution of E. carolinianus when compared to E. tomentosus.

In both Figures 8 and 9 the Mariner's Museum population does not show a greater variation in range than the other populations although E. carolinianus was sympatric with the other two species in this area. The other populations sampled consisted solely of E. carolinianus growing alone.

Fig. 8. Comparative histogram of E. carolinianus and E. tomentosus.

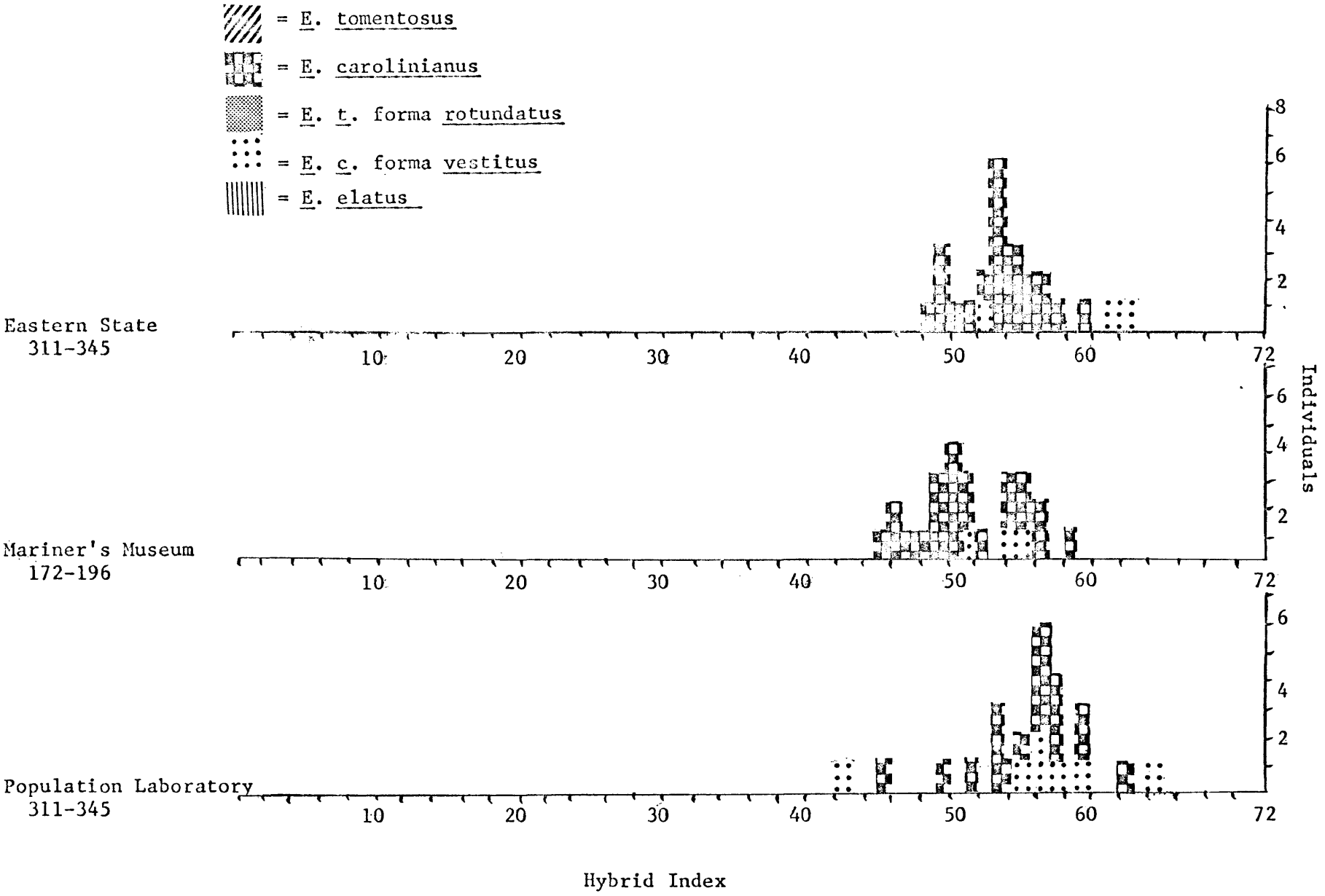


Fig. 8 continued

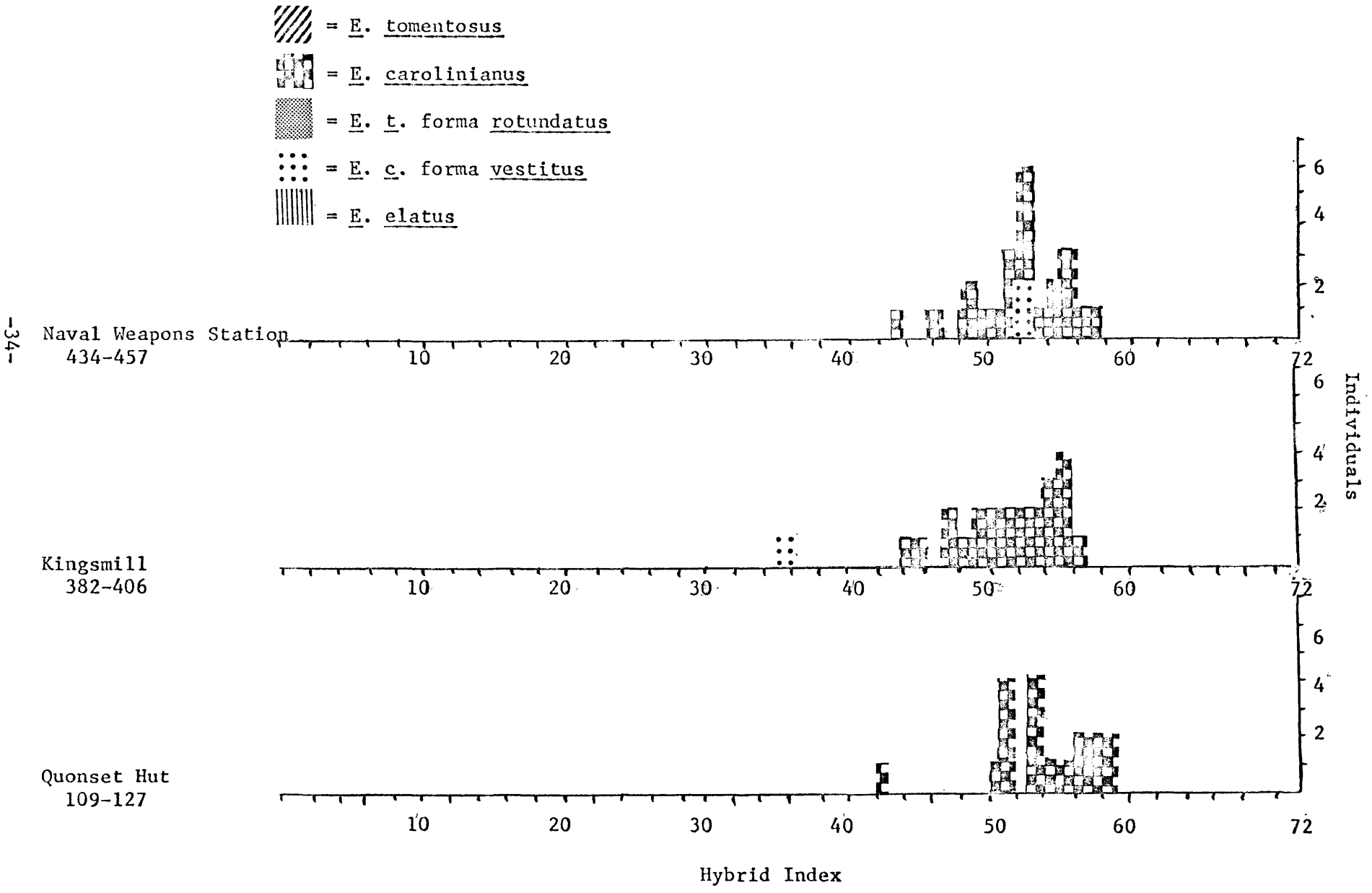


Fig. 9. Comparative histogram of E. carolinianus and E. nudatus.

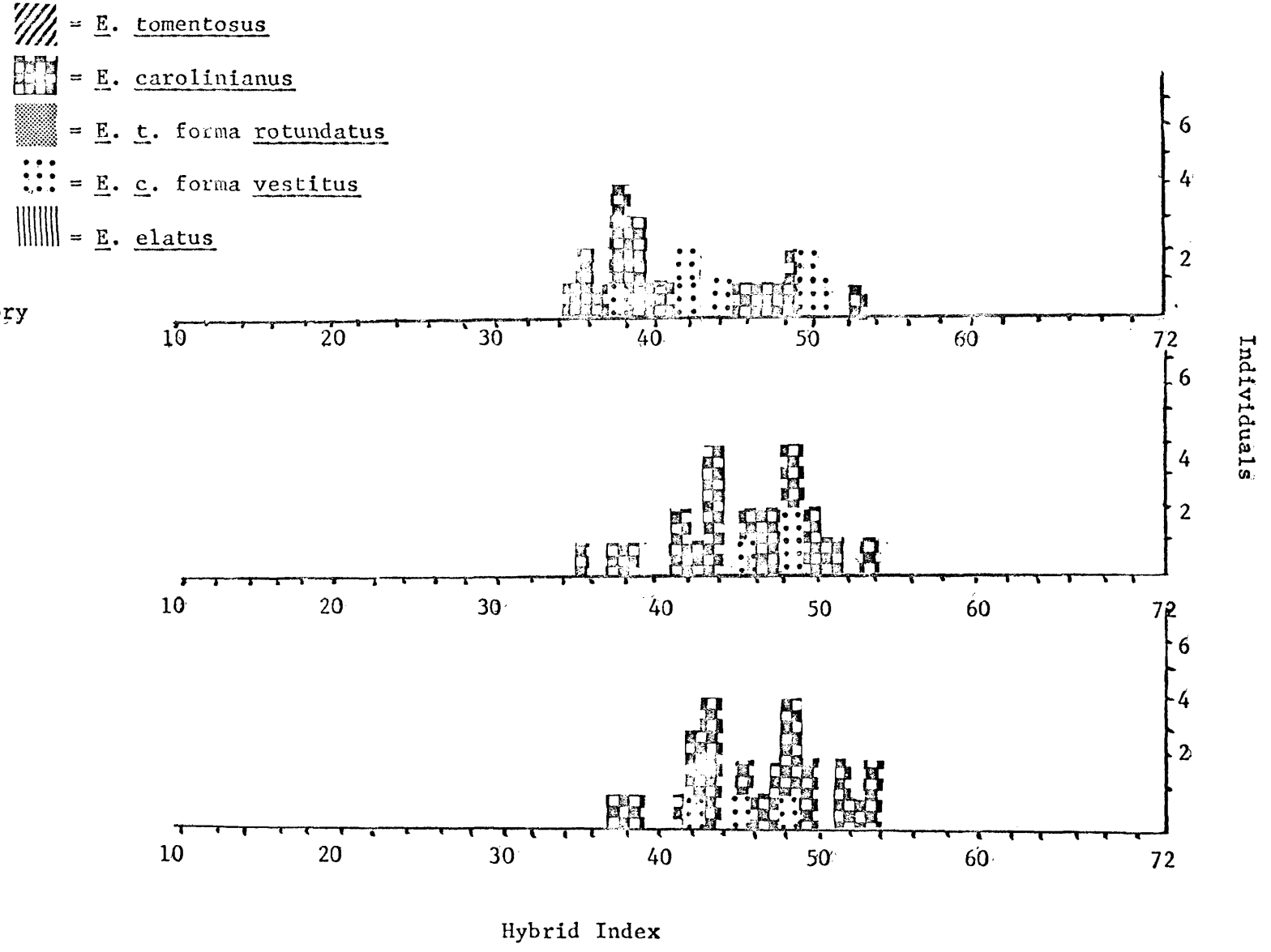
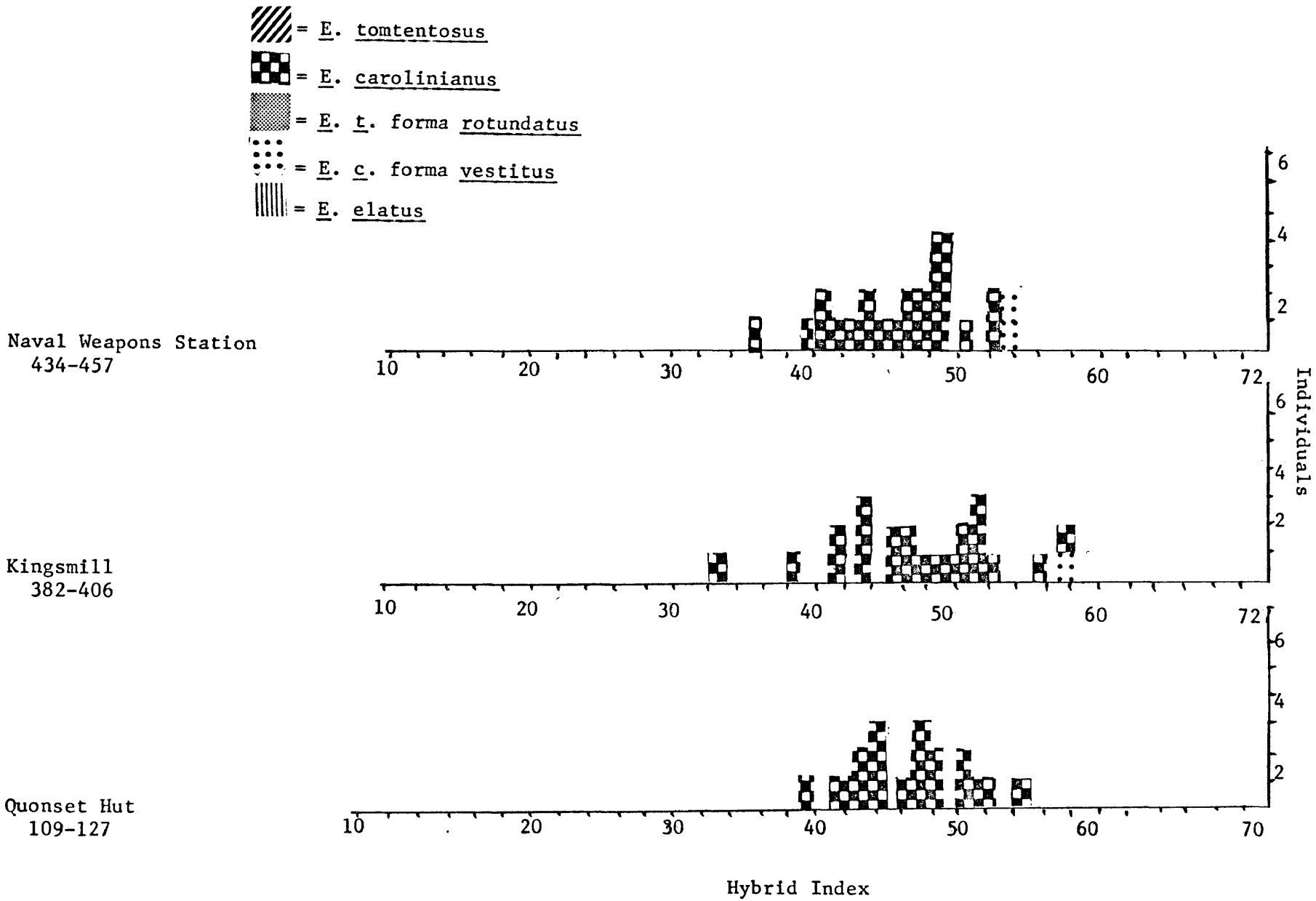


Fig. 9. continued



The forma vestitus of E. carolinianus was found in all but the Quonset Hut population. This form was not numerous and showed no discrete pattern in the frequency distributions of hybrid index values.

POLYGONAL AND SCATTER DIAGRAMS

The quantitative data from all three species of the Mariner's Museum population have been adapted to polygonal graphs as devised by Davidson (1947). The graphs are used for comparison of patterns involving several characteristics of two or more taxa. Average values of all eighteen categories were calculated for all three Series. Each polygonal graph represents one Series. The score for each character is placed at the proper distance from the center of a different radius of the circle. The polygon formed by connecting the points on the radii is representative of the taxon. The polygons of two species were superimposed on each graph and the coincidence of the polygons at certain points suggests relationship between the taxa.

A list of the average scores of each characteristic and numbers corresponding to the characteristics is found on the following page.

Figure 10 shows a coincidence or overlap in leaf length and bract length between E. tomentosus and E. carolinianus, and only slight differences in leaf apex, number of glomerules and leaf index. There is overall resemblance of polygons in two areas: in characteristics concerned with leaf size (#3-6) and in characteristics of reproductive structures (#8-12).

In Figure 11 the characteristics of glomerule and head number, length of the first internode and leaf length at the first node show identical scores for E. nudatus and E. tomentosus. Bract length and

POLYGONAL DIAGRAMS

Mariner's Museum Population, showing the average values of twenty-five plants of E. tomentosus and E. carolinianus and eighteen plants of E. nudatus.

