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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

THE GENUS *GALIUM* (RUBIACEAE) IN THE SOUTHEASTERN UNITED STATES

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

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BY

CHERYL ANN LAWSON

Norman, Oklahoma

1976

THE GENUS GALIUM (RUBIACEAE)

IN THE SOUTHEASTERN UNITED STATES

APPROVED BY

DISSERTATION COMMITTEE

To

DR. GEORGE J. GOODMAN

from the last of a long line

of grateful students

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THE GENUS *GALIUM* (RUBIACEAE) IN THE SOUTHEASTERN UNITED STATES

CHAPTER I

INTRODUCTION

This study involves a taxonomic treatment of the *Galium* species found in the southeastern United States. Included are keys, descriptions, distributions, illustrations, and taxonomic and nomenclatural notes. Geographically, the study area is the southeastern United States bounded by and including Delaware, Maryland, West Virginia, and Kentucky on the north and Arkansas and Louisiana on the west. The boundaries are those of the proposed *Vascular Flora of the Southeastern United States* to be edited by a board chaired by A. E. Radford. Portions of the following treatment of *Galium* are to be included in this proposed flora.

The species of *Galium* found in the southeastern United States have been treated over the centuries numerous times in regional manuals and floras and in botanical works dating back, for our purposes, to Linnaeus' (1753) *Species Plantarum*. Few studies have presented in-depth information on groups or single species of *Galium*

known to occur in the southeastern United States. In Wiegand's (1897) study of G. trifidum and its North American allies, he treated eleven species, six of which occur in the southeastern United States. Later, Weatherby and Blake (1916) completed the most thorough study to that time of G. pilosum and its varieties. Galium tinctorium and G. obtusum were more fully clarified in a study by Fernald (1935). Two years later Fernald (1937) presented his work on G. circaezans. Cytotaxonomical studies of G. boreale were published by Löve and Löve (1954). Moore (1975) studied the morphological, cytological, and physiological aspects of G. aparine. Recently, Puff (1975) presented the leaf flavonoid chemistry of some species of Galium. Two of the species he studied occur in the southeastern United States - G. obtusum and G. tinctorium. His data support my concept of these two species. In the area of study, occasional state treatments have appeared such as Winston's (1939) study of the Rubiaceae of Middle Tennessee and Wells and Sharp's (1966) study of the Coffeoideae of Tennessee.

Presented here are the results of a critical examination of twenty-two species and nine varieties of Galium. Of the twenty-two species, two, G. palustre and G. tricornutum, have been previously unknown in the southeastern United States.

Study material included my own collections of populations, potted plants brought from the field to the

greenhouse, and over 6300 sheets of herbarium specimens from the following herbaria:

AUA, CLEMS, DUKE, FSU, GA, GH, LONG,[1] MISSA, MO, NCU, NO, NSC, NY, OKL, PH, TENN, UARK, US, USF, VDB, VPI, VSC, WCUH, WVA.

Field studies were carried out in the summer of 1973 and spring of 1974.[2] All field material collected is deposited at OKL with duplicates to be distributed.

Measurements were made on these collections and the borrowed specimens. Many of the resulting measurements are given as ( ) X - Y ( ) with the parenthetical measurements representing the minimum and maximum values found and with the non-parenthetical measurements, X - Y, representing the mean measurement plus or minus one standard deviation.

Some of the species may be confused because of morphological similarity during certain periods in the life cycle with one or more other species. Each of the confusing pairs is discussed under one of the species. Figure 1 shows groups of similar species, the arrows indicating the confusing species pairs. A species with no arrow indicates there is little confusion in the southeastern United States.