Characteristic	E. tomentosus		E. carolinianus		E. nudatus	
	Series		Series		Series	
	I	II	I	III	II	III
1. Leaf Base	0.7	0.6	3.5	1.6	3.6	0.7
2. Leaf Apex	0.3	0.8	0.7	2.1	2.9	1.1
3. Leaf Length	2.7	2.4	2.6	2.0	3.0	2.0
4. Leaf Width	2.9	1.7	3.7	2.0	3.0	2.0
5. Leaf Index	3.2	1.8	4.0	2.0	3.6	2.0
6. Leaf Width Index	3.6	0.0	3.1	3.2	1.8	1.8
7. Length of Pappus	0.2	0.6	2.4	2.0	3.3	2.0
8. Number of Heads	1.8	2.0	2.4	2.7	2.0	0.9
9. Number of Glomerules	0.8	2.0	2.8	2.8	2.0	1.2
10. Length of First Internode	1.9	2.0	3.9	3.8	2.0	0.8
11. Leaf Length at First Node	0.9	2.0	2.2	1.6	2.0	0.5
12. Bract Length	1.6	0.4	1.6	2.0	1.0	2.0
13. Density of Bract Pubescence	0.9	0.7	2.1	3.7	3.2	1.6
14. Bract Pubescence	0.0	0.0	4.0	4.0	3.8	0.2
15. Density of Stem Pubscence	0.6	1.7	2.9	1.1	2.7	1.4
16. Stem Pubescence	0.3	0.5	4.0	3.4	3.8	0.2
17. Density of Leaf Pubescence	0.6	1.4	2.3	3.2	2.4	3.1
18. Leaf Pubescence	0.0	0.1	4.0	3.5	3.5	0.7

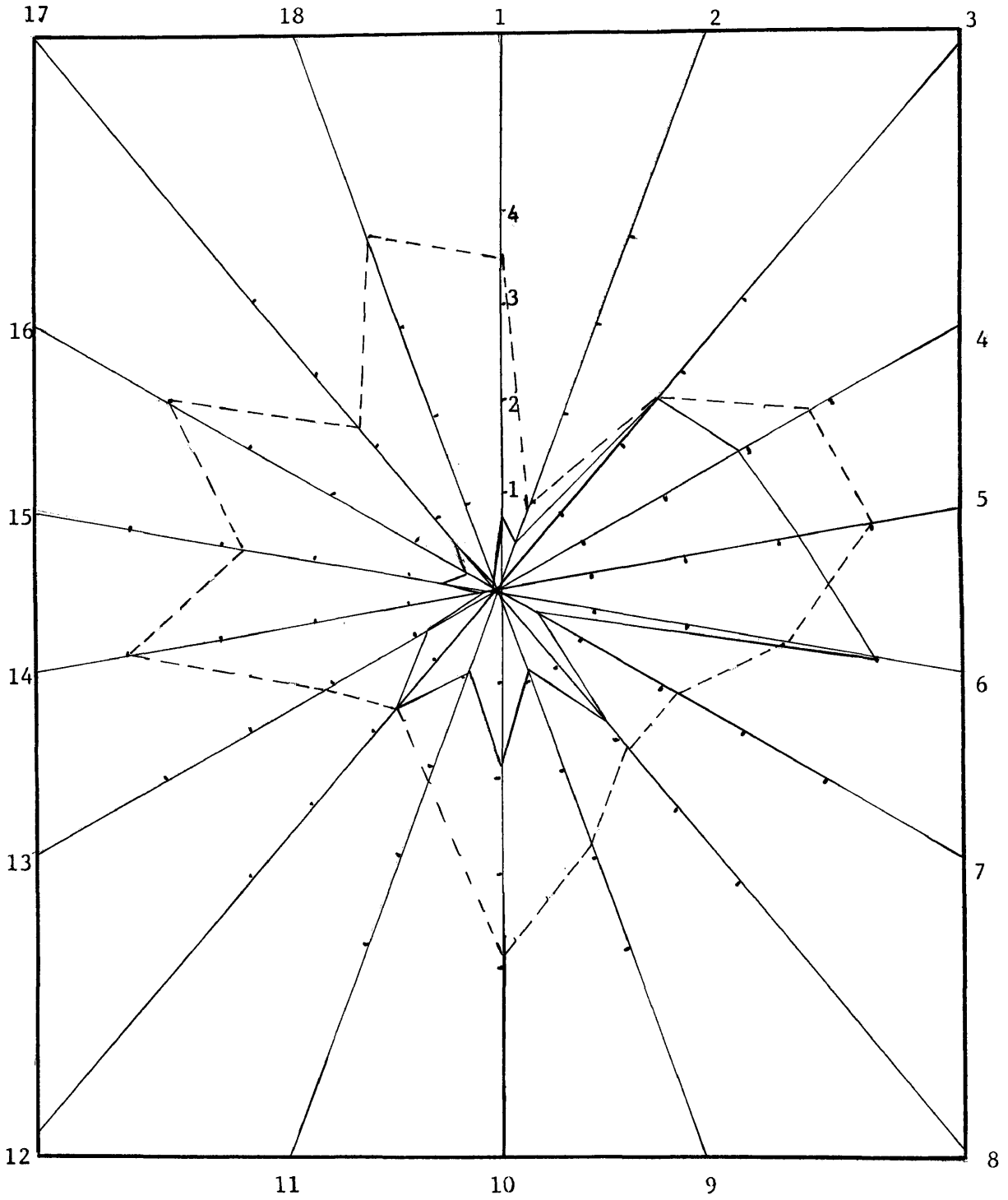
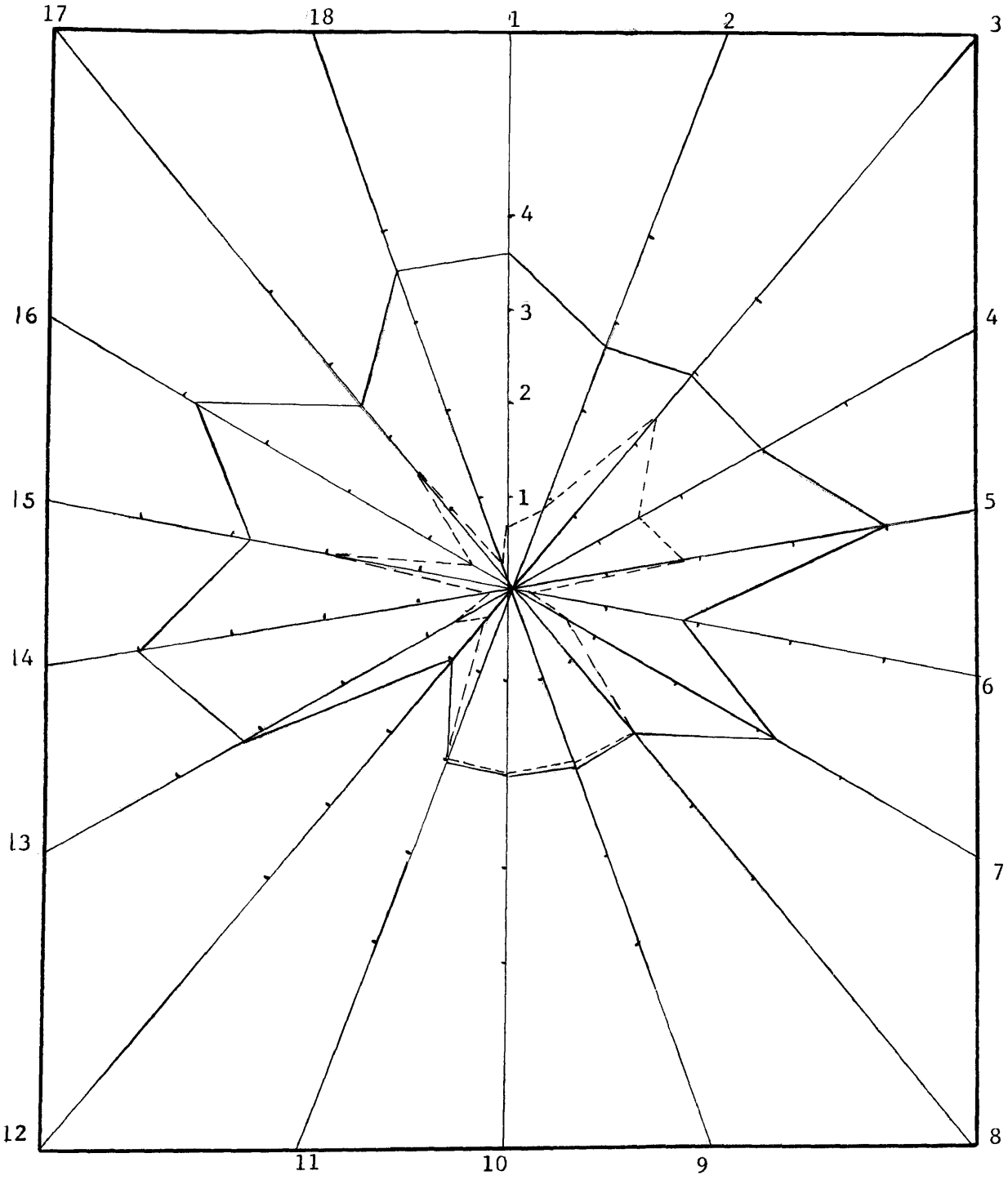


Fig. 10. Polygon of E. tomentosus and E. carolinianus of the Mariner's Museum Population.



__=E. nudatus
--=E. tomentosus

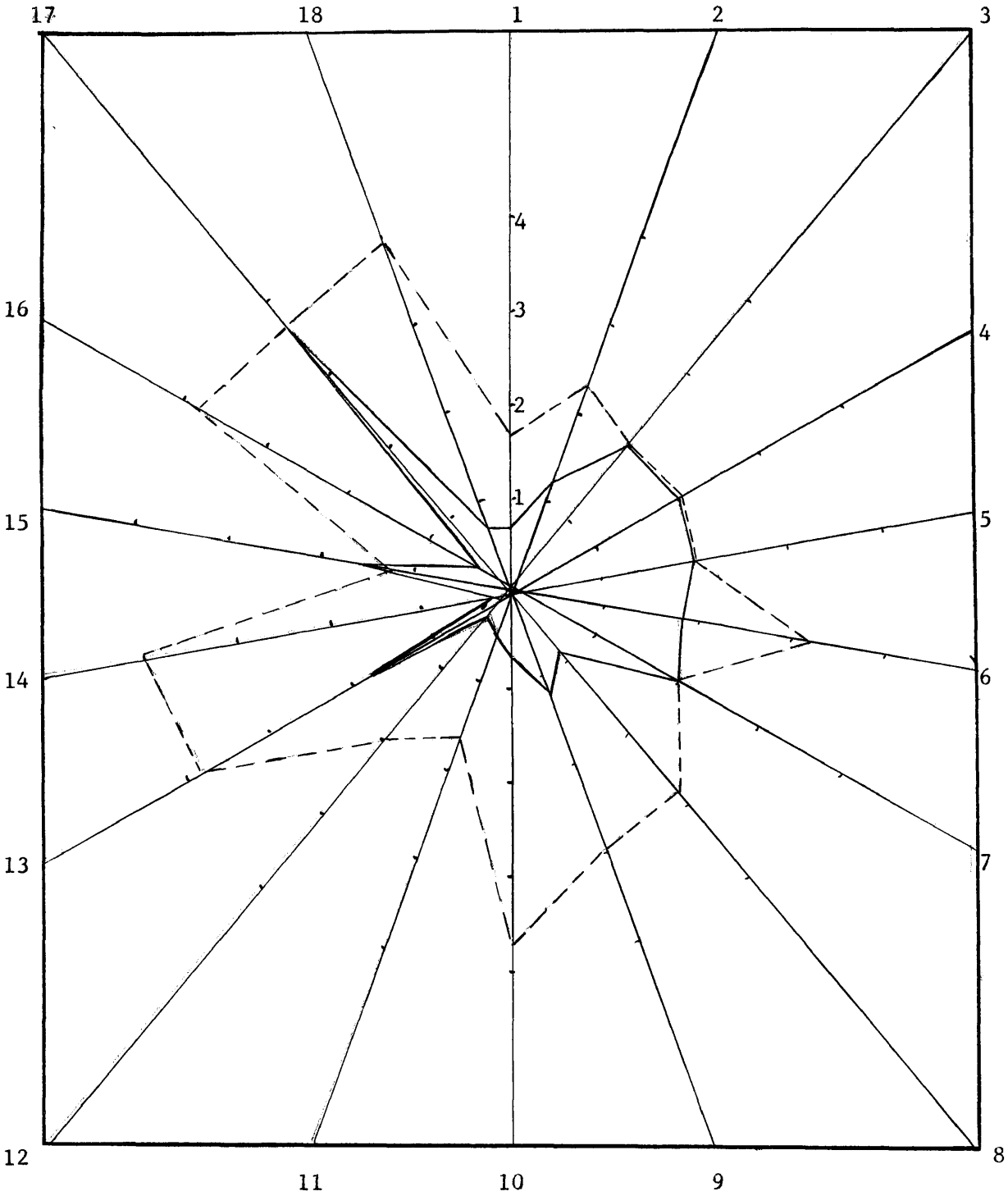
Fig.11. Polygon of E. tomentosus and E. nudatus of the Mariner's Museum Population.

leaf length are also very similar; however, there is a wide divergence in all other characteristics. The overall diagram shows a slight correlation in the area of leaf size and in the area of reproductive structures and internode size.

Coincidence of E. nudatus and E. carolinianus in Figure 12 includes the leaf length, leaf width index, length of pappus, and density of leaf pubescence characteristics and little difference is shown in the density of bract pubescence, reproductive structures and internode length.

An equal amount of overlap between polygons is illustrated in all three figures. There is a close relationship of leaf and bract length between E. tomentosus and E. carolinianus. Similar patterns of reproductive structures and internode morphology characterize E. tomentosus and E. nudatus. Coincidence of leaf size and stem and leaf pubescence density are most marked in E. nudatus and E. carolinianus. Although all three Elephantopus species seem to be closely related the two polygons in each figure are distinct and correspond to the separate species.

The correlation of several characteristics may be studied with pictorialized scatter diagrams as devised by Anderson (1936). Six of the most distinctive characteristics among the three species of the Mariner's Museum population were selected. The leaf base was plotted along the abscissa and the leaf width index along the ordinate. Three symbols were chosen to represent the species. Four additional characters were represented by a bar in each of the major compass



__=E. nudatus
--=E. carolinianus

Fig. 12. Polygon of E. carolinianus and E. nudatus of the Mariner's Museum Population.

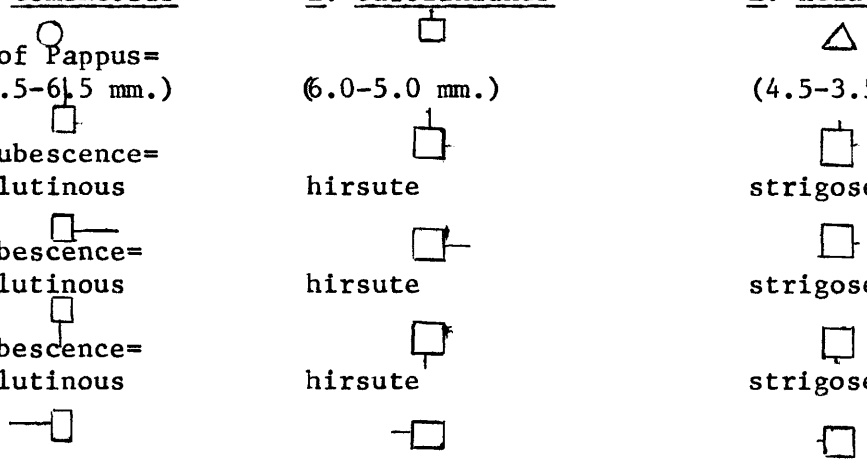
directions. Three divisions in each category were depicted by three different lengths of the bar. A key to the symbols is found below.

Abscissa = Leaf Base (0°-100°)

Ordinate = Leaf Width Index (0.0 -.07)

Species =

	E. tomentosus	*E. carolinianus*	*E. nudatus*
Length of Pappus=	(7.5-6.5 mm.)	(6.0-5.0 mm.)	(4.5-3.5 mm.)
Bract Pubescence=	velutinous	hirsute	strigose
Stem pubescence=	velutinous	hirsute	strigose
Leaf Pubescence=	velutinous	hirsute	strigose



The three species as represented by pictorial figures seem to congregate at axes of a triangle with *E. carolinianus* at the top and *E. nudatus* and *E. tomentosus* at either base angle. The most overlap of figures is shown along the side from *E. carolinianus* to *E. tomentosus* and from *E. carolinianus* to *E. nudatus* but a few individuals are scattered in the wider gap between *E. tomentosus* and *E. nudatus*.

Most individuals of *E. tomentosus* and one of *E. nudatus* have a medium length pappus. *E. carolinianus* individuals show a medium to short pappus. Pubescence seems to be strigose in *E. nudatus*, hirsute in *E. carolinianus* and velutinous in *E. tomentosus* with only slight variation between all combinations of the species.