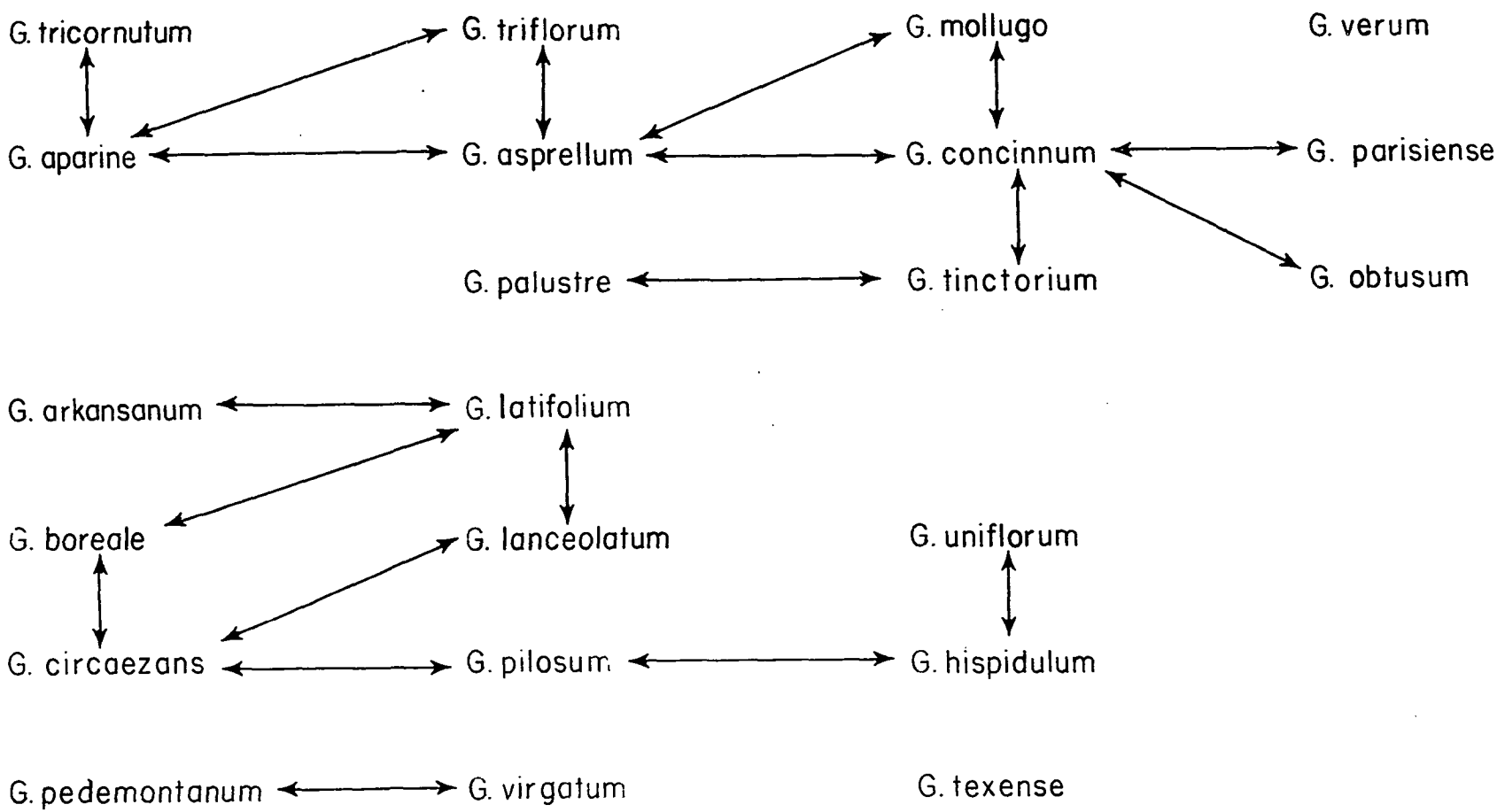
---

[1]Longwood College, Farmville, Virginia.

[2]Travel supported by a National Science Foundation Traineeship from the University of Oklahoma Graduate College.

FIGURE 1

Groups of similar species with arrows indicating the confusing species pairs. A species with no arrow indicates little confusion in the southeastern United States.


G. tricornutum
G. triflorum
G. mollugo
G. verum
G. aparine
G. asprellum
G. concinnum
G. parisiense
G. palustre
G. tinctorium
G. obtusum
G. arkansanum
G. latifolium
G. boreale
G. lanceolatum
G. uniflorum
G. circaezans
G. pilosum
G. hispidulum
G. pedemontanum
G. virgatum
G. texense

CHAPTER II

GENERAL MORPHOLOGY

Roots.—Perennial species are found most commonly, with G. aparine, G. parisiense, G. pedemontanum, G. texense, and G. tricornutum comprising the annuals. One species, G. hispidulum, is stoloniferous, and G. mollugo and G. triflorum are rhizomatous.

Stems.—The stems are four-sided and square in cross section. Usually the stem angles are noticeably thickened. It is on these angles that the indumentum, when present on the stem, generally will be found. Only occasionally will the sides of the stem also exhibit pubescence.

The presence and absence, amount, and type of indumentum is variable among the species and sometimes within a single species. Hairs may be scabrous, scaberulous, villous, villosulous, hispid, flattened-hispid, or uncinate. Occasionally a combination of two types of indumentum may be found on individuals of a species. The direction of growth of these hairs is equally as variable and includes straight-spreading, descending, ascending, curved, antrorse, or retrorse.

The stems are generally erect or ascending, but reclining, prostrate, or matted ones may be found in certain species. The branching pattern varies from simple to branching near the base of the plant to branching once or twice at either the upper or lower nodes or both.

Inflorescences.—For the most part, the inflorescences are cymose. Variations and modifications of this cymose nature is seen throughout the species. For example, a compound dichasium is present in G. latifolium, G. texense, and usually in G. tricornutum. The dichasium has been reduced to its simplest form in G. uniflorum and G. hispidulum. The cyme is modified in G. circaezans and G. lanceolatum by the loss of flowers from the same side of each dichotomy, thereby forming helicoid cymes. Cymose panicles and simple and compound cymes are found in the other species with the exception of G. virgatum. Here the flowers are sessile and axillary and develop racemosely on the virgate stem.

In many of the species the axillary inflorescences develop in the upper portion of the plant and, thus, frequently appear terminal.

Flowers.—The flowers are perfect with obsolete calyx lobes and very short corolla tubes. There are four stamens and two style branches.

The corollas are rotate although campanulate ones are known to occur in some of the species of Galium of the western United States. Galium and Asperula have been separated

on the basis of rotate versus campanulate corollas; however, campanulate corollas in Galium are considered by Dempster and Ehrendorfer (1965) to be an atavism.

Three or four connate lobes with or without an apical appendage comprise each corolla. Only in G. tinctorium were three-lobed corollas found, and these along with four-lobed ones.

The presence of a caudate corolla lobe as opposed to one which is acute, obtuse, or slightly or broadly apiculate is a fairly useful diagnostic character. Only corolla lobes of G. verum, G. parisiense, G. concinnum, and G. asprellum are known to exhibit both caudate and non-caudate apices.

Corollas are mostly white with varying shades of greenish white and yellowish white also abundant. Shades of light green, greenish yellow, and yellow occur also. Sometimes in G. palustre a rose-tinged corolla is found. Purple corolla lobes may be found in G. arkansanum, and ones which are purple at least on the inner surface occur in G. latifolium and G. pilosum. In G. lanceolatum the corolla lobes are purple when dry. These purple corolla lobes may be distinguished even in dried specimens from corollas of other colors. Differentiation between yellow, white, green, and rose corolla lobes is difficult in dried material.

Corolla lobes are mostly glabrous, but in five species they may be either glabrous or pubescent on the outer surface. In G. texense the margins and submargins of the

lobes are consistently beset with long, straight hairs, while at least the inner surface of the corolla lobes in G. palustre is muriculate.

The corollas vary from minute to quite showy. Measurements of the corolla lobe length were made from the point of connation to the apex. If an apical appendage were present, it was excluded from the lobe length measurement. The width of each corolla lobe was made at its widest point.

Galled corollas my be found occasionally in some species.

Fruits.—The fruits, when ripe, separate into two spherical, ovoid, or slightly reniform, indehiscent, one-seeded carpels. These fruits are usually dry, but in G. hispidulum and G. uniflorum berries are formed.

Ovaries and fruits may be glabrous or glabrate or covered with uncinate, straight, or curved hairs. In addition to these fruit types, muriculate fruits are often found in G. parisiense, and tuberculate ones in G. tricornutum. In G. arkansanum the fruits appear glabrous, but are roughened and often papillate. Within a species, fruits are consistently glabrous or glabrate or bear uniform processes or hairs with the exception of G. parisiense, in which the fruits my be muriculate or uncinate hairy, and G. boreale, in which they are glabrous, glabrate, or pubescent with straight or curved hairs.

Only mature fruits were measured, and these measurements represent individual carpel lengths and widths.

Leaves.—Leaves, their number, shape, size, apex, and indumentum, are also variable between the species. These leaf characters are frequently useful diagnostically.

Whorls of leaves and stipular appendages are all referred to as leaves. The size and shape of the stipular appendages are generally the same as the true leaves; however, in G. texense there is a slight difference in size between the two. Dempster (1973) pointed out that the midnerve of the true leaves is connected directly to the vertical vascular system of the stem and that the midnerve of the stipular appendages is directly connected only to a vascular ring leading to the basal connection of the true leaves. Also, the stipular appendages lack axillary buds.

Leaves vary from four to up to twelve per whorl and are sometimes only opposite. Generally, however, leaf number ranges between four to six per whorl. The leaves are sessile with entire margins.

The shape of the leaves ranges in varying degrees from linear, elliptical, oblong, ovate, lanceolate, oblanceolate, to obovate.

Likewise, the leaf apices vary from obtuse, acute, acuminate, cuspidate, mucronate, and mucronulate to apices with rounded tips. Within a species there may be slight variations in apices, but generally the apex type is of

diagnostic value in differentiating species. The above apices are illustrated in Figure 2.