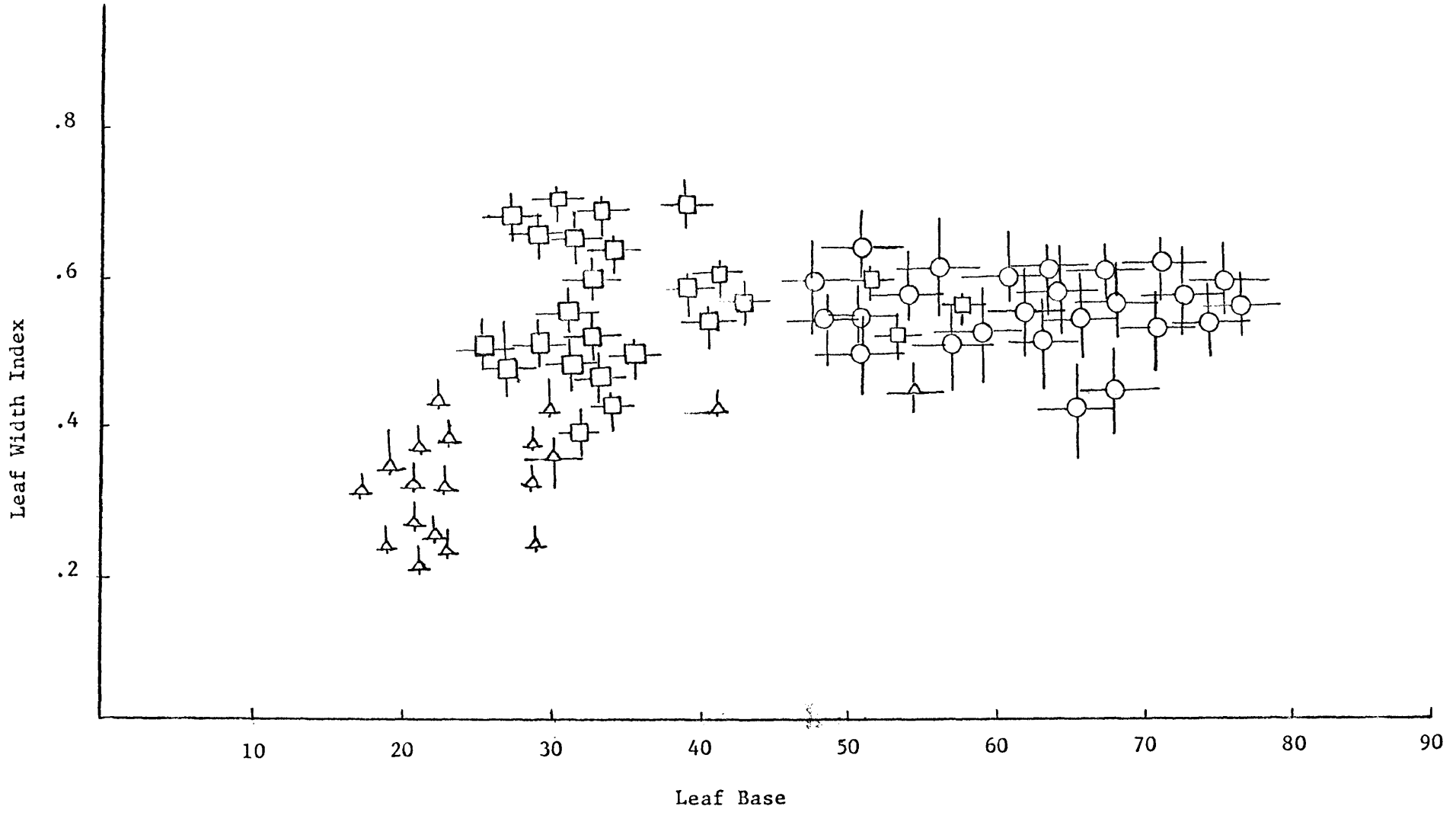


Fig. 13. Pictorial scatter diagram of all three species of the Mariner's Museum Population.

POLLINATION AND HYBRIDIZATION STUDIES

A major factor in the biology of angiosperms is the type of breeding system present, that is to what extent floral and genetic mechanisms promote inbreeding vs. outbreeding. Self-compatibility of flower heads prior to anthesis, and examining them later to see if any viable seeds have been set.

All taxa of Elephantopus studied were found to be self-compatible.[1] First generation seedlings were produced

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[1]Plants showing positive results in self-compatibility tests:

* - produced first generation seedlings,

** - produced mature achenes.

I-39 E. tomentosus*
I-9 E. carolinianus*
X-3 E. tomentosus**
II-4 E. carolinianus**
IV-69 E. nudatus**
IX-6 E. c. forma vestitus**
IV-4 E. t. forma rotundatus**
II-10 E. t. forma rotundatus**

from self-pollinated achenes of E. tomentosus and E. carolinianus. Mature achenes were produced by plants of E. carolinianus forma vestitus, E. tomentosus forma rotundatus and E. nudatus though limited time prevented actually growing the first generation seedlings.

That Elephantopus species are self-compatible is no surprise as the flower heads are relatively small and inconspicuous as composites go. In nature, considerable insect visitation was observed, as previously noted, suggesting that a great deal of cross-pollination commonly occurs. The ability to self-pollinate often contributes to the taxonomic problems found in many angiosperm genera. More particularly, it causes great practical difficulties in attempting to make artificial hybrids between species in the greenhouse. Mechanical emasculation of the tiny composite floret is not usually feasible. However, washing the heads with distilled water to destroy their own pollen does increase the chances of achieving a cross-pollination.

The production of artificial hybrids was attempted with plants from ten greenhouse cultures. Crosses were attempted using all possible combinations of the five taxa and as both paternal and maternal parents. A total of 136 crosses was hence attempted; however, achenes from only 58 of the crosses produced first generation seedlings. Due to the relatively slow growth of these seedlings, their actual identity as hybrids versus selfs of the maternal parent could not be determined by the time of this writing. The crosses involved are summarized in Table 3.

Cross-pollination producing first generation seedlings was recorded involving all five taxa; however, the largest number of

TABLE 3. SUMMARY OF CROSSES PRODUCING SEEDLINGS

Parents	Number of Crosses Producing Seedlings: Few	Several
E. carolinianus x *E. tomentosus*	2	1
E. c. forma *vestitus* x *E. tomentosus*	10	3
E. carolinianus x *E. t.* forma *rotundatus*	3	4
E. c. forma *vestitus* x *E. nudatus*	4	1
E. c. forma *vestitus* x. *E. t.* forma *rotundatus*	7	0
E. carolinianus x *E. nudatus*	3	1
E. tomentosus x *E. nudatus*	3	1
E. t. forma *rotundatus* x *E. nudatus*	10	2
E. tomentosus x *E. t.* forma *rotundatus*	1	2

successful crosses seem to be between E. c. forma vestitus x E. tomentosus, E. c. forma vestitus x E. t. forma rotundatus, and E. t. forma rotundatus x E. nudatus. These are independent results and not relative to the number of crosses attempted in each category. No great importance can be attached to the absolute or relative numbers of seedlings produced, however, until they are mature enough for accurate identification. A more detailed list of the actual plants utilized in this attempted series of hybridizations is presented in the appendix.

Interbreeding, as revealed by the presence of partly sterile hybrids, can often be detected by the study of pollen grain fertility. The relative number of well-filled pollen grains heavily stained by cotton blue is compared with the number of abortive, unstained grains. Such pollen counts based on at least 150 grains each, were taken of plants from six field populations and from eight greenhouse cultures. The mean count was determined for each taxon, wild population, and greenhouse culture.

Field populations of E. nudatus and E. tomentosus at the Mariner's Museum showed a mean fertility of 93.9% and 90.6% respectively (Table 4). Six field populations of E. carolinianus sampled showed means ranging from 77.6% to 97.4%. With the possible exception of the Glebe Land population, low fertility was associated merely with occasional individuals rather than characterizing a population as a whole.

Cultivated populations are considered separately from field populations inasmuch as greenhouse conditions sometimes significantly

TABLE 4. POLLEN STAINABILITY, FIELD POPULATIONS

Field Population	Species	Date of Pollen Count	Per cent Stainability	Population Mean
Mariner's Museum	1. E. nudatus	18 Sept. 66	95.6	
	2. E. nudatus	18 Sept. 66	90.4	
	3. E. nudatus	18 Sept. 66	95.6	
				Mean = 93.9
Mariner's Museum (valley)	1. E. tomentosus	18 Sept. 66	90.8	
	2. E. tomentosus	18 Sept. 66	96.7	
	3. E. tomentosus	18 Sept. 66	77.7	
	4. E. tomentosus	18 Sept. 66	97.8	
	5. E. tomentosus	18 Sept. 66	87.3	
				Mean = 90.6
Mariner's Museum (valley)	1. E. carolinianus	18 Sept. 66	92.3	
	2. E. carolinianus	18 Sept. 66	91.2	
	3. E. carolinianus	18 Sept. 66	93.4	
	4. E. carolinianus	18 Sept. 66	87.9	
	5. E. carolinianus	18 Sept. 66	95.6	
	6. E. carolinianus	18 Sept. 66	89.6	
				Mean = 91.7
Population Laboratory	1. E. carolinianus	22 Sept. 66	96.5	
	2. E. carolinianus	22 Sept. 66	97.1	
	3. E. carolinianus	222 Sept. 66	94.6	
	4. E. carolinianus	22 Sept. 66	96.9	
				Mean = 96.3
"Far" Eastern State	1. E. carolinianus	22 Sept. 66	91.1	
	2. E. carolinianus	22 Sept. 66	90.3	
	3. E. carolinianus	22 Sept. 66	93.3	
	4. E. carolinianus	22 Sept. 66	91.1	
	5. E. carolinianus	22 Sept. 66	41.9	
				Mean = 81.5
"Near" Eastern State	1. E. carolinianus	22 Sept. 66	76.6	
	2. E. carolinianus	22 Sept. 66	96.7	
	3. E. carolinianus	22 Sept. 66	94.5	
	4. E. carolinianus	22 Sept. 66	93.7	
	5. E. carolinianus	22 Sept. 66	96.8	
				Mean = 91.7
Glebe Land	1. E. carolinianus	30 Sept. 66	77.9	
	2. E. carolinianus	30 Sept. 66	90.7	
	3. E. carolinianus	30 Sept. 66	54.3	
	4. E. carolinianus	30 Sept. 66	76.7	
	5. E. carolinianus	30 Sept. 66	88.5	
				Mean = 77.6

TABLE 4. (CONTINUED)

Population	Species	Date of Pollen Count	Per cent Stainability	Population Mean
Kingsmill	1. E. carolinianus	30 Sept. 66	96.2	
	2. E. carolinianus	30 Sept. 66	92.8	
	3. E. carolinianus	30 Sept. 66	98.6	
	4. E. carolinianus	30 Sept. 66	100.0	
	5. E. carolinianus	30 Sept. 66	99.6	
				Mean = 97.4

modify fertility. In the greenhouse, the five taxa under consideration showed a fertility range as found in Table 5.

A more complete tabulation of the pollen fertility of greenhouse populations on which the above data were based is presented in Table 6. Here all the taxa which originated from a single station are listed together as one culture and an overall mean for the combination of taxa calculated. Only two such cultures had a mean below 90% fertility and here again this appears to be merely a matter of occasional individuals rather than whole populations being characterized by lowered pollen viability.

In conclusion, the occurrence of lowered pollen fertility was not characteristic of any particular population or taxon. The greatest number of plants from both the greenhouse and field showed a normal fertility of 90-100%. Individuals showing substantially less than this value need to be reinvestigated morphologically and to have their fertility and cytology studied further if greenhouse stocks can be maintained.

TABLE 5. POLLEN STAINABILITY, IN THE FIVE TAXA OF GREENHOUSE CULTURES

Taxon	Number of Individuals	Mean Fertility	Range
E. carolinianus	19	93.9%	(82.8-100.0%)
E. c. forma *vestitus*	18	86.2%	(42.5-99.6%)
E. tomentosus	9	95.1%	(79.7-99.6%)
E. t. forma *rotundatus*	8	93.1%	(57.6-99.1%)
E. nudatus	4	94.8%	(90.1-98.9%)

TABLE 6. POLLEN STAINABILITY, GREENHOUSE CULTURES

Population	Culture Number	Species	Date of Pollen Count	Per cent Stainability	Population Mean
I	2	*E. carolinianus*	1 Sept. 66	92.9	
	3	*E. carolinianus*	8 Sept. 66	86.9	
	9	*E. carolinianus*	8 Sept. 66	98.6	
	8	*E. c.* forma *vestitus*	1 Sept. 66	63.1	
	12	*E. c.* forma *vestitus*	19 Sept. 66	57.5	
	15	*E. c.* forma *vestitus*	8 Sept. 66	42.5	
	34	*E. tomentosus*	1 Sept. 66	94.2	
	29	*E. t.* forma *rotundatus*	19 Sept. 66	99.1	
					Mean = 79.4
II	1	*E. carolinianus*	19 Sept. 66	88.7	
	5	*E. carolinianus*	8 Sept. 66	94.9	
	14	*E. carolinianus*	1 Sept. 66	100.0	
	13	*E. tomentosus*	1 Sept. 66	93.8	
	13	*E. tomentosus*	19 Sept. 66	99.6	
	11	*E. tomentosus*	1 Sept. 66	99.1	
	7	*E. t.* forma *rotundatus*	1 Sept. 66	98.7	
	8	*E. t.* forma *rotundatus*	3 Sept. 66	57.6	
	10	*E. t.* forma *rotundatus*	8 Sept. 66	97.9	
	12	*E. t.* forma *rotundatus*	19 Sept. 66	95.9	
					Mean = 93.2
IV	12	*E. t.* forma *rotundatus*	1 Sept. 66	98.3	
	12	*E. t.* forma *rotundatus*	19 Sept. 66	98.5	
	14	*E. t.* forma *rotundatus*	1 Sept. 66	98.8	
	60	*E. nudatus*	19 Sept. 66	92.3	
	74	*E. nudatus*	1 Sept. 66	98.8	
					Mean = 97.3

TABLE 6. (continued)

Population	Culture Number	Species	Date of Pollen Count	Percent Stainability	Population Mean
V.	5	E. tomentosus	1 Sept. 66	98.9	
	9	E. tomentosus	1 Sept. 66	99.0	
	11	E. tomentosus	13 Sept. 66	94.3	
	13	E. carolinianus	8 Sept. 66	90.0	
	13	E. carolinianus	19 Sept. 66	94.2	
	14	E. carolinianus	3 Sept. 66	82.8	
	14	E. carolinianus	19 Sept. 66	96.5	
	15	E. carolinianus	19 Sept. 66	97.5	
	15	E. carolinianus	19 Sept. 66	90.9	
	16	E. carolinianus	19 Sept. 66	97.6	
	17	E. carolinianus	8 Sept. 66	95.4	
	17	E. carolinianus	19 Sept. 66	95.8	
					Mean = 94.5
VII	6	E. carolinianus	8 Sept. 66	87.5	
	5	E. c. forma vestitus	19 Sept. 66	99.1	
	7	E. c. forma vestitus	3 Sept. 66	96.1	
	7	E. c. forma vestitus	19 Sept. 66	97.0	
					Mean = 94.9
VIII	5	E. carolinianus	19 Sept. 66	98.8	
	3	E. c. forma vestitus	3 Sept. 66	97.1	
	6	E. c. forma vestitus	3 Sept. 66	97.6	
	6	E. c. forma vestitus	3 Sept. 66	94.1	
	6	E. c. forma vestitus	19 Sept. 66	99.5	
	8	E. c. forma vestitus	3 Sept. 66	94.2	
	8	E. c. forma vestitus	8 Sept. 66	94.4	
					Mean = 96.5

TABLE 6. (continued)

Population	Culture Number	Species	Date of Pollen Count	Per cent Stainability	Population Mean
IX	1	*E. carolinianus*	3 Sept. 66	97.3	
	5	*E. c.* forma *vestitus*	3 Sept. 66	64.0	
	5	*E. c.* forma *vestitus*	19 Sept. 66	94.0	
	6	*E. c.* forma *vestitus*	3 Sept. 66	96.4	
	6	*E. c.* forma *vestitus*	19 Sept. 66	96.7	
	8	*E. c.* forma *vestitus*	1 Sept. 66	93.1	
	8	*E. c.* forma *vestitus*	3 Sept. 66	75.5	
					Mean = 86.8
X	3	*E. tomentosus*	8 Sept. 66	79.9	
	4	*E. tomentosus*	8 Sept. 66	96.7	
	11	*E. nudatus*	1 Sept. 66	97.2	
	17	*E. nudatus*	1 Sept. 66	91.1	
					Mean = 91.2

DISCUSSION

Anderson (1936) devised a hybrid index method to study hybridization between Tradescantia canaliculata and T. virginiana in seven localities. He found that the hybrids tended to back-cross with one parental species while only a few combinations with the second species were detected. Anderson concluded that the process of hybridization varies with the conditions of the environment and according to the species involved. In certain cases the variability produced was thought to constitute a major source of raw material for natural selection.

One of the most important aspects of Anderson's work is the possibility of expressing qualitative categories as quantitative values. This insures a more objective technique in determining the deviation and mode in any population. According to Gay (1960) any remaining analysis of the data involves visual estimation of differences between frequency polygons of samples and introduces subjectivity.