In all the species the midnerve is prominent, but the two lateral nerves may be present or absent. These lateral nerves also may be prominent or obscure. Vein number is consistent in most species; however, in a few the number may vary on occasion from one to three.

The pubescence on the leaves shows the same variation as on the stem angles. On individual plants the stem and leaf pubescence frequently will be similar. However, the upper and lower surfaces, veins, and margins of the same leaf may vary in the presence and absence and type of indumentum.

Secretory glands are found scattered or near the apex on the lower leaf surface in most species containing four-leaved whorls. This observation has been made in other European and North American Galium species having the four leaves/whorl. Rarely, G. mollugo, a species containing mostly six to eight leaves/whorl, may show a few such glands on the lower leaf surface.

These glands, containing a phytosterine (Dempster and Ehrenforfer, 1965), often form a useful taxonomic character. Dempster and Ehrendorfer (1965) reported that these glands have been associated with a downward bending of the leaf and are the apparent cause of the reflexion of leaf apices.

Since there is variation in leaf size on each individual, measurements have been limited to the largest, middle-stem leaves. These are referred to in the descriptions as "largest leaves."

FIGURE 2

LEAF APICES

A - obtuse

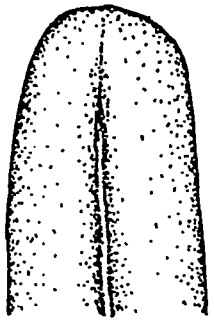
B - acute

C - acuminate

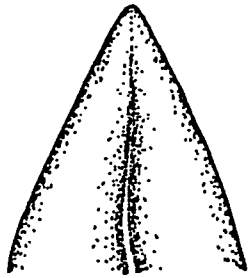
D - cuspidate

E - mucronate

F - mucronulate



A



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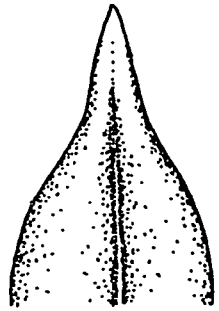

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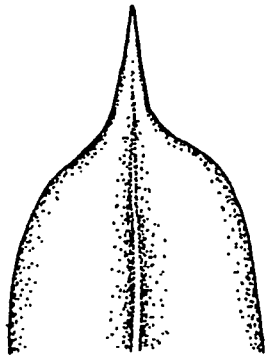

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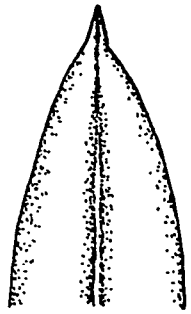
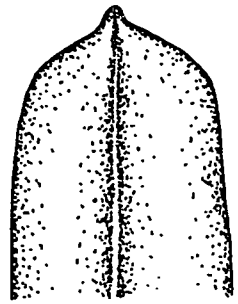


E



F

CHAPTER III

KEYS TO SPECIES

Key to Plants in Vegetative Condition

A. Leaves in whorls of 4 on the main stem (often appearing as 6 or 8 in G. virgatum because of the subtending bracts of the sessile flowers).

B. Leaves with 1 prominent nerve and lacking any obscure or inconspicuous lateral nerves.

C. Angles of the stem with long, villous and retrorse, flattened-hispid hairs throughout, the hispid hairs often more abundant and dense on the upper stem angles. . . . . 14. G. pedemontanum

CC. Angles of the stem glabrous or pubescent, but not as in C above.

D. Secretory glands absent on the lower leaf surface.

E. Largest leaves mostly 4.7 - 7.1 mm long, acute, sometimes obtuse, and often tipped with a stiff, straight hair; margins of the leaves with

straight , spreading, apically directed or slightly descending hairs 0.2 - 0.4 mm long (these hairs frequently flattened and broadened at the base); stems simple or branching mostly near the base, glabrate to moderately pubescent on the angles with stiff, straight, spreading or descending hairs up to 0.4 mm long. . . . . 22. G. virgatum

EE. Largest leaves mostly 9.6 - 18 mm long, mostly obtuse and lacking a stiff, straight hair at the tip; margins of the leaves glabrous or with flattened-hispid or scabrous hairs up to 0.2 mm long (these hairs more or less descending); stems usually branching once at each node, glabrous or retrorsely scabrous with hairs up to 0.1 mm long.

F. Stems retrorsely scabrous or rarely nearly glabrous on the angles, the nodes occasionally hairy. . . 17. G. tinctorium

FF. Stems frequently with hairy nodes, otherwise glabrous or nearly so on the angles. . 11. G. obtusum

DD. Secretory glands scattered on the lower leaf surface or only near the apex in G. texense (20x or greater magnification may be necessary).