Sibley (1954) proposed additional means of analysis using a Mean Hybrid Index to measure the degree of hybridization in each population. The same results are sometimes obtained in both hybridizing and non-hybridizing populations. To avoid this ambiguity Gay (1960) has combined the deviation of the Hybrid Index of the specimen from the nearer of the two extreme values of the Hybrid Index scale. The Hybrid Number represents the degree of hybridity or degree of gene mixture within a specimen. The Mean Hybrid Number is plotted against the Mean Hybrid Index. A graph representing the two species and hybrids forms a triangle

and all specimens interpreted in terms of these three components will fall within this triangle on the same graph. Each population is plotted as a whole and the distance is a measure of the proportion in the population of the component represented by the apex opposite that side.

This seems to decrease the amount of subjectivity when comparing populations. However, Gay mentions several shortcomings of this method such as two populations having an identical M. H. I. and M. H. No. but a different composition. Secondly, it is not known if the difference in these statistics between populations is significant. Additionally not all variations in a population can be described by this method (Gay, 1960).

Although, this method can be applied to material of the genus Erica (Gay, 1960) it cannot be safely used in this study since hybrid material must be definitely identifiable and score values determined before the analysis is undertaken.

In Anderson's original work (1936), the index values assigned to given characteristics were not consistent, giving more weight to some than to others. If two intermediates were found for one characteristic, then the range of the index score was extended from 0-2 to 0-3. However, one series of three characteristics was only given an extreme index value of 1. Anderson gave them half the normal weight because these characteristics were all different measures of the same quality, the distribution of stomata on the upper epidermis.

In 1962, Hatheway proposed a Weighted Hybrid Index. Using data obtained from a study on the stemless white violets, he constructed a pictorial scatter diagram illustrating ten characteristics of each of

25 specimens. Two plants having opposite extreme characteristics were chosen to represent either end of a hybrid index scale. Characteristics from the hybrid index were then used to construct scatter diagrams: one an unweighted diagram combining five aspects of pubescence along one axis and four aspects of petal venation along the other axis; the second, a weighted scatter diagram representing the relationship between the number of branches in the submidvein of the spur petal and the number of hairs on the pedicel. Correlation between the venation and the pubescence was much higher for the weighted scatter diagram and the individual specimens showed a more distinct distribution. Hatheway (1962) states that an index composed of only a few well-selected characters can be more meaningful than an unweighted index since the variation in certain characters may have nothing to do with introgression and only confuse an otherwise orderly pattern of variation. He believes that the contribution of the character to an index should be in proportion to its usefulness in demonstrating a known or suspected relationship.

An unweighted hybrid index was used in the present study of Elephantopus since no single pair of characteristics showed a marked correlation. If a character was not found to vary between two species a standard score of intermediate value was given to all specimens. This would merely introduce consistency and would have no differential effect on the total hybrid score. Unless individual scatter diagrams were constructed for all combinations of characters showing some degree of variation it would be difficult to select the "most useful" characters. Characters showing any degree of variation all contribute to the phenotype of the specimen. They have a cumulative effect on the overall morphology and aspect of the individual

and should not be disregarded in the analysis. Often the more subtle characteristics, whether adaptive or non-adaptive, are overlooked. They could be significant in the Hybrid Index.

In many cases, population analysis using two unweighted Hybrid Index scales showed that the frequency distribution deviated from the normality in a bi- or tri-modal pattern. Although E. tomentosus, E. carolinianus and E. nudatus are broadly sympatric in overall range, all three were found growing together in only one location, Mariner's Museum: E. tomentosus and E. carolinianus were both found in the College Woods.

The histogram comparing E. tomentosus and E. nudatus from Mariner's Museum shows several modes on the E. tomentosus side and only one mode on the E. nudatus side; however, four specimens from the E. nudatus group extend into the intermediate zone. There seems to be variation in both species although it is more abrupt in E. tomentosus with a gradation of variants toward the mode of E. nudatus.

This scattered frequency distribution could indicate the presence of hybrids and a more pronounced backcrossing of the hybrids with E. nudatus than with E. tomentosus.

Comparison of E. tomentosus and E. carolinianus of the same population also indicates possible hybridization. Widespread intermediates are not found but both species have a wide range of hybrid indices diminishing gradually in frequency toward the hybrid zone. Absence of hybrids strictly

intermediate between the species could be due to character combinations which are inappropriate to the prevalent ecological condition. Backcrosses showing greater resemblance to either parent species are more likely to survive since they are better able to compete with the parent species and probably would also show a greater fertility than F_1 hybrids.

The highest degree of intergradation can be seen between E. nudatus and E. carolinianus of the Mariner's Museum population. The E. nudatus frequency distribution has only one mode and E. carolinianus is bi-modal while both species show overlapping specimens within the hybrid zone. There seems to be an even distribution within the intermediate zone in addition to areas of backcrossing.

In the fourth histogram three groups of E. tomentosus were compared with a hypothetical E. nudatus population. All groups were multi-modal but showed a concentrated distribution around the modes. E. tomentosus from both the Mariner's Museum Roadside had a wider range with four specimens showing some intermediate variation which could be due to hybridization with adjacent E. nudatus plants.

All groups of E. tomentosus compared to E. carolinianus in the fifth histogram were bi-modal with a continual gradation of the frequency distribution from the modes toward the second species.

Six populations of E. carolinianus were compared in the sixth histogram and seem to illustrate two patterns of distribution. Populations from Mariner's Museum and the Quonset Hut are bi-modal and have few or no individuals extending into the intermediate region. This could mean that hybridization has taken place and only progeny from backcrosses

have been established, which could explain the presence of two close modes. The Naval Weapons Station and Kingsmill populations show a gradual decrease of frequencies from the mode toward the hybrid zone which could correspond to introgression although no E. tomentosus plants were observed in the immediate area in either case. Most specimens from the Population Laboratory area are concentrated around the mode and a few are scattered along both extremes of the range. The variation shown by specimens in these fringe areas could be due to individual genetic variation and not to hybridization. Specimens at both ends of the range belong to forma vestitus.

In the last histogram the same six populations of E. carolinianus were compared to E. nudatus. All populations have similar ranges. Only one mode is found in the Population Laboratory and Naval Weapons Station populations and the rest of the populations are bi-modal. Areas of backcrossing seem to be indicated in all populations, with a distinct gradation of hybrid frequencies within a short range from the mode in the direction of E. nudatus.

The histograms seem to indicate hybridization between all three species and this is also illustrated by the polygons and pictorial scatter diagrams.

The polygons give a visual comparison since each polygon represents the mean value of all the specimens for each characteristic. The similarity of the polygons can be observed at a glance and the specific categories in which both species are similar can be noted. Some overlap was found in characters between all combinations of the three species but the greatest amount of similarity was shown between E. carolinianus and E. nudatus and between E. carolinianus and E. tomentosus.

The same pattern was shown in the pictorial scatter diagram (Figure 13). Individuals corresponding to the three species were concentrated in three areas. The specimens of E. carolinianus were grouped slightly above but between E. tomentosus and E. nudatus. Variation in the characteristics could also be seen in areas where two species overlapped.

The origins of the distribution patterns described for these three species is thought to be due to hybridization and establishment of introgressants. Although artificial hybrids have not been produced, there is no reason to believe that both natural and aritficial hybridization is not possible. Crosses were attempted in the greenhouse and progeny were produced from every combination of species and form. The seedlings were too immature to analyze with a hybrid index. However, because the native pollen of the maternal plants was destroyed with distilled water it is probable that some of the second generation seedlings are hybrids.

The three species and two forms of Elephantopus are known to have the same chromosome number 2n=22 (Baldwin and Speese, 1955). This eliminates the possibility of chromosome sterility between the parent species due to different ploidy levels. Likewise this same number of chromosomes could be expected in the hybrids.

Any sterility or partial sterility could be due to chromosomal aberrations in the form of duplications, deficiencies, translocations, or inversions or to genetic incompatibility. Although cytogenetic analysis from chromosome squash slides of the hybrids was not attempted in this study, it is possible to detect the presence of such aberrations at meiosis. The specific causes of hybrid sterility will

not be known until this can be done.

Although not prevalent, a few putative hybrids were collected from the field and can be described as follows:

1. #109 E. carolinianus resembles E. tomentosus. The specimen has round leaves with a narrow apex and a short tapered base; heads and glomerules few with short bracts.

2. #118 E. carolinianus resembles E. nudatus. The specimen has long leaves, round-oval in shape, extensively tapered to the base. The bracts and pappus are short.

3. #269 E. carolinianus resembles E. tomentosus. The specimen has short leaves gradually tapered to the base. The stem pubescence is velutinous and the leaf pubescence is dense; heads and glomerules are few; long internodes.

4. #270 E. carolinianus resembles E. tomentosus. The specimen has short leaves with a narrow apex, evenly tapered to the base. The stem pubescence is velutinous and the leaf is densely velutinous; heads few with short bracts; long internodes.

5. #324 E. carolinianus resembles E. nudatus. The specimen has long slender leaves, round in shape, gradually tapered to the base. The pappus and bracts are short; leaf pubescence dense.

6. #320 E. carolinianus resembles E. nudatus. The leaves are gradually tapered at apex and base. The internodes are short; heads few and bracts short.

7. #451 E. carolinianus resembles E. tomentosus. The specimen has oval-shaped leaves with little tapering at the base. The pappus is short; heads and glomerules few; bract pubescence is dense.

8. #398 E. carolinianus resembles E. nudatus. The leaves are short, round-ovate with a narrow base and apex; the glomerules few.

9. #163 E. nudatus resembles E. carolinianus. The specimen has oblong-ovate leaves which are abruptly tapered to the base. The pubescence of bract, stem and leaf is hirsute.

10. #132 E. tomentosus resembles E. carolinianus. The specimen has oval leaves; small bracts subtending the inflorescence.

Unfortunately all of these specimens were nearly or quite past blooming when collected so that no pollen or insufficient pollen was available for study of fertility.

Probable hybrids such as these listed above seem to be present in natural populations in very small numbers with larger numbers of individuals showing only slight variation from the average. There is no evidence that extensive hybridization is obliterating the differences between the three species. Several barriers or partial barriers may exist between the species preventing the three from merging into a single polymorphic species. The factors tending to promote and to restrict successful hybridization are listed below.

Promoting Hybridization	Restricting Hybridization
1. Wide overlap of species geographically.	1. High degree of autogamy.
2. Somewhat similar habitat preferences.	2. Partial sterility of hybrids.
3. Similar blooming period; floral parts of similar size and structure; pollinating agents in common.	3. Lack of hybrid habitats.
4. Identical chromosome numbers.	

Most of the advantages for successful pollination seem to be at the gamete or zygote level. Chromosomal inter-fertility is suggested for all three species. Cross-pollination is favored for the species are all sympatric and have similar blooming seasons. E. nudatus was observed to blossom first during the last two weeks of August. E. tomentosus was in full bloom during the last week of August when E. carolinianus first began to bloom. The blooming seasons do not correspond exactly but in all cases a few plants from all three species were blooming at the same time. The petal color is similar in all three species, attracting the same type of pollinating agent and the

transfer of pollen is accomplished by non-selective pollinators. Since the floral parts of all three species are similar in size and structure there would be no mechanical disadvantage concerning the transfer or development of foreign pollen.

Disadvantages at the gamete level might include the high degree of autogamy which may lessen the chance of fertilization by foreign pollen. Perhaps the low pollen fertility found in a few cases indicates gemetic sterility in the hybrid progeny. Most of the disadvantages for successful hybridization, however, appear to be at the ecological level.

F_1 hybrids usually show an intermediate morphology between the parents but the second generation is extremely variable with a large number of individuals resembling the original parent species. Anderson (1947) suggests that physiological differences segregate in the same way as morphological ones and that the F_1 hybrids require a habitat intermediate between the parent habitats. The persistence of the F_1 hybrids and of any second hybrid generation recombinations might require habitats seldom or never found in close juxtaposition to one another.

Anderson (1947) believes that only through hybridization of the habitat can hybrids and hybrid recombinations be preserved in nature. This can be accomplished through the intervention of man; however, the habitats produced may still be much like the parental habitats. This may explain the establishment of backcrosses instead of hybrids for they are much like the parents and are more likely to find ecological niches suited to them.

Hybrid habitats were described by Riley (1938) in his work with colonies of Iris. He found two colonies of hybrids between two colonies of the pure species in an area disturbed by man. Apparently the ecological barrier had been broken down, providing conditions suitable for producing hybrids. Riley found that onee the hybrids were formed they became established in the recently disturbed area.

This situation could also apply to Elephantopus since all three species studied seem to have slightly different ecological ranges. According to Steyermark (1963) E. carolinianus was found in sparsely wooded lowlands, valleys and ravines and along streams in alluvial thickets and Tatnall (1946) also record E. carolinianus in damp woods. In this study E. carolinianus was also found in open dry woods and commonly bordering fields or pastures in little to moderate shade. E. tomentosus was found in dry open woods with little underbrush and moderate to dense shade. E. nudatus occurred in open pine woods in sand or gravel in moderate shade and with no underbrush. The absence of hybrid recombination habitats may be a factor in isolating these species. There may be no habitat distinctive enought so that the hybrids could indefinitely compete against teh most suitable parent species.

Most of the histograms seem to indicate the presence of introgressants gradually extending from the mode toward the intermediate hybrid area. In most cases purely intermediate hybrids were not present. This could be influenced by inappropriate hybrid habitats as noted above so that progeny produced by backcrossing to the parents would have a more similar ecological tolerance to the parents and would be more likely to survive in habitats occupied by the parents.

Elephantopus, like many other herbaceous perennials, is an invader of pasturelands and paths in wooded areas which are all sites of rapid ecological succession. If the hybrids were less vigorous vegetatively than the parents this instability of the habitat would decrease their relative chances of success in establishing new colonies or in dominating them. The smaller number of hybrid achenes produced compared to parental achenes would also be a disadvantage for the continual establishment of hybrids.

The distribution of forma vestitus and forma rotundatus showed no distinctive pattern within their respective species and could not be correlated with hybridization, nor with specific populations or geographic areas. Variation was found within each form and it is thought that slight genetic variation within each species is responsible for the occurence of these forms. Hence their nomenclatural status as forms rather than varieties or subspecies appears to be the correct one.

The polygons and pictorial scatter diagrams show that the three species are very closely related and according to Sibley (1963) this would indicate that in the past they were derived from common stock. During the following period of isolation the three species achieved a high degree of morphological difference in pubescence, leaf and bract shape but less in other characters. Gleason (1922), Gleason and Cronquist (1963) and Fernald (1950) have uniformly recognized the three as valid species. Although sympatric, the three species can be recognized as distinct even in areas such as the Mariner's Museum Park where plants were actually growing within a few yards of each other.

The morphological distinction has not been obliterated even though it appears that widespread hybridization definitely does take place among the three species especially between E. carolinianus in combination with each of the other species. Variation and the occasional occurrence of hybrids has been noted in all populations including the Mariner's Museum Park. The presence of introgressants seems to be indicated in the histograms between all three species.

One explanation for interbreeding between species may be the distruction of mature communities. Elephantopus is a noted invader of disturbed areas, and disturbance such as the clearing of wooded areas for paths or pastureland may provide the ecological niches necessary for introgressants and hybrids espécially adapted for secondary successional series.

A breakdown in such ecological barriers probably occurred with the clearing of natural vegetation by man. This process has taken place in eastern Virginia for the last 360 years. A short period of hybridization also seems to be suggested by the great variability within each population. If selection has occurred before man began to make wide ecological changes, the hybrid populations would probably occur as a chain of intermediate populations (Sibley, 1963).

Additional information concerning the variation patterns of Elephantopus could be obtained by studying artificial hybrids. Descriptions of the actual characteristics shown in the F_1 hybrids and in later generations would be valuable. Fertility of these hybrids should be tested, followed by cytogenetic studies of the causes of any sterility noted. Further work might also involve quantitative ecological study of the habitat

coupled with reciprocal transplants.

SUMMARY

1. The morphology and patterns of variation were studied in three sympatric species and two forms of Elephantopus in Virginia.

2. Methods of investigation included both field and laboratory work. Progeny were produced by artificial hybridization between all combinations of the five taxa, although the seedlings were too immature to analyze.

3. Approximately twenty-five specimens of each species present in seven population areas were analyzed with a hybrid index method. Histograms and other diagrams constructed from these data seem to indicate the presence of introgressants primarily, rather than first generation hybrids.

4. Identical pollinating agents were noticed for all three species and pollen fertility tests taken from natural populations and culture plants showed a consistently high fertility with only a few plants depressed to 40-80% fertility.

5. Cytological information, data from artificial crosses and high pollen fertility suggest that hybridization is possible between all combinations of the taxa.

6. The comparative rarity of first generation hybrids may be due to genetic barriers between species, the inability of hybrids to compete in habitats with rapid ecological succession, or a lack of distinctive

hybrid habitats. Establishment of interspecific hybrids may depend on the presence of intermediate habitats distinctive enough that the hybrid has advantages over the parent species. Perhaps further intervention by man will provide the habitats suitable for intermediate populations or stimulate the evolution of one polymorphic species.

APPENDIX

World distribution of Elephantopus.

1. Species recorded from North America north of the Isthmus of Panama include:

*E. angustifolius Sw.
Distribution: American Tropics

E. arenarius Britton & Wilson
Type Locality: Vicinity of Los Indios, Isle of Pines.
Distribution: Isle of Pines, Cuba.

E. carolinianus Willd.
Elephantopus violaceus Schultz-Bip. 1847.
Elephantopus flexuosus, Rafin.

Type Locality: Carolina.
Distribution: New Jersey to Florida, Kansas, and Texas, Pa., W. Va., O., Ind., Ill., Mo; Cuba and Puerto Rico.

E. colimensis Sess & Moc.
Distribution: Mexico.

E. dilatatus Gleason
Type Locality: Banks of the Rio Ceibo, Buenos Aires Costa Rica.
Distribution: Mexico, Guatemala, Costa Rica, Central America.

E. elatus Bertol.
Elephantopus elatus intermedius Gleason

Type Locality: Alabama.
Distribution: South Carolina to Florida, Louisiana, and southern Arkansas.

E. glaber Sesse & Moc.
Distribution: Mexico.

E. hypomalacus Blake
Type Locality: Orotina, Costa Rica, alt. about 180 meters.
Distribution: Mexico, Guatemala, Costa Rica, Central America.

* Denotes species found in more than one geographic zone.

E. littoralis Sesse & Moc.
Distribution: Mexico.

E. mollis H. B. K.
Type Locality: Venezuela.
Distribution: Cuba and Mexico and south into tropical Puerto Rico, Jamaica and other islands.

E. nudatus A. Gray
Type Locality: Oxford, Delaware.
Distribution: Delaware to Florida, Arkansas, and Louisiana.

E. pratensis C. Wright
Type Locality: Cuba.
Distribution: Cuba and Isle of Pines.

*E. scaber L.
Type Locality: East Indies.
Distribution: Introduced into Costa Rica and Guatemala from the East Indies.

E. tomentosus L.
Elephantopus nudicaulis Poir.
Elephantopus carolinianus simplex Nutt.
Elephantopus nudicaulis, Ell.

Type Locality: Virginia.
Distribution: se. Va. to Florida and Texas, n. to Md., W. Va., and Ky.

2. Species recorded from South America include:

*E. angustifolius Sw.
Distribution: American Tropics.

E. arenosus Kraschen
Distribution: Brazil.

E. biflorus Sch. Bip.
Distribution: Brazil.

E. elongatus Hook.
Distribution: Brazil.

E. erectus Gleason
Distribution: Sao Paulo, Brazil.

E. hirtiflorus DC.
Distribution: Brazil.

E. Martii Grah.
Distribution: Brazil.

E. micropappus Less.
Distribution: Brazil.

E. mollis H. B. K.
Type Locality: Venezuela.
Distribution: Cuba and Mexico, and south into tropical South America.

E. palustris. Hook.
Distribution: Brazil.

E. paniculatus Mart.
Distribution: Brazil.

E. pilosus Philipson
Distribution: Antigua; Trinidad; Guiana; Brazil.

E. racemosus Hook
Distribution: Brazil.

E. Riedelii Sch. Bip.
Distribution: Brazil.

E. riparius Gardn.
Distribution: Brazil.

E. spicatus Aubl.
Distribution: Guiana.

E. vaginatus Hook.
Distribution: Brazil.

E. virgatus Desa
Distribution: Guiana.

3. Species recorded in the Far East include:

E. ciliatus Zell & Moc.
Distribution: Java.

E. Bodinieri Gagnep.
Distribution: Indo-China (Anam); Hong Kong.

*E. scaber L.
Type Locality: East Indies.
Distribution: Ceylon, Formosa, Malaysian and Australasian islands, Africa. Introduced into Costa Rica and Guatemala from the East Indies.

E. sericeus R. Grah.
Distribution: West Indies.

E. sinuatus Zoll. & Moc.
Distribution: Java.

4. Species recorded in Africa include:

E. Gossiverleri S. Moore
Distribution: Angola.

E. Mendoncae Philipson
Distribution: Angola.

*E. scaber L.
Type Locality: East Indies.
Distribution: Ceylon, Formosa, Malaysian and Australasian islands, Africa. Introduced into Costa Rica and Guatemala from the East Indies.

E. senegalensis Oliver.
Distribution: Tropical Africa.

E. vernonioides S. Moore.
Distribution: Angola.

Fig. A. E. nudatus showing (A) habit (plant IV-49) and (B) inflorescence (plant IV-63).

Fig. B. E. tomentosus showing (A) habit (plant X-1) and (B) inflorescence (plant IV-35).

Fig. C. E. carolinianus showing (A) habit (plant III-8) and (B) inflorescence (plant IX-3).

Fig. D. E. tomentosus forma rotundatus Fern. (plant IV-35).

Fig. E. (A) E. carolinianus forma vestitus Fern. (plant IX-3) (B) Comparative photograph showing E. tomentosus forma rotundatus Fern. (plant IV-35), E. nudatus (plant IV-49), and E. carolinianus forma vestitus Fern. (plant IX-3).

Location of Experimental Populations

I. College Woods	College Woods, Campus side of Lake, College of William and Mary, Williamsburg, James City County, Virginia.
II. Colonial Parkway	Along highway between Jamestown and Williamsburg, James City County, Virginia.
III. College Woods	College Woods, College of William and Mary, Williamsburg, James City County, Virginia.
IV. Mariner's Museum	Along highway in Mariner's Museum Park, Newport News.
V. College Woods	Along lumbering paths, far side of Lake Matoaka, College of William and Mary, Williamsburg, James City County, Virginia.
VI. College Woods	Along path on campus side, College of William and Mary, Williamsburg, James City County, Virginia.
VII. Eastern State "Far"	Along Francis Street near the old site of Eastern State Hospital, Williamsburg, James City County, Virginia.
VIII. Eastern State "Near"	Along Henry Street near old site of Eastern State Hospital, Williamsburg, James City County Virginia.
IX. Population Laboratory	Along Henry Street in the vicinity of Population Laboratory, College of William and Mary, Williamsburg, James City County, Virginia.
X. Mariner's Museum	Along highway through Mariner's Museum Park Newport News, Virginia.
Kingsmill Historical Site	Colonial Parkway between Williamsburg and Jamestown.
Quonset Hut Number 5	College of William and Mary, Williamsburg, Virginia.

Bellfield Plantation Site	Colonial Parkway between Williamsburg and Yorktown.
Ringfield Picnic Area	Colonial Parkway between Williamsburg and Yorktown.
Naval Weapons Station	Colonial Parkway between Williamsburg and Yorktown.
Glebe Land Historical Site	Colonial Parkway between Williamsburg and Jamestown.

Series I

E. tomentosus vs E. carolinianus

Characteristics

	Character State and Score				
	0	1	2	3	4
Leaf Base	-65°	64°-55°	54°-45°	44°-35°	34°-
Leaf Apex	-69°	70°-75°	76°-81°	82°-87°	88°-
Leaf Length	-22 cm.	21-18 cm.	17-14 cm.	13-10 cm.	9- cm.
Leaf Width	-9 cm.	8 cm.	7 cm.	6 cm.	5 cm.
Leaf Index	-.66	.65-.61	.60-.56	.55-.51	.50-
Leaf Width Index	-.40	.41-.45	.46-.50	.51-.55	.56
Length of Pappus	-7.0 mm.	6.5-6.0 mm.	5.5-5.0 mm.	4.5-4.0 mm.	3.5- mm.
No. of Heads	-8	9-10	11-12	13-14	15-
No. of Glomerules	-5	6-8	9-11	12-14	15-
Length of First Internode	-21 cm.	20-15 cm.	14-9 cm.	8-3 cm.	2- cm.
Leaf Length of First Node	-2 cm.	3-5 cm.	6-8 cm.	9-11 cm.	12- cm.
Bract Length	-1.00 cm.	1.25 cm.	1.50 cm.	.175 cm.	2.00 cm.
Density of Bract Pubescence	dense		moderate		slight
Bract Pubescence	velutin-ous				hirsute
Density of Stem Pubescence	dense		moderate		slight
Stem Pubescence	velutin-ous				hirsute
Density of Leaf Pubescence	dense		moderate		slight
Leaf Pubescence	velutin-ous				hirsute

Series II

E. tomentosus vs E. nudatus

Characteristics

	Character State and Score				
	0	1	2	3	4
Leaf Base	-62°	61°-49°	48°-36°	35°-23°	22°-
Leaf Apex	-89°	88°-73°	72°-57°	56°-41°	40°-
Leaf Length	-22 cm.	21-18 cm.	17-14 cm.	13-10 cm.	9- cm.
Leaf Width	-9 cm.	8-7 cm.	6-5 cm.	4-3 cm.	2- cm.
Leaf Index	-.64	.63-.51	.50-.38	.37-.25	.24-
Leaf Width Index	-.41	.40-.36	.35-.31	.30-.26	.25-
Length of Pappus	-7.0 mm.	6.5 mm.	6.0 mm.	5.5 mm.	5.0 mm.
No. of Heads	-				-
No. of Glomerules					
Length of First Internode					
Leaf Length of First Node	-	-	-	-	-
Bract Length	1.25 cm.	1.00 cm.	0.75 cm.	0.50 cm.	0.25 cm.
Density of Bract Pubescence	dense		moderate		slight
Bract Pubescence	velutinous				strigose
Density of Stem Pubescence	dense		moderate		slight
Stem Pubescence	velutinous				strigose
Density of Leaf Pubescence	dense		moderate		slight
Leaf Pubescence	velutinous				strigose

Series III

E. nudatus vs E. carolinianus

Characteristics	Character State and Score				
	0	1	2	3	4
Leaf Base	-24°	25°-27°	28°-30°	31°-33°	34°-
Leaf Apex	-40°	41°-56°	57°-72°	73°-88°	89°-
Leaf Length					
Leaf Width					
Leaf Index	-				
Leaf Width Index	-.25	.26-.35	.36-.45	.46-.55	.56-
Length of Pappus	-	-	-	-	-
No. of Heads	-8	9-10	11-12	13-14	15-
No. of Glomerules	-5	6-8	9-11	12-14	15-
Length of First Internode	-15 cm.	14-11 cm.	10-7 cm.	6-3 cm.	2- cm.
Leaf Length at First Node	-3 cm.	4-6 cm.	7-9 cm.	10-12 cm.	13- cm.
Bract Length					
Density of Bract Pubescence	slight				moderate
Bract Pubescence	strigose				hirsute
Density of Stem Pubescence	slight		moderate		dense
Stem Pubescence	strigose	-	-		hirsute
Density of Leaf Pubescence	strigose				moderate
Leaf Pubescence	strigose				hirsute

Hybrid Data Sheet

Population: Mariner's Museum Valley 221-268
Series: I

Date: 4/10/67

Species: E. tomentosus with E. carolinianus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Leaf Index	Leaf Width Index	Length of Pappus	No. of Heads	No. of Glomerules	Length of First Internode	Leaf Length of First Node	Bract Length	Density of Bract Pubescence	Bract Pubescence	Density of Stem Pubescence	Stem Pubescence	Density of Leaf Pubescence	Leaf Pubescence	Total Index Value
* 1	221	2	4	3	3	4	4	0	2	2	2	1	0	0	0	0	0	0	0	27
* 2	222	0	1	4	4	3	4	0	2	0	1	0	1	0	0	2	4	0	0	26
* 3	223	0	4	3	2	4	4	0	4	0	3	1	1	0	0	0	0	0	0	26
4	224	1	2	2	2	4	4	0	3	0	0	1	4	2	0	2	0	0	0	27
* 5	224	0	4	3	3	3	4	0	2	0	1	1	1	0	0	2	0	0	0	24
* 6	226	2	3	4	4	4	4	2	3	0	1	0	2	0	0	0	0	2	0	31
* 7	227	2	3	0	0	4	4	0	3	4	1	1	4	2	0	0	4	2	0	34
8	228	0	4	3	2	2	4	0	2	1	1	1	1	0	0	2	0	0	0	24
* 9	230	0	4	3	3	3	4	0	2	0	2	2	2	2	0	2	0	2	0	31
*10	231	0	4	3	3	3	4	0	1	0	2	1	2	2	0	2	0	2	0	29
*11	232	0	4	2	1	2	4	0	1	2	2	1	2	0	0	0	0	0	0	23
*12	233	0	4	3	1	1	0	0	1	2	3	2	2	2	0	0	0	0	0	21
*13	234	1	4	3	4	4	4	0	0	0	2	4	0	0	0	2	0	2	0	30
*14	235	0	2	2	2	4	4	0	1	0	2	1	1	2	0	0	0	2	0	23
*15	236	2	2	2	2	4	4	0	1	0	2	1	1	0	0	0	0	2	0	23
*16	237	2	4	3	3	0	4	1	0	0	2	0	0	2	0	0	0	0	0	21
*17	238	0	4	3	3	2	4	1	2	0	1	2	0	0	0	0	0	0	0	22
*18	239	0	1	4	4	3	4	1	0	0	4	0	0	2	0	0	0	0	0	23
*19	240	0	4	2	1	2	0	0	2	2	1	1	1	2	0	0	0	0	0	18
*20	241	2	1	1	1	4	4	0	0	1	1	1	4	2	0	0	0	0	0	22
*21	242	0	4	2	1	4	4	0	3	2	3	1	2	0	0	0	0	0	0	26
*22	243	0	3	3	2	4	4	1	2	0	2	0	2	0	0	0	0	0	0	24
*23	244	1	1	3	4	4	4	0	1	1	2	1	2	0	0	0	0	0	0	24
*24	245	0	4	3	3	4	4	0	2	1	2	1	4	2	0	0	0	0	0	30
*25	246	2	2	3	4	4	3	0	3	0	2	0	2	0	0	0	0	0	0	25

* Denotes a form of the species.

Hybrid Index Data Sheet

Population: Mariner's Museum Valley 172-196
Series: I

Date: 4/9/67

Species: E. carolinianus with E. tomentosus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per Cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Length	Stem Density	Stem Length	Leaf Density	Leaf Length	Total Index Value
1	172	4	0	2	4	4	2	2	1	4	4	2	0	2	4	2	4	2	4	47
2	173	4	2	2	2	4	4	2	4	4	4	3	0	4	4	2	4	2	4	55
3	174	2	0	3	4	4	4	2	2	4	4	3	1	2	4	4	4	2	4	53
4	175	4	0	2	4	4	2	1	2	4	4	3	2	2	4	2	4	2	4	50
5	176	3	0	3	4	4	4	3	3	2	4	2	1	2	4	2	4	2	4	51
6	177	4	1	2	4	4	1	3	2	4	4	3	2	2	4	0	4	4	4	52
7	178	4	2	2	4	4	3	2	4	4	4	1	2	2	4	4	4	2	4	56
8	179	4	2	2	3	4	4	2	4	4	4	3	3	2	4	2	4	2	4	57
9	180	4	0	3	4	4	4	3	3	0	4	1	4	2	4	4	4	4	4	56
10	181	4	0	2	4	4	2	2	3	4	4	2	4	2	4	4	4	2	4	55
11	182	4	1	3	4	4	0	2	2	3	3	3	4	2	4	2	4	2	4	51
12	183	4	1	1	0	4	4	2	3	4	3	3	1	2	4	2	4	2	4	48
13	184	3	1	2	3	4	4	3	2	3	4	4	0	2	4	4	4	4	4	55
14	185	3	0	3	4	4	4	3	1	1	4	3	1	0	4	4	4	4	4	51
15	186	4	1	3	4	4	2	2	4	2	4	2	0	2	4	4	4	2	4	52
16	187	4	1	2	4	4	1	2	1	1	3	1	2	1	3	3	3	1	3	52
17	188	4	1	3	4	4	2	2	2	1	4	1	2	0	4	2	4	2	4	46
18	189	4	0	3	4	4	4	1	4	4	4	1	1	1	4	4	4	1	4	57
19	190	4	1	2	3	3	3	2	4	4	4	1	2	2	4	4	4	4	4	59
20	191	3	1	3	4	4	4	2	3	4	4	1	1	2	4	2	4	0	4	50
21	192	4	0	3	4	4	3	3	1	3	4	3	1	2	4	2	4	2	4	51
22	193	1	0	4	4	4	4	4	1	1	4	2	0	2	4	2	4	2	4	57
23	194	2	1	3	4	4	4	4	0	1	4	2	0	2	4	2	4	2	4	47
24	195	3	1	4	4	4	3	3	1	0	4	1	4	4	4	4	4	4	4	56
25	196	4	0	3	4	4	4	2	2	4	3	2	0	4	4	2	4	0	4	50