G. Apices of the leaves acute (sometimes obtuse in G. virgatum).

H. Largest leaves mostly less than 9.6 mm long; apices of the leaves often tipped with a stiff, straight hair.

I. Secretory glands scattered over the lower leaf surface . . . . 22. G. virgatum

II. Secretory glands present only near the apex on the lower leaf surface; two leaves of each whorl slightly larger than the other two . . . . 16. G. texense

HH. Largest leaves mostly greater than 14 mm long; apices of the leaves not tipped with a stiff, straight hair.

J. Upper leaf surface muriculate, glabrate or with short, scabrous,

ascending hairs 0.08 - 0.16 mm long along the margins and midrib (these hairs sometimes scattered over the upper leaf surface); leaves mostly linear or narrowly elliptical to sometimes linear oblong, largest leaves mostly 2.3 - 3.4 mm wide. . . . . 20. G. uniflorum

JJ. Upper leaf surface with straight, ascending hairs up to 0.4 mm long on the midnerve (these hairs often appressed and parallel to the midnerve); margins with straight, spreading or slightly ascending hairs up to 0.5 mm long; leaves lanceolate to linear, largest leaves mostly 4.7 - 8.8 mm wide. . . . . 2. G. arkansanum

GG. Apices of the leaves mucronulate or acuminate (only slightly so in G. uniflorum).

K. Apices of the leaves mostly mucronulate; leaves broadly to narrowly elliptical to broadly oblong; largest leaves mostly 5.4 - 9.4 mm wide. . . . . 15. G. pilosum

KK. Apices of the leaves acuminate, at least slightly so.

L. Upper leaf surface muriculate, glabrate or with short, scabrous, ascending hairs 0.08 - 0.16 mm long along the margins and midrib (these hairs sometimes scattered over the upper surface); leaves mostly linear to narrowly elliptical to sometimes linear oblong, slightly acuminate, largest leaves mostly 2.3 - 3.4 mm wide. . . . . 20. G. uniflorum

LL. Upper leaf surface muriculate, glabrous or with stiff, vertical or slightly curved, ascending hairs 0.14 - 0.4 mm long; margins glabrous to densely hispid with hairs 0.2 - 0.4 mm long; leaves mostly elliptical but varying from ovate to oblong to occasionally oblanceolate, acuminate, largest leaves mostly 3.5 - 5.3 mm wide . . . 7. G. hispidulum

BB. Leaves with 3 nerves, the two lateral nerves sometimes obscure or less conspicuous than the midnerve.

M. Angles of the stem with long, villous (0.6 - 1.6 mm long) and retrorse, flattened-hispid (0.1 - 0.4 mm long) hairs throughout, the hispid hairs often more abundant and dense on the upper stem angles. . 14. G. pedemontanum

MM. Angles of the stem glabrous or pubescent, but not as in M above.

N. Apices of the leaves usually mucronulate; leaves broadly to narrowly elliptical to broadly oblong, midnerve prominent, lateral nerves two, obscure. . 15. G. pilosum

NN. Apices of the leaves acuminate, acute, obtuse, or occasionally the tips rounded.

O. Leaves linear to lanceolate (at least on the upper portion of the stem in G. lanceolatum).

P. Apices of the leaves acute.

Q. Midnerve only occasionally more prominent than the lateral nerves; leaves lanceolate, commonly broadly so, mostly 33 - 46.5 mm long and 10.8 - 16 mm wide. . . . . 9. G. latifolium

QQ. Midnerve prominent, the lateral nerves obscure; leaves linear to lanceolate, mostly 26.2 - 37.8 mm long and 4.7 - 8.8 mm wide. . . . . 2. G. arkansanum

PP. Apices of the leaves obtuse or rounded (if nearly acute in G. boreale, the tips rounded).

R. Stems glabrous or with retrorsely scaberulous or straight, spreading or descending hairs on the

angles and sometimes on the sides, glabrous or occasionally densely pubescent at the nodes; leaves linear to lanceolate throughout, largest leaves mostly 22 - 39.8 mm long and 2.8 - 6.6 mm wide. . 4. G. boreale

RR. Stems mostly glabrous or with a few straight, spreading hairs scattered on the angles and sides or at the nodes; leaves lanceolate above and elliptical on the lower portion of the stem, largest leaves mostly 42.6 - 55.3 mm long and 12.7 - 17.8 mm wide. . . . . . 8. G. lanceolatum

OO. Leaves elliptical, ovate, oblong, or oblanceolate.