Hybrid Index Data Sheet

Population: Mariner's Museum Roadside 128-152
Series: I

Date: 4/7/67

Species: E. tomentosus with E. carolinianus

Number	Specimen Number	Leaf Base	LEaf Apex	Leaf Lenght	Leaf Width	Per Cent Length	Leaf Index	Length pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Length	Stem Density	Stem Length	Leaf Density	Leaf Length	Total Index Value
1	128	1	3	3	4	4	4	0	0	0	1	0	0	3	0	3	0	0	0	34
2	129	2	3	3	3	4	4	0	0	0	1	1	2	2	0	2	0	2	0	29
3	130	1	3	2	2	1	4	0	2	1	2	1	2	0	0	2	0	2	0	35
4	131	1	4	2	3	4	4	1	0	0	2	0	0	0	0	2	0	2	0	25
5	132	0	4	2	2	3	4	0	0	0	2	0	0	0	0	0	0	0	0	17
6	133	0	1	3	3	4	4	0	0	0	1	1	3	0	0	3	0	3	0	23
7	134	1	4	3	3	4	4	1	0	0	3	0	1	0	0	0	0	2	0	26
8	135	0	4	3	3	2	4	1	1	0	1	1	1	0	0	0	0	2	0	23
9	136	0	4	3	4	4	4	0	1	0	1	1	2	0	0	2	0	4	0	30
10	137	4	0	2	4	4	1	1	2	3	2	0	0	2	4	4	0	4	0	37
*11	138	1	1	3	4	4	4	1	1	1	1	0	0	2	0	2	0	4	0	29
*12	140	0	2	2	2	4	4	0	1	1	1	1	2	0	0	2	0	0	0	22
*13	141	0	3	4	4	4	4	0	0	0	2	1	2	0	0	2	0	0	0	26
*14	142	0	3	3	3	4	4	1	0	0	1	0	0	0	0	2	0	2	0	23
*15	143	1	0	2	4	4	4	0	0	0	1	0	1	0	0	2	0	0	0	20
*16	144	3	3	2	2	4	4	0	1	0	2	1	2	0	0	0	0	2	0	26
*17	145	1	0	3	4	4	4	0	0	0	1	1	2	2	0	2	0	2	0	26
*18	146	0	2	4	4	2	4	0	0	0	1	0	1	2	0	2	0	2	0	24
*19	147	0	4	3	2	0	4	0	1	1	1	1	0	0	0	2	0	0	0	19
20	148	1	1	2	1	4	4	1	1	0	1	1	2	0	0	2	0	0	0	21
*21	149	0	4	2	1	3	4	1	4	0	1	1	2	2	0	4	0	2	0	31
*22	180	1	4	2	2	4	4	1	0	1	1	1	0	0	0	2	0	0	0	23
*23	151	0	1	4	4	4	4	0	0	0	2	1	0	0	0	2	0	2	0	24
*24	152	2	2	3	4	4	4	1	3	4	0	1	0	2	0	0	0	0	4	34

Hybrid Index Data Sheet

Population: Mariner's Museum Valley 221-268
Series: II

Date: 4/10/67

Species: E. tomentosus with E. nudatus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per Cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st. Int.	Bract Length	Bract Density	Bract Texture	Stem Density	Stem Texture	Leaf Density	Leaf Texture	Total Index Value
* 1	221	2	1	3	2	2	0	0	2	2	2	2	1	0	0	0	0	0	0	19
* 2	222	0	1	4	0	1	0	0	2	2	2	2	1	0	0	2	0	0	0	17
* 3	223	0	0	3	1	2	0	0	2	2	2	2	0	0	0	0	4	0	0	18
4	224	1	1	2	1	2	0	0	2	2	2	2	0	2	0	2	4	0	0	23
* 5	225	0	0	3	2	1	0	0	2	2	2	2	0	0	0	2	0	0	0	16
* 6	226	1	1	4	2	2	0	4	2	2	2	2	0	0	0	0	0	2	0	24
* 7	227	1	1	0	0	2	0	0	2	2	2	2	0	2	0	0	0	2	0	16
8	228	0	0	3	1	1	0	0	2	2	2	2	0	0	0	2	0	0	0	15
* 9	230	0	0	3	2	1	0	0	2	2	2	2	0	2	0	2	4	2	0	24
*10	231	0	0	3	2	1	0	0	2	2	2	2	0	2	0	2	4	2	0	24
*11	232	0	0	2	1	1	0	0	2	2	2	2	0	0	0	0	4	0	0	16
*12	233	0	0	3	1	1	0	0	2	2	2	2	0	2	0	0	0	0	0	15
*13	234	0	0	3	2	2	0	0	2	2	2	2	1	0	0	2	4	2	0	24
*14	235	0	1	2	1	2	0	0	2	2	2	2	0	2	0	0	4	2	0	22
*15	236	2	1	2	1	2	0	0	2	2	2	2	0	0	0	0	4	2	0	22
*16	237	1	1	3	2	2	0	1	2	2	2	2	1	2	0	0	4	0	0	25
*17	238	0	0	3	2	1	0	1	2	2	2	2	1	0	0	0	4	0	0	20
*18	239	0	2	4	3	1	0	1	2	2	2	2	1	2	0	0	0	0	0	22
*19	240	0	0	2	1	1	0	0	2	2	2	2	0	2	0	0	0	0	0	14
*20	241	1	1	1	1	2	0	0	2	2	2	2	0	2	0	0	4	0	0	20
*21	242	0	1	2	1	2	0	0	2	2	2	2	0	0	0	0	4	0	0	21
*22	243	0	1	3	2	2	0	1	2	2	2	2	0	0	0	0	4	0	0	23
*23	244	1	2	3	3	2	0	0	2	2	2	2	0	0	0	0	4	0	0	20
*24	245	0	0	3	1	2	0	0	2	2	2	2	0	2	0	0	4	0	0	20
*25	246	1	1	3	2	3	0	0	2	2	2	2	0	0	0	0	0	0	0	18

Hybrid Index Data Sheet

Population: Mariner's Museum Roadside 128-152

Date: 4/7/67

Series: II

Species: E. tomentosus with E. nudatus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per Cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Texture	Stem Density	Stem Texture	Leaf Density	Leaf Texture	Total Index Value
1	128	1	1	3	2	2	0	0	2	2	2	2	1	2	0	2	0	0	0	22
2	129	1	1	3	2	2	0	0	2	2	2	2	0	2	0	2	0	2	0	23
3	130	1	1	2	1	2	0	0	2	2	2	2	0	2	0	2	0	2	0	21
4	131	1	0	2	2	2	0	0	2	2	2	2	1	0	0	2	0	2	0	20
5	132	0	0	2	1	1	0	0	2	2	2	2	1	0	0	0	0	0	0	13
6	133	0	1	3	2	2	0	0	2	2	2	2	0	0	0	2	0	2	0	20
7	134	1	0	3	2	2	0	2	2	2	2	0	0	0	0	0	0	2	0	20
8	135	0	0	3	2	1	0	2	2	2	2	2	0	0	0	0	0	2	0	18
9	136	0	1	3	2	2	0	0	2	2	2	2	0	0	0	2	0	4	0	22
10	137	3	2	2	3	3	1	2	2	2	2	2	1	2	0	4	0	4	0	35
*11	138	1	1	3	2	2	0	2	2	2	2	2	1	2	0	2	0	4	0	28
*12	140	0	1	1	1	2	0	0	2	2	2	2	0	0	0	2	0	0	0	15
*13	141	0	1	4	2	2	0	0	2	2	2	2	0	0	0	2	4	0	0	23
*14	142	0	1	2	2	2	0	1	2	2	2	2	1	0	0	2	0	2	1	21
*15	143	1	2	3	2	3	0	0	2	2	2	2	0	0	0	2	0	0	0	21
*16	144	2	1	2	1	2	0	0	2	2	2	2	0	0	0	0	0	2	0	18
*17	145	1	2	3	2	2	0	0	2	2	2	2	0	2	0	2	4	2	0	28
*18	146	0	1	4	2	1	0	0	2	2	2	2	0	2	0	2	0	2	0	22
*19	147	0	0	3	1	0	0	0	2	2	2	2	1	0	0	2	0	0	0	15
20	148	1	2	2	1	2	0	1	2	2	2	2	0	0	0	2	0	0	0	19
*21	149	0	0	2	1	2	0	2	2	2	2	2	0	2	0	4	0	2	0	23
*22	150	1	0	2	1	2	0	1	2	2	2	2	1	0	0	2	0	0	0	18
*23	151	0	1	4	3	2	0	1	2	2	2	2	1	0	0	2	0	2	0	24
*24	152	1	1	3	2	2	0	1	2	2	2	2	0	2	0	0	4	0	4	28

Hybrid Index Data Sheet

Population: Mariner's Museum Roadside 153-171
Series: II

Date: 4/9/67

Species: E. nudatus with E. tomentosus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Texture	Stem Density	Stem Texture	Leaf Density	Leaf Texture	Total Index Value
1	153	4	4	3	4	4	1	4	2	2	2	2	3	4	4	2	4	2	4	55
2	154	2	2	4	3	2	0	3	2	2	2	2	2	2	4	2	4	2	0	40
3	155	3	3	3	4	1	4	2	2	2	2	2	2	0	4	4	4	2	4	51
4	156	3	3	3	3	3	2	4	2	2	2	2	0	4	4	4	4	2	4	51
5	157	4	3	2	3	4	3	4	2	2	2	2	1	4	4	2	4	4	4	54
6	158	4	3	3	3	3	1	4	2	2	2	2	1	4	4	2	4	2	4	50
7	160	4	2	4	1	3	2	4	2	2	2	2	1	4	4	4	4	4	4	53
8	161	4	3	4	4	4	3	4	2	2	2	2	2	4	4	4	4	2	4	56
9	162	4	2	3	3	3	0	4	2	2	2	2	3	4	4	2	4	2	4	50
10	163	3	2	3	3	3	1	2	2	2	2	2	1	2	0	4	0	4	0	36
11	164	4	3	3	3	4	2	4	2	2	2	2	1	2	4	2	4	4	4	52
12	165	3	3	4	2	4	3	4	2	2	2	2	2	2	4	2	4	2	4	51
31	166	4	4	3	4	4	4	4	2	2	2	2	0	2	4	2	4	2	4	53
14	167	4	3	3	3	4	3	4	2	2	2	2	2	4	4	2	4	2	4	54
15	168	4	3	2	3	4	2	3	2	2	2	2	0	4	4	2	4	2	4	51
16	169	4	3	3	3	3	2	4	2	2	2	2	0	4	4	4	4	2	4	52
17	170	4	3	3	3	4	2	0	2	2	2	2	0	2	4	0	4	2	4	43
18	171	3	3	3	3	4	0	0	2	2	2	2	0	4	4	4	4	2	4	46

Hybrid Index Data Sheet

Population: Mariner's Museum Roadside 153-171
Series: III

Date: 4/9/67

Species: E. nudatus with E. carolinianus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per Cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Texture	Stem Density	Stem Texture	Leaf Density	Leaf Texture	Total Index Value
1	153	0	0	2	2	2	2	2	0	3	1	1	2	0	0	2	0	2	0	23
2	154	4	1	1	1	1	4	1	1	1	1	0	1	4	0	1	0	4	4	39
3	155	1	1	2	2	2	2	2	1	1	1	1	2	0	0	0	0	4	0	26
4	156	1	1	2	2	2	1	2	3	2	0	1	2	0	0	0	0	4	0	23
5	157	0	1	2	2	2	1	2	1	0	0	0	2	0	0	2	0	0	0	15
6	158	0	1	2	2	2	2	2	0	1	0	0	2	0	0	2	0	4	0	20
7	160	0	2	2	2	2	3	2	0	1	0	1	2	0	0	0	0	0	0	17
8	161	0	1	2	2	2	1	2	1	0	0	0	2	4	0	0	0	4	0	21
9	162	0	2	2	2	2	3	2	0	0	1	0	2	0	0	0	0	4	0	20
10	163	3	2	2	2	2	4	2	0	0	2	0	2	4	4	0	4	0	4	37
11	164	0	1	2	2	2	1	2	0	2	1	0	2	4	0	2	0	0	0	21
12	165	1	1	2	2	2	1	2	0	0	2	0	2	4	0	2	0	4	0	25
13	166	0	0	2	2	2	0	2	1	1	0	1	2	4	0	2	0	4	0	23
14	167	0	1	2	2	2	1	2	0	2	2	1	2	0	0	2	0	4	0	23
15	168	0	1	2	2	2	1	2	3	1	1	1	2	0	0	2	0	4	0	24
16	169	0	0	2	2	2	2	2	2	2	0	1	2	0	0	0	0	4	0	21
17	170	0	1	2	2	2	1	2	2	3	1	1	2	4	0	2	0	4	0	31
18	171	3	1	2	2	2	2	2	1	1	0	0	2	0	0	0	0	4	0	22

Hybrid Index Data Sheet

Population: Mariner's Museum Valley 172-196
Series: III

Date: 4/9/67

Species: E. carolinianus with E. nudatus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per Cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Texture	Stem Density	Stem Texture	Leaf Density	Leaf Texture	Total Index Value
1	172	0	2	2	2	2	3	2	1	4	4	1	2	4	4	2	4	4	4	47
* 2	173	2	2	2	2	2	2	2	3	4	4	0	2	4	4	2	4	4	4	49
3	174	1	2	2	2	2	4	2	2	4	4	1	2	4	4	0	4	4	4	48
4	175	1	2	2	2	2	3	2	2	4	4	3	2	4	4	2	4	4	4	51
5	176	4	1	2	2	2	1	2	3	2	4	2	2	4	4	2	4	4	4	49
* 6	177	0	2	2	2	2	2	2	2	4	4	2	2	4	4	4	4	0	4	46
* 7	178	0	3	2	2	2	3	2	4	4	4	1	2	4	4	0	4	4	4	49
8	179	0	3	2	2	2	4	2	4	4	4	3	2	4	4	2	4	4	4	54
9	180	0	2	2	2	2	2	2	3	0	4	1	2	4	4	0	4	0	4	38
10	181	0	2	2	2	2	1	2	3	4	4	2	2	4	4	0	4	4	4	46
11	182	2	3	2	2	2	4	2	2	3	3	3	2	4	4	2	4	4	4	52
12	183	0	3	2	2	2	4	2	3	4	3	1	2	4	4	2	4	4	4	50
13	184	4	2	2	2	2	4	2	4	1	3	2	2	4	4	0	0	0	4	42
14	185	4	2	2	2	2	4	2	1	0	4	3	2	4	4	0	4	0	4	44
15	186	1	2	2	2	2	3	2	4	2	4	2	2	0	4	0	4	4	4	44
16	187	3	2	2	2	2	3	2	2	2	4	1	2	4	4	0	4	4	4	47
17	188	0	2	2	2	2	3	2	2	1	4	0	2	4	4	2	4	4	4	44
18	189	0	2	2	2	2	4	2	1	4	4	2	2	4	4	0	4	4	0	43
19	190	2	3	2	2	2	4	2	4	4	4	1	2	4	4	0	4	0	4	48
20	191	4	2	2	2	2	4	2	3	4	4	1	2	4	4	2	4	4	0	50
21	192	0	2	2	2	2	3	2	1	3	4	2	2	4	4	2	0	4	0	39
22	193	4	1	2	2	2	4	2	1	1	4	1	2	4	4	2	0	4	4	44
23	194	4	2	2	2	2	4	2	0	1	4	1	2	4	4	0	0	4	4	42
24	195	4	1	2	2	2	3	2	0	1	4	1	2	0	4	0	4	0	4	36
25	196	0	2	2	2	2	4	2	2	4	3	2	2	4	4	2	4	4	4	49

Hybrid Index Data Sheet

Population: Population Lab. 269-310
Series: I

Date: 4/13/67

Species: E. carolinianus with E. tomentosus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Length	Stem Density	Stem Length	Leaf Density	Leaf Length	Total Index Value
* 1	269	2	2	3	3	4	4	2	1	0	4	2	2	2	4	4	0	0	4	43
2	270	4	2	2	3	4	4	2	3	2	4	2	2	4	4	4	0	0	0	46
3	271	4	1	2	2	4	4	2	2	1	4	2	0	4	4	4	4	4	4	52
4	272	4	4	0	1	0	4	2	4	3	4	3	1	4	4	4	4	4	4	54
5	273	4	4	0	2	4	1	2	4	1	4	4	4	4	4	4	4	4	4	58
6	274	3	2	3	4	4	4	3	4	1	4	4	2	4	4	4	4	4	4	63
* 7	275	3	3	3	4	4	4	2	4	4	4	1	2	4	4	0	4	4	4	58
* 8	276	4	3	3	3	4	4	2	4	4	4	4	2	4	4	4	4	4	4	65
* 9	277	3	3	2	3	4	4	2	3	4	4	2	2	4	4	4	4	4	4	60
*10	278	4	4	3	2	4	4	2	4	2	4	3	1	2	4	4	4	2	4	57
*11	279	3	4	2	2	4	4	2	4	3	4	3	1	4	4	2	4	2	4	56
12	280	4	4	2	3	4	4	3	4	2	4	3	3	4	4	2	4	2	4	60
13	281	4	4	2	2	4	4	3	4	2	3	3	4	4	4	0	4	2	4	57
14	282	4	4	0	0	4	4	2	4	2	4	4	4	4	4	2	4	2	4	56
15	283	4	3	2	3	4	4	2	1	2	4	3	2	4	4	2	4	2	4	54
16	284	3	3	4	4	4	4	2	4	2	4	3	2	4	4	0	4	2	4	57
17	285	4	2	3	4	4	4	2	4	4	4	1	2	4	4	4	4	2	4	60
18	286	1	0	4	4	4	4	2	2	2	4	2	4	4	4	4	4	4	4	57
19	287	1	2	3	4	4	4	4	0	1	4	2	2	4	4	4	4	4	4	55
20	288	4	3	1	2	4	3	2	2	2	4	3	0	4	4	4	0	4	4	50
21	289	1	2	3	4	4	4	2	4	3	4	3	2	4	4	4	4	2	4	58
22	290	4	4	2	3	4	3	2	2	3	4	1	0	4	4	4	4	2	4	54
23	291	2	2	3	4	4	4	3	1	4	4	1	4	4	4	4	4	2	4	58
24	292	2	0	4	4	4	4	3	2	1	4	1	4	4	4	4	4	4	4	57
*25	294	4	2	2	2	4	4	3	3	1	4	4	2	4	4	4	4	2	4	57

Hybrid Index Data Sheet

Population: Population Lab. 269-310
Series: III

Date: 4/13/67

Species: E. carolinianus with E. nudatus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Texture	Stem Density	Stem Texture	Leaf Density	Leaf Texture	Total Index Value
* 1	269	4	3	2	2	2	4	2	1	0	4	2	2	2	4	0	4	0	4	42
2	270	2	3	2	2	2	4	2	3	2	4	2	2	0	4	0	0	0	4	38
3	271	3	2	2	2	2	4	2	2	2	4	1	2	0	4	0	0	0	4	36
4	272	0	4	2	2	2	3	2	4	3	4	3	2	0	0	0	4	0	4	39
5	273	0	4	2	2	2	2	2	4	1	4	4	2	0	4	0	4	0	4	41
6	274	4	3	2	2	2	4	2	4	1	4	4	2	0	4	0	4	0	4	46
* 7	275	4	3	2	2	2	4	2	4	4	4	1	2	0	4	4	4	0	4	50
* 8	276	4	3	2	2	2	4	2	4	4	4	4	2	0	0	0	4	0	4	45
* 9	277	4	3	2	2	2	4	2	3	4	4	2	2	0	0	0	4	0	4	42
*10	278	4	4	2	2	2	4	2	4	2	4	3	2	0	4	0	4	4	4	51
*11	279	4	4	2	2	2	4	2	4	3	4	3	2	0	0	2	4	4	4	50
12	280	1	4	2	2	2	4	2	4	2	4	3	2	0	4	2	4	4	4	48
13	281	3	4	2	2	2	4	2	4	2	3	3	2	0	4	0	4	4	4	49
14	282	1	3	2	2	2	4	2	4	2	4	3	2	0	4	2	4	4	4	49
15	283	2	3	2	2	2	4	2	1	2	4	3	2	0	4	2	4	4	4	47
16	284	4	3	2	2	2	4	2	4	2	4	2	2	0	4	4	4	4	4	53
17	285	3	3	2	2	2	4	2	4	4	4	0	2	0	0	0	4	0	4	40
18	286	4	2	2	2	2	4	2	2	2	4	2	2	0	0	0	4	0	4	38
19	287	4	3	2	2	2	4	2	0	1	4	2	2	0	0	0	4	0	4	36
20	288	0	3	2	2	2	3	2	2	2	4	3	2	0	0	0	4	0	4	35
21	289	4	3	2	2	2	4	2	4	3	4	3	2	0	0	0	0	4	0	39
22	290	0	3	2	2	2	3	2	2	3	4	1	2	0	0	0	4	4	4	38
23	291	4	3	2	2	2	4	2	1	4	4	1	2	0	0	0	0	4	4	39
24	292	4	3	2	2	2	4	2	2	1	4	1	2	0	0	0	4	0	4	37
*25	294	2	3	2	2	2	4	2	3	1	4	3	2	0	0	0	0	4	4	38

Hybrid Index Data Sheet

Population: Quonset Hut 5
109-137
Series: I

Date: 4/15/67

Species E. carolinianus
with E. tomentosus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Length	Stem Density	Stem Length	Leaf Density	Leaf Length	Total Index Value
1	109	2	2	2	0	2	4	2	1	2	3	4	1	4	4	0	4	2	4	43
2	110	4	2	1	2	4	4	2	4	4	3	3	1	4	4	0	4	2	4	52
3	111	3	4	2	0	4	4	2	4	4	3	4	2	4	4	0	4	2	4	54
4	112	3	4	2	2	4	4	2	3	4	3	3	2	4	4	2	4	0	4	54
5	113	4	4	3	4	4	4	2	4	2	3	2	1	4	4	2	4	2	4	57
6	114	4	3	2	2	4	4	5	4	4	3	3	1	4	4	2	4	2	4	59
7	115	4	2	2	2	4	4	3	3	4	3	3	2	4	4	4	4	2	4	58
8	116	4	4	1	1	4	2	3	2	4	3	3	2	4	4	0	4	2	4	51
9	117	4	1	2	2	4	4	3	3	2	3	4	2	4	4	2	4	2	4	54
10	118	4	4	1	2	4	3	2	4	3	3	4	1	4	4	2	4	2	4	55
11	119	4	2	2	2	4	4	2	4	4	3	3	2	4	4	0	4	0	4	52
12	120	4	2	2	3	4	4	2	3	4	3	3	2	4	4	2	4	2	4	56
13	121	4	2	2	3	4	4	2	2	4	3	4	2	2	4	2	4	2	4	54
14	122	4	3	2	2	4	4	2	2	1	3	3	4	4	4	0	4	2	4	52
15	123	4	2	2	1	3	4	2	4	4	2	4	2	4	4	2	4	0	4	52
16	124	4	4	2	1	4	4	2	2	4	4	4	2	2	4	4	4	2	4	57
17	125	3	3	2	1	4	4	2	4	4	3	4	2	4	4	4	4	2	4	58
18	126	4	2	1	1	4	4	2	4	4	3	4	2	4	4	2	4	2	4	51
19	127	4	3	2	2	4	4	2	4	4	3	3	4	2	4	4	4	2	4	59

Hybrid Index Data Sheet

Population: Quonset Hut 5
109-127
Series: III

Date: 4/15/67

Species: E. carolinianus
with E. nudatus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Texture	Stem Density	Stem Texture	Leaf Density	Leaf Texture	Total Index Value
1	109	4	3	2	2	2	4	2	1	2	3	4	2	0	4	4	4	4	4	51
2	110	4	3	2	2	2	4	2	4	4	3	3	2	0	4	4	4	4	4	55
3	111	4	4	2	2	2	4	2	4	4	3	4	2	0	4	4	0	4	4	53
4	112	4	4	2	2	2	4	2	3	4	3	4	2	0	4	2	0	4	0	46
5	113	0	4	2	2	2	4	2	4	2	3	3	2	0	4	4	0	4	4	46
6	114	4	3	2	2	2	4	2	4	4	3	3	2	0	4	2	0	4	4	49
7	115	3	3	2	2	2	4	2	3	4	3	3	2	0	4	0	0	2	4	43
8	116	0	4	2	2	2	4	2	2	4	3	3	2	0	4	4	0	2	4	44
9	117	0	3	2	2	2	4	2	2	4	3	4	2	0	4	2	0	2	4	42
10	118	0	4	2	2	2	4	2	4	3	3	4	2	0	0	2	0	2	4	40
11	119	0	4	2	2	2	4	2	4	4	3	3	2	0	4	4	4	4	4	52
12	120	0	3	2	2	2	4	2	3	4	3	3	2	0	4	2	0	4	4	44
13	121	0	3	2	2	2	4	2	2	4	3	4	2	4	4	2	0	4	4	48
14	122	0	4	2	2	2	4	2	3	4	3	3	2	0	4	4	4	4	4	51
15	123	3	4	2	2	2	4	2	4	4	2	4	2	0	4	2	0	4	4	49
16	124	3	4	2	2	2	4	2	2	4	4	4	2	0	4	0	0	4	4	49
17	125	4	3	2	2	2	4	2	4	4	3	4	2	0	4	0	0	4	4	48
18	126	0	3	2	2	2	4	2	4	4	3	4	2	0	4	2	0	4	4	46
19	127	1	3	2	2	2	4	2	4	4	3	3	2	0	4	0	4	4	4	48

Hybrid Index Data Sheet

Population: Naval Weapons Station
434-457
Series: I

Date: 4/19/67

Species: E. carolinianus
with E. tomentosus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Length	Stem Density	Stem Length	Leaf Density	Leaf Length	Total Index Value
1	434	4	0	2	3	4	2	2	4	4	3	4	2	2	4	4	4	4	4	56
2	435	4	4	2	3	4	4	2	4	3	3	3	2	4	4	2	4	2	4	58
3	436	4	4	1	2	4	4	3	3	2	4	4	1	4	0	4	4	2	4	54
4	437	4	0	2	4	4	1	3	4	4	3	2	2	2	4	4	4	2	4	53
5	438	4	1	1	2	4	3	2	4	4	3	3	4	2	4	2	4	2	4	53
6	439	4	1	2	3	4	3	2	3	4	4	1	1	4	4	2	4	2	4	52
7	440	4	1	1	3	4	1	2	4	3	4	4	4	4	4	2	4	2	4	53
8	441	4	2	3	4	4	4	2	1	3	4	2	4	2	4	2	4	2	4	55
9	442	4	2	2	2	4	1	2	1	1	4	2	2	4	4	2	4	2	4	47
10	443	4	2	1	3	4	2	3	4	2	4	4	4	4	4	2	4	2	4	57
11	444	4	1	3	4	4	4	2	2	4	3	3	1	2	4	4	4	2	4	55
12	446	4	0	1	2	4	3	2	4	4	3	4	2	2	4	2	4	0	4	49
13	447	4	3	0	3	4	0	2	3	4	4	4	2	4	4	2	0	4	4	51
14	448	4	0	0	2	4	1	2	4	4	3	4	4	4	4	2	4	2	4	52
15	449	4	2	1	3	4	2	2	3	3	4	4	4	4	0	2	4	2	4	52
16	450	4	2	1	2	4	3	2	4	0	3	4	2	4	4	4	4	2	4	53
17	451	1	2	3	4	4	4	1	1	1	3	1	3	0	4	2	4	2	4	44
18	452	4	1	2	3	4	3	3	4	4	3	3	2	2	4	4	4	2	4	56
19	453	4	1	1	2	4	3	2	4	1	1	3	4	4	4	2	4	2	4	50
*20	454	4	1	1	2	4	4	2	3	4	4	4	2	2	4	2	4	2	4	53
21	455	4	4	2	3	4	4	2	4	3	4	2	2	2	4	2	4	2	4	56
22	456	4	1	1	4	4	0	3	4	3	3	4	2	4	4	0	4	0	4	49
*23	457	4	4	0	0	4	4	3	4	4	4	4	2	2	4	0	4	2	4	53

Hybrid Index Data Sheet

Population: Naval Weapons Station 434-457
Series: III

Date: 4/19/67

Species: E. carolinianus with E. nudatus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Percent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Texture	Stem Density	Stem Texture	Leaf Density	Leaf Texture	Total Index Value
1	434	0	2	2	2	2	3	2	4	4	3	4	2	4	4	0	0	0	4	42
2	435	4	4	2	2	2	4	2	4	3	3	3	2	0	4	2	0	4	4	49
3	436	2	3	2	2	2	3	2	3	2	4	4	2	0	4	0	4	4	4	47
4	437	0	2	2	2	2	3	2	4	4	3	3	2	4	4	0	4	4	4	49
5	438	0	3	2	2	2	3	2	4	4	3	4	2	4	4	2	4	4	4	53
6	439	0	2	2	2	2	3	2	3	4	4	1	2	0	0	2	4	4	4	41
7	440	0	2	2	2	2	2	2	4	3	4	4	2	0	4	2	0	4	4	43
8	441	0	3	2	2	2	4	2	1	3	4	1	2	4	4	2	0	4	4	44
9	442	0	3	2	2	2	2	2	1	1	4	1	2	0	0	2	4	4	4	36
10	443	0	3	2	2	2	3	2	4	2	4	4	2	0	0	2	0	4	4	40
11	444	1	2	2	2	2	4	2	2	4	3	3	2	4	4	0	4	4	4	49
12	446	0	2	2	2	2	3	2	4	4	3	3	2	4	4	2	4	4	4	51
13	447	0	3	2	2	2	2	2	3	4	4	4	2	0	4	2	4	4	4	48
14	448	0	2	2	2	2	2	2	4	4	3	4	2	0	4	2	4	4	4	47
15	449	0	3	2	2	2	3	2	3	3	4	4	2	0	4	2	4	4	4	48
16	450	0	3	2	2	2	3	2	4	0	3	4	2	0	4	2	4	4	4	45
17	451	4	3	2	2	2	4	2	1	1	3	1	2	4	4	2	4	4	4	49
18	452	0	3	2	2	2	3	2	4	4	3	3	2	4	4	0	0	4	4	46
19	453	0	2	2	2	2	3	2	4	1	3	4	2	0	4	2	0	4	4	41
*20	454	0	3	2	2	2	4	2	3	4	4	4	2	4	4	2	4	4	4	54
21	455	4	4	2	2	2	3	2	4	3	4	3	2	4	4	2	0	4	4	53
*22	456	0	2	2	2	2	1	2	4	3	4	4	2	0	4	4	0	4	4	44
*23	457	0	4	2	2	2	4	2	4	4	4	4	2	4	4	4	0	4	4	54

Hybrid Index Data Sheet

Population: Far Eastern State
311-345
Series: I

Date: 4/14/67

Species: E. carolinianus
with E. tomentosus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Length	Stem Density	Stem Length	Leaf Density	Leaf Length	Total Index Value
*1	311	3	4	3	3	4	4	2	4	4	4	4	2	4	4	4	4	2	4	63
*2	312	3	4	2	3	4	4	2	1	4	4	4	0	2	4	2	4	2	4	53
*3	313	4	4	1	2	4	4	4	4	4	4	4	1	4	4	4	4	2	4	62
4	314	4	0	2	4	4	1	2	2	3	4	4	2	2	4	2	4	2	4	50
5	315	4	2	2	4	4	3	4	2	4	4	4	1	2	4	4	4	2	0	54
6	316	4	1	3	4	4	3	2	2	4	4	2	1	2	4	4	4	2	4	54
7	317	3	1	2	3	4	4	2	3	4	4	4	1	4	4	4	4	2	4	57
8	318	4	0	2	4	4	3	2	3	4	4	4	1	2	4	2	4	2	4	53
9	319	4	0	2	4	4	1	3	4	4	4	4	1	4	4	4	4	2	4	57
10	320	2	1	3	3	4	4	4	0	4	4	4	1	4	4	2	4	2	4	54
11	321	4	0	2	3	4	4	2	1	3	4	4	1	2	4	2	4	2	4	50
12	322	3	1	3	4	4	4	2	4	4	4	4	1	2	4	4	4	2	4	58
13	323	2	1	2	3	4	4	3	3	4	4	4	4	4	4	4	4	2	4	60
14	324	4	0	2	4	4	1	2	4	4	4	3	1	4	4	4	4	2	4	55
15	325	4	0	2	4	4	2	2	2	2	4	4	1	2	4	2	4	2	4	49
16	326	4	0	2	3	4	4	2	4	2	4	3	1	2	4	2	4	4	4	52
17	327	3	2	3	4	4	4	0	1	2	4	3	1	2	4	4	4	2	4	51
18	328	4	1	2	3	4	4	2	3	4	4	4	2	2	4	2	4	2	4	55
19	329	4	2	3	4	4	1	2	3	2	4	4	1	2	4	4	4	2	4	54
20	330	4	2	3	4	4	4	2	3	3	4	3	1	2	4	2	4	2	4	55
21	331	4	2	2	3	4	4	2	4	4	4	4	1	2	4	2	4	2	4	56
22	336	4	3	2	4	4	3	2	4	4	4	4	0	4	2	2	4	2	4	56
23	337	4	3	2	3	4	3	2	2	4	4	4	1	2	4	2	4	2	4	54
24	338	4	1	2	2	4	4	2	3	4	4	3	1	2	4	4	4	2	4	54
25	339	2	1	3	4	4	4	2	2	2	4	3	1	2	4	2	4	2	4	50

Hybrid Index Data Sheet

Population: Far Eastern State
311-345
Series: III

Date: 4/14/67

Species: E. carolinianus
with E. nudatus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Texture	Stem Density	Stem Texture	Leaf Density	Leaf Texture	Total Index Value
*1	311	4	4	2	2	2	4	2	4	4	4	4	2	0	0	0	0	4	4	46
*2	312	4	4	2	2	2	4	2	1	4	4	4	2	4	0	2	0	4	4	49
*3	313	1	4	2	2	2	4	2	4	4	4	4	2	0	0	0	0	4	4	43
4	314	0	2	2	2	2	2	2	4	4	4	4	2	4	0	2	0	4	4	44
5	315	0	3	2	2	2	3	2	2	4	4	4	2	4	4	0	0	4	4	46
6	316	2	3	2	2	2	3	2	2	4	4	4	2	0	4	0	4	4	4	48
7	317	4	3	2	2	2	4	2	3	4	4	4	2	0	0	0	4	4	4	48
8	318	1	2	2	2	2	3	2	3	4	4	4	2	4	4	2	4	4	4	53
9	319	1	2	2	2	2	2	3	2	4	4	4	4	2	0	4	0	0	4	44
10	320	4	3	2	2	2	4	2	0	4	4	4	2	0	0	2	0	4	0	39
11	321	4	2	2	2	2	4	2	1	3	4	4	2	4	4	2	4	4	4	54
12	322	4	2	2	2	2	4	2	4	4	4	4	2	0	0	0	0	4	4	44
13	323	4	2	2	2	2	4	2	3	4	4	4	2	0	0	0	0	4	4	43
14	324	1	2	2	2	2	2	2	4	4	4	3	2	0	0	0	0	4	4	38
15	325	3	2	2	2	2	3	2	1	2	4	4	2	4	0	2	0	4	4	43
16	326	4	2	2	2	2	4	2	3	2	4	3	2	4	0	2	0	0	4	42
17	327	4	3	2	2	2	4	2	1	1	4	3	2	4	4	2	4	4	4	52
18	328	0	3	2	2	2	3	2	3	4	4	4	2	4	4	2	0	4	4	49
19	329	0	3	2	2	2	2	2	3	2	4	4	2	4	4	0	0	4	4	44
20	330	1	3	2	2	2	4	2	3	3	4	3	2	4	4	2	0	4	4	49
21	331	0	3	2	2	2	4	2	3	4	4	4	2	4	4	2	4	4	4	54
22	336	0	3	2	2	2	3	2	4	4	4	4	2	4	4	2	0	4	4	50
23	337	0	3	2	2	2	3	2	2	4	4	4	2	4	4	2	4	4	4	52
24	338	0	3	2	2	2	4	2	3	4	4	3	2	4	4	0	0	4	4	47
25	339	4	3	2	2	2	4	2	2	2	4	3	2	4	4	2	4	4	0	50