S. Leaves with usually prominent lateral nerves, ovate or elliptical, minutely or inconspicuously acuminate or

occasionally the tips rounded, largest leaves mostly 19.6 - 31.5 mm long and 9.6 - 15.1 mm wide. . . . 5. G. circaezans

SS. Leaves with obscure lateral nerves, mostly elliptical but varying from ovate to oblong to occasionally oblanceolate, acuminate, largest leaves mostly 8.3 - 13.2 mm long and 3.5 - 5.3 mm wide. 7. G. hispidulum

AA. Leaves in whorls of 5 or more on the main stem, sometimes 4 and 5, 4 to 6, or rarely 4 and 6 on the same plant (sometimes with but 2 leaves at some nodes in G. obtusum and G. palustre).

T. Angles of the stem villosulous throughout or only in the inflorescence; leaves in whorls of 6 to 12, cuspidate. . . . . 21. G. verum

TT. Angles of the stems glabrous or pubescent, but not villosulous.

U. Angles of the stem retrorsely scabrous (sparsely so in G. concinnum) or retrorsely hispid on the stem angles excluding the nodes.

V. Apices of the leaves obtuse or mostly so.

W. Leaves in whorls of 4 to 6 on the same plant, sometimes opposite,

6 - 11 mm long and 1.6 - 2.3 mm wide, mostly obtuse. . . 12. G. palustre

WW. Leaves in whorls of 4, 5, or 6 on the same plant, mostly 9.6 - 15.5 mm long and 1.8 - 3.1 mm wide, obtuse. . . . . 17. G. tinctorium

VV. Apices of the leaves mucronate or cuspidate.

X. Margins of the leaves usually antrorsely scabrous (occasionally glabrous or retrorsely scabrous near the base in G. concinnum).

Y. Leaves in whorls of 6 or whorls of 4 and 6 on the same plant, usually more than 8 mm long.

Z. Leaves usually 18 - 34.6 mm long and 5.4 - 8.7 mm wide . . . 19. G. triflorum

ZZ. Leaves usually 11.3 - 15.9 mm long and 1.6 - 2.4 mm wide. . 6. G. concinnum

YY. Leaves in whorls of 6 or 7, sometimes 5 or 8, usually 4.6 - 7.9 mm long and 0.8 - 1.3 mm wide. . . 13. G. parisiense

XX. Margins of the leaves retrorsely scabrous throughout (also usually antrorsely scabrous distally in G. tricornutum).

a. Upper leaf surface with slightly uncinate to uncinate hairs; leaves in whorls of 6 to 8, sometimes 9. . 1. G. aparine

aa. Upper leaf surface glabrous or with a few appressed, apically directed hairs near the margins and sometimes on the midnerve.

b. Leaves in whorls of 6; margins of the leaves retrorsely scabrous throughout. . 3. G. asprellum

bb. Leaves in whorls of 6 to 10; margins of the leaves retrorsely scabrous throughout and also usually antrorsely scabrous distally . . . 18. G. tricornutum

UU. Angles of the stems glabrous or nearly so or pubescent, but the hairs not as in U above (occasionally retrorsely short hispid and long, straight hairy on the same stem angles in G. triflorum).

c. Apices of the leaves obtuse; stems frequently with hairy nodes, otherwise glabrous or nearly so; leaves in whorls of 4, sometimes 5 (rarely 6) on the same plant, side branches occasionally with 2 leaves/node. . . . . 11. G. obtusum

cc. Apices of the leaves mucronate or cuspidate.

d. Leaves in whorls of 6, narrowly elliptical to oblanceolate, mucronate or cuspidate, largest leaves mostly 18 - 34.6 mm long and 5.4 - 8.7 mm wide. . . . . 19. G. triflorum

dd. Leaves in whorls of 6 to 8, rarely 12, obovate to oblanceolate to linear, cuspidate, largest leaves mostly 10.5 - 15.2 mm long and 1.9 - 3.3 mm wide. 10. G. mollugo

Key to Plants in Flowering Condition

A. Lobes of the corolla caudate, sometimes only slightly so, (the appendages 0.1 - 0.8 mm long, often folded inside or broken off).

B. Flowers sessile or subsessile in helicoid cymes.

C. Lobes of the corolla usually pubescent on the outer surface, sometimes glabrous, abruptly caudate; flowers light green to light yellow; leaves ovate or elliptical, minutely acuminate or the tips rounded. . . 5. *G. circaezans*

CC. Lobes of the corolla glabrous, slightly or narrowly caudate; flowers yellowish, turning dull purple in drying; leaves lanceolate above and elliptical on the lower portion of the stem, narrowing to a rounded or obtuse tip. . . . . 8. *G. lanceolatum*

BB. Flowers pedicellate.

D. Leaves in whorls of 4.

E. Lobes of the corolla usually purple at least on the inner surface.

F. Leaves broadly to narrowly elliptical to broadly oblong, usually mucronulate, midnerve prominent, lateral nerves two, obscure or absent; lobes of the corolla usually greenish on the outer surface. . 15. *G. pilosum*

FF. Leaves lanceolate to linear.

G. Leaves 3-nerved, the midnerve only occasionally more prominent than the lateral nerves, lanceolate, commonly broadly so, mostly 33 - 46.5 mm long and 10.8 - 16 mm wide; inflorescence a compound dichasium, bibracteate at each of the up to four branchings. . . . . 9. G. latifolium

GG. Leaves generally 1-nerved, prominent, the lateral nerves absent or obscure, linear to lanceolate, mostly 26.2 - 37.8 mm long and 4.7 - 8.8 mm wide; inflorescence a compound cyme, two or three times branched. . . . . 2. G. arkansanum

EE. Lobes of the corolla whitish, yellowish, or greenish, but not purple.

H. Leaves mostly elliptical but varying from ovate to oblong to occasionally oblanceolate, acuminate, largest leaves mostly 8.3 - 13.2 mm long and 3.5 - 5.3 mm wide; inflorescence a simple dichasium; flowers borne

2 - 3 at the ends of axillary, naked peduncles, yellow green to light green. . . . . 7. G. hispidulum

HH. Leaves mostly linear or narrowly elliptical to sometimes linear oblong, acute to slightly acuminate, largest leaves mostly 19.5 - 26.6 mm long and 2.3 - 3.4 mm wide; inflorescence a simple dichasium with lateral branches most frequently reduced or obsolete, thus appearing as a monochasium; flowers borne singly, sometimes 2, or rarely 3 at the ends of axillary, naked puduncles, white to light green. . . 20. G. uniflorum

DD. Leaves in whorls of 6 or more, rarely in whorls of 5 and more or whorls of 4 and 6 on the same plant.

I. Angles of the stem villosulous throughout or only in the inflorescence; leaves in whorls of 6 to 12, cuspidate. . . . . 21. G. verum

II. Angles of the stem glabrous or pubescent, but not villosulous.

J. Leaves in whorls of 6 only, or whorls of 4 and 6 on the same plant.

K. Margins of the leaves usually antrorsely scabrous (occasionally glabrous or retrorsely scabrous near the base in G. concinnum).

L. Leaves in whorls of 6 or occasionally reduced to 4 in the upper branches, linear to narrowly oblong, elliptical, or oblanceolate, cuspidate, largest leaves mostly 11.3 - 15.9 mm long and 1.6 - 2.4 mm wide; ovaries glabrous. . . . . 6. G. concinnum

LL. Leaves in whorls of 6, narrowly elliptical to oblanceolate, mucronate to cuspidate, largest leaves 18 - 34.6 mm long and 5.4 - 8.7 mm wide; ovaries pubescent. . . . . 19. G. triflorum

KK. Margins of the leaves mostly retrorsely scabrous; lobes of

the corolla only slightly caudate; ovaries glabrous. . . . . 3. G. asprellum

JJ. Leaves in whorls of 6 and more, rarely in whorls of 5 and more on the same plant.

M. Stems retrorsely scabrous on the angles; leaves in whorls of 6 or 7, sometimes 5 or 8. . . . . 13. G. parisiense

MM. Stems glabrous to densely pubescent on the lower angles and sides with straight, spreading or descending hairs (occasionally also pubescent on the upper angles); leaves in whorls of 6 to 8, rarely 12. . . . . 10. G. mollugo

AA. Lobes of the corolla acute, obtuse, or slightly or broadly apiculate.

N. Flowers sessile, supported by very short, axillary peduncles and subtended by two leaf-like bracts, developing racemosely on the virgate stem; lobes of the corolla acute, yellow-white to white. . . . . 22. G. virgatum

NN. Flowers pedicellate.

O. Pedicels long villous; lobes of the corolla acute to slightly rounded, pale yellow to white. . . . . 14. G. pedemontanum

OO. Pedicels glabrous or pubescent, but not long villous.

P. Margins and submargins of the corolla lobes beset with long, straight hairs up to 0.4 mm long; lobes of the corolla acute, light green to yellow. . 16. G. texense

PP. Margins and submargins of the corolla without long, straight hairs.

Q. Leaves in whorls of 4.

R. Leaves 3-nerved, lateral nerves present but usually less conspicuously so; lobes of the corolla slightly or broadly apiculate, white. . . . . 4. G. boreale

RR. Leaves 1-nerved; lobes of the corolla obtuse or acute.