Hybrid Index Data Sheet

Population: King's Mill
382-406

Date: 4/15/67

Series: I

Species: E. carolinianus
with E. tomentosus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per Cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Length	Stem Density	Stem Length	Leaf Density	Leaf Length	Total Index Value
1	382	3	0	3	4	4	4	2	3	3	4	2	2	4	4	4	4	2	4	56
2	383	1	1	3	3	4	4	2	3	1	3	2	0	0	4	4	4	2	4	45
3	384	4	3	3	1	4	4	2	4	3	4	2	1	2	4	4	4	0	4	53
4	385	2	3	3	4	4	4	2	1	2	3	3	1	2	4	2	4	2	4	50
5	386	2	2	3	4	4	4	1	0	3	4	2	1	2	4	2	4	0	4	46
6	387	2	1	3	3	4	4	1	3	4	4	2	1	2	4	2	4	0	1	48
7	388	4	2	2	4	4	2	2	2	3	4	2	2	4	4	4	4	2	4	55
8	389	4	3	3	3	4	4	2	4	4	3	2	1	2	4	2	4	2	4	55
9	390	4	2	3	4	4	4	2	2	2	4	2	2	2	4	4	4	2	4	55
10	391	1	3	4	4	4	4	2	3	3	4	1	2	4	4	4	4	2	4	57
11	392	4	2	2	3	4	3	2	2	4	4	2	0	2	4	2	4	2	4	50
12	393	3	1	3	4	4	4	4	2	1	4	3	0	2	4	2	4	2	4	51
13	394	3	1	3	4	4	4	2	0	1	4	1	2	2	4	4	4	2	4	49
14	395	3	2	3	3	4	4	1	1	2	3	1	0	1	4	4	4	2	4	52
15	396	3	1	3	4	4	4	3	0	0	4	2	0	2	4	4	4	2	4	48
16	397	4	1	3	2	4	4	2	2	1	4	2	2	2	4	4	4	2	4	51
17	398	4	1	2	3	4	4	3	2	0	3	4	2	4	4	4	4	2	4	54
18	399	4	2	2	3	4	3	2	2	0	3	3	2	4	4	4	4	4	4	54
19	400	4	2	2	3	4	4	2	3	3	4	4	2	2	4	2	4	2	4	56
20	401	4	3	2	2	4	4	2	3	4	4	3	1	4	4	2	4	2	4	56
21	402	3	1	2	3	4	4	2	4	3	3	3	2	2	4	2	4	2	4	53
22	403	3	2	2	2	4	4	3	4	3	3	2	2	4	4	4	4	2	4	56
23	404	4	1	3	4	4	4	1	3	0	3	3	1	2	4	4	4	2	4	52
*24	405	1	2	2	0	3	0	2	3	4	4	4	1	0	4	2	0	0	4	36

Hybrid Index Data Sheet

Population: King's Mill
382-406
Series: III

Date: 4/15/67

Species: E. carolinianus
with E. nudatus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per Cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length in 1st Int.	Bract Length	Bract Density	Bract Texture	Stem Density	Stem Texture	Leaf Density	Leaf Texture	Total Index Value
1	382	4	2	2	2	2	4	2	3	3	4	1	2	0	4	0	2	2	2	47
2	383	4	3	2	2	2	4	2	2	1	4	2	2	4	4	0	0	2	4	44
3	384	1	3	2	2	2	4	2	4	3	4	2	2	4	4	0	4	4	4	51
4	385	1	3	2	2	2	4	2	1	2	3	2	2	4	4	2	4	4	4	48
5	386	4	3	2	2	2	4	2	0	2	3	2	2	4	4	2	4	4	4	52
6	387	4	3	2	2	2	4	2	3	4	4	2	2	4	4	2	4	4	4	56
7	388	0	3	2	2	2	2	2	2	3	4	2	2	0	4	0	4	4	4	42
8	389	0	3	2	2	2	4	2	4	4	3	2	2	4	4	2	4	4	4	52
9	390	0	3	2	2	2	4	2	2	2	4	2	2	4	4	0	4	4	4	47
10	391	4	3	2	2	2	4	2	3	3	4	1	2	0	4	0	0	4	4	44
11	392	4	3	2	2	2	3	2	2	4	4	1	2	4	4	2	4	4	4	53
12	393	4	3	2	2	2	4	2	2	1	4	8	2	4	4	2	4	4	4	58
13	394	4	2	2	2	2	4	2	0	1	4	1	2	4	0	0	4	4	4	42
14	395	4	3	2	2	2	4	2	2	3	4	2	2	4	4	0	4	4	4	52
15	396	4	2	2	2	2	4	2	0	0	4	2	2	4	4	0	4	4	4	46
16	397	0	2	2	2	2	4	2	2	0	1	4	2	0	4	0	4	4	4	39
17	398	0	3	2	2	2	3	2	2	0	1	2	2	0	4	0	4	0	4	33
18	399	0	3	2	2	2	4	2	3	3	1	4	2	4	4	2	4	4	4	50
19	400	0	3	2	2	2	4	2	3	4	4	2	3	0	4	2	4	4	4	49
20	401	4	2	2	2	2	4	2	4	3	3	3	2	4	4	2	0	4	4	51
21	402	4	3	2	2	2	4	2	4	3	3	3	2	0	4	0	0	4	4	46
22	403	0	2	2	2	2	4	2	2	1	2	3	2	4	4	0	4	4	4	44
23	404	0	2	2	2	2	4	2	2	0	3	3	2	4	4	0	4	4	4	44
*24	405	4	3	2	2	2	4	2	3	4	4	4	2	4	4	2	4	4	4	58

Hybrid Index Data Sheet

Population: College Woods

Date: 4/12/67

510-545
Series: I

Species: E. tomentosus
with E. carolinianus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per Cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Length	Stem Density	Stem Length	Leaf Density	Leaf Length	Total Index Value
* 1	510	1	4	3	3	4	4	1	1	0	1	0	0	2	0	4	0	2	0	30
2	511	3	1	2	3	0	4	1	0	0	2	0	2	0	0	4	0	2	0	24
3	512	1	4	2	0	0	4	1	0	0	2	0	0	0	0	0	0	4	0	18
* 4	512b	0	3	3	3	3	4	1	0	0	1	0	2	2	0	2	0	0	0	24
5	513	1	3	1	1	4	4	0	2	0	2	0	2	2	0	4	0	2	0	28
* 6	514	4	1	2	3	4	4	0	0	0	2	0	2	0	0	0	0	2	0	24
* 7	515	2	2	2	3	4	4	0	2	0	1	0	1	0	0	4	0	2	0	27
* 8	516	1	0	3	3	4	4	0	0	0	0	0	1	0	0	2	0	2	0	20
9	517	1	3	2	1	4	4	0	0	0	2	0	1	0	0	2	0	2	0	22
10	518	2	0	2	3	4	4	0	0	0	2	1	4	0	0	2	0	2	0	26
11	519	3	1	2	3	4	4	1	0	0	1	0	0	0	0	2	0	2	0	23
12	520	2	4	2	1	4	4	0	0	0	1	1	2	0	0	4	0	0	0	25
*13	521	1	3	3	3	4	4	2	0	0	1	1	0	0	0	0	0	2	0	24
14	522	2	4	2	1	4	4	2	0	0	0	1	0	2	0	2	0	2	0	26
15	523	0	2	2	1	2	4	0	0	1	1	1	1	0	0	2	0	0	0	17
16	524	3	2	3	3	4	4	0	0	0	0	1	1	0	0	4	0	2	0	27
17	525	3	3	2	2	4	4	0	0	0	0	1	2	2	0	2	0	2	0	27
18	526	4	2	2	3	4	4	0	0	0	3	0	2	0	0	2	0	2	0	28
19	527	3	4	1	2	4	4	0	0	0	2	1	0	0	0	2	0	2	0	25
20	528	4	3	1	3	4	2	1	0	0	2	1	2	2	0	2	0	2	0	29
21	529	3	3	0	0	4	4	0	0	0	1	1	0	2	0	2	0	0	0	20
22	530	4	3	2	3	4	2	0	0	0	3	1	1	2	0	2	0	2	0	30
23	531	0	4	3	3	4	4	0	0	0	1	1	1	2	0	2	0	2	0	27
24	532	3	4	3	4	4	4	0	1	0	2	0	1	2	0	2	0	2	0	32
25	533	2	2	1	2	4	4	0	3	0	1	1	2	2	0	0	0	2	0	26

Hybrid Index Data Sheet

Population: College Woods
510-545
Series: II

Date: 4/12/67

Species: E. tomentosus
with E. nudatus

Number	Specimen Number	Leaf Base	Leaf Apex	Leaf Length	Leaf Width	Per Cent Length	Leaf Index	Length Pappus	No. Florets	No. Heads	First Internode	Leaf Length 1st Int.	Bract Length	Bract Density	Bract Texture	Stem Density	Stem Texture	Leaf Density	Leaf Texture	Total Index Value
* 1	510	1	0	3	2	2	0	2	2	2	2	2	1	2	0	4	0	2	0	27
2	511	2	1	2	0	0	0	1	2	2	2	2	0	0	0	4	0	2	0	20
3	512	1	0	2	0	0	0	1	2	2	2	2	1	0	0	4	0	4	0	21
* 4	512b	0	1	3	2	1	0	1	2	2	2	2	0	2	0	2	0	0	0	20
5	513	1	1	1	1	2	0	0	2	2	2	2	0	2	0	4	0	2	0	22
* 6	514	2	1	2	2	2	0	0	2	2	2	2	0	0	0	0	4	2	0	23
* 7	515	1	1	2	2	2	0	0	2	2	2	2	0	0	0	4	4	2	0	26
* 8	516	1	0	3	2	2	0	0	2	2	2	2	0	0	0	2	0	2	0	20
9	517	2	1	2	1	2	0	0	2	2	2	2	0	0	0	2	4	2	0	24
10	518	2	0	2	2	3	0	0	2	2	2	2	0	0	0	2	0	2	0	21
11	519	3	2	2	2	3	0	1	2	2	2	2	1	0	0	2	0	2	0	26
12	520	1	0	2	1	2	0	0	2	2	2	2	0	0	0	4	0	0	0	18
*13	521	1	1	3	2	2	0	2	2	2	2	2	2	0	0	0	4	2	0	27
14	522	1	0	2	1	2	0	4	2	2	2	2	1	2	0	2	0	2	0	25
15	523	0	2	2	1	1	0	0	2	2	2	2	0	0	0	2	0	0	0	16
16	524	2	1	3	2	2	0	0	2	2	2	2	0	0	0	4	0	2	0	24
17	525	2	1	2	1	2	0	0	2	2	2	2	0	2	0	2	0	2	0	22
18	526	3	1	2	2	2	0	0	2	2	2	2	0	0	0	2	0	2	0	22
19	527	2	0	1	1	2	1	0	2	2	2	2	2	0	0	2	0	2	0	21
20	528	3	1	1	2	3	2	1	2	2	2	2	0	2	0	2	0	2	0	27
21	529	2	1	0	0	3	0	0	2	2	2	2	1	2	0	2	4	0	0	23
22	530	3	1	2	2	3	0	0	2	2	2	2	0	2	0	2	0	2	0	25
23	531	0	0	3	2	2	0	0	2	2	2	2	0	2	0	2	0	2	0	21
24	532	2	0	3	2	2	0	0	2	2	2	2	0	2	0	2	4	2	0	27
25	533	2	1	1	1	2	0	0	2	2	2	2	0	2	0	0	0	2	0	19

List of parent crosses producing first generation seedlings.

x - few seedlings
xx - several seedlings

Pistillate Plant	x	Staminate Plant	Number of Seedlings
IV-34 E. tomentosus		IV-52 E. nudatus	xx
IV-52 E. nudatus		IV-34 E. tomentosus	x
V-6 E. tomentosus		X-15 E. nudatus	x
IV-64 E. nudatus		VI-5 E. tomentosus	x
V-12 E. tomentosus		I-14 E. carolinianus	xx
I-14 E. carolinianus		V-12 E. tomentosus	x
I-23 E. tomentosus		I-3 E. carolinianus	x
II-13 E. tomentosus		I-24 E. t. forma rotundatus Fern.	x
II-11 E. tomentosus		I-28 E. t. forma rotundatus Fern.	xx
IV-14 E. t. forma rotundatus Fern.		V-10 E. tomentosus	xx
V-8 E. tomentosus		I-8 E. c. forma vestitus Fern.	xx
V-9 E. tomentosus		IX-4 E. c. forma vestitus Fern.	xx
IX-4 E. c. forma vestitus Fern.		V-9 E. tomentosus	x
IV-10 E. tomentosus		VII-5 E. c. forma vestitus Fern.	x
I-15 E. c. forma vestitus Fern.		V-11 E. tomentosus	x
VIII-6 E. c. forma vestitus Fern.		X-5 E. tomentosus	x
IX-9 E. c. forma vestitus Fern.		X-1 E. tomentosus	x
V-15 E. c. forma vestitus Fern.		V-5 E. tomentosus	x
IX-8 E. c. forma vestitus Fern.		VI-6 E. tomentosus	xx
VI-6 E. tomentosus		IX-88 E. c. forma vestitus Fern.	xx
IX-8 E. c. forma vestitus Fern.		VI-6 E. tomentosus	x
II-12 E. t. forma rotundatus Fern.		X-8 E. nudatus	x
IV-22 E. t. forma rotundatus Fern.		IV-50 E. nudatus	x
I-20 E. t. forma rotundatus Fern.		X-13 E. nudatus	x
V-1 E. t. forma rotundatus Fern.		IV-66 E. nudatus	x
IV-37 E. t. forma rotundatus Fern.		IV-69 E. nudatus	x

cont.

Pistillate Plant	x	Staminate Plant	Number of Seedlings
IV-69 E. nudatus		IV-37 E. t. forma rotundatus Fern.	xx
IV-14 E. t. forma rotundatus Fern.		V-16 E. nudatus	xx
V-16 E. nudatus		IV-14 E. t. forma rotundatus Fern.	x
IV-51 E. nudatus		II-8 E. t. forma rotundatus Fern.	x
IV-65 E. nudatus		V-2 E. t. forma rotundatus Fern.	x
IV-71 E. nudatus		IV-33 E. t. forma rotundatus Fern.	x
IV-63 E. nudatus		IV-39 E. t. forma rotundatus Fern.	x
II-6 E. t. forma rotundatus Fern.		I-2 E. carolinianus	xx
I-2 E. carolinianus		II-6 E. t. forma rotundatus Fern.	x
V-4 E. t. forma rotundatus Fern.		VI-3 E. carolinianus	xx
IV-25 E. t. forma rotundatus Fern.		V-14 E. carolinianus	xx
V-14 E. carolinianus		IV-25 E. t. forma rotundatus Fern.	x
II-7 E. t. forma rotundatus Fern.		II-5 E. carolinianus	xx
II-5 E. carolinianus		II-7 E. t. forma rotundatus Fern.	xx
I-19 E. t. forma rotundatus Fern.		I-5 E. carolinianus	x
IV-15 E. t. forma rotundatus Fern.		VIII-3 E. c. forma vestitus Fern.	x
IV-28 E. t. forma rotundatus Fern.		VII-8 E. c. forma vestitus Fern.	x
VII-8 E. c. forma vestitus Fern.		IV-28 E. t. forma rotundatus Fern.	x
I-29 E. t. forma rotundatus Fern.		VIII-4 E. c. forma vestitus Fern.	x
VIII-4 E. c. forma vestitus Fern.		I-29 E. t. forma rotundatus Fern.	x
IV-19 E. t. forma rotundatus Fern.		IX-3 E. c. forma vestitus Fern.	x
IX-6 E. c. forma vestitus Fern.		III-4 E. t. forma rotundatus Fern.	x
X-16 E. nudatus		X-16 E. nudatus	x
X-11 E. nudatus		VII-1 E. carolinianus	xx
X-10 E. nudatus		V-17 E. carolinianus	x

cont.

Pistillate Plant	x	Staminate Plant	Number of Seedlings
X-11 E. nudatus		V-13 E. carolinianus	x
V-13 E. carolinianus		X-11 E. nudatus	x
IX-1 E. carolinianus		X-18 E. nudatus	x
IV-68 E. nudatus		VIII-3 E. c. forma vestitus Fern.	xx
IV-61 E. nudatus		VIII-8 E. c. forma vestitus Fern.	x
X-17 E. nudatus		IX-7 E. c. forma vestitus Fern.	x
VII-1 E. c. forma vestitus Fern.		X-11 E. nudatus	x

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