S. Stems frequently with hairy nodes, otherwise glabrous or nearly so; lobes of the corolla mostly acute, white. . . . . 11. G. obtusum

SS. Stems with retrorse hairs, rarely nearly glabrous; lobes of the corolla obtuse or acute, white. . . . . 17. G. tinctorium

QQ. Leaves in whorls of 5 or more, sometimes 4 and 5, 4 to 6, or rarely 4 and 6 on the same plant (sometimes with but 2 leaves at some nodes in G. obtusum and G. palustre).

T. Angles of the stem villosulous throughout or only in the inflorescence; leaves in whorls of 6 to 12, cuspidate; lobes of the corolla acute, yellow. . . . . 21. G. verum

TT. Angles of the stem glabrous or pubescent, but not villosulous.

U. Leaves in whorls of 4 and 5, 4 to 6 or rarely 4 and 6 on the same plant (sometimes with but 2 leaves at some nodes in G. obtusum and G. palustre).

V. Leaf apices cuspidate, leaves in whorls of 6

or occasionally reduced to 4 in the upper branches; lobes of the corolla acute, white . . 6. G. concinnum

VV. Leaf apices mostly obtuse, but not cuspidate.

W. Stems frequently with hairy nodes, otherwise glabrous or nearly so; leaves in whorls of 4, sometimes 5 (rarely 6) on the same plant; side branches occasionally with 2 leaves/node; lobes of the corolla mostly acute, white. . 11. G. obtusum

WW. Stems with retrorse hairs, rarely nearly glabrous.

X. Fruits numerous usually borne 2 - 3 at the ends of several-times forked lateral and terminal peduncles; leaves in whorls of 4 to 6, sometimes opposite; lobes of the corolla obtuse or acute, white or rose-tinged. . . 12. G. palustre

XX. Fruits usually borne 2 - 3 at the ends of simple lateral and terminal peduncles; leaves in whorls of 4, 5, or 6 on the same plant; lobes of the corolla obtuse or acute, white. . . . . 17. G. tinctorium

UU. Leaves in whorls of 6 or more, without any whorls of 5 (rarely in G. parisiense) or opposite.

Y. Margins of the leaves antrorsely scabrous (occasionally glabrous or retrorsely scabrous near the base in G. concinnum).

Z. Leaves in whorls of 6, largest leaves mostly 11.3 - 15.9 mm long and 1.6 - 2.4 mm wide; ovaries glabrous 6. G. concinnum

ZZ. Leaves in whorls of 6 or 7, sometimes 5 or 8, largest leaves 4.6 - 7.9 mm long and 0.8 - 1.3 mm wide; ovaries muriculate or hairy 13. G. parisiense

YY. Margins of the leaves retrorsely scabrous throughout or if antrorsely scabrous distally, the pedicels retrorsely scabrous.

a. Upper leaf surface with slightly uncinate to uncinate hairs; leaves in whorls of 6 to 8, sometimes 9; pedicels glabrous or glabrate; lobes of the corolla mostly acute, white; ovaries pubescent. . . .

1. G. aparine

aa. Upper leaf surface glabrous or with a few appressed, apically directed hairs near the margins and sometimes on the midnerve.

b. Leaves in whorls of 6; pedicels glabrous; lobes of the corolla acute, white or yellowish; ovaries glabrous 3. *G. asprellum*

bb. Leaves in whorls of 6 to 10; pedicels retrorsely scabrous; lobes of the corolla acute, white; ovaries tuberculate. . . 18. *G. tricornutum*

Key to Plants in Fruiting Condition

A. Fruits pubescent with uncinate, straight, or curved hairs.

B. Leaves in whorls of 4 (appearing 6 or 8 in G. virgatum).

C. Leaves 1-nerved with no obscure lateral nerves.

D. Fruits sessile, supported by very short, axillary peduncles and subtended by two leaf-like bracts, developing racemosely on the virgate stem; lower leaf surface often with scattered secretory glands; leaf apices acute, sometimes obtuse. . . . . 22. G. virgatum

DD. Fruits pedicellate in axillary, compound dichasia or simple and compound cymes.

E. Lower leaf surface with scattered secretory glands; leaf apices mucronulate. . . . 15. G. pilosum

EE. Lower leaf surface with secretory glands present only near the apex; leaf apices acute and often tipped with a stiff, straight hair. . . . . 16. G. texense

CC. Leaves 3-nerved, the lateral nerves sometimes less conspicuous than the midnerve.

F. Fruits pedicellate.

G. Leaves broadly to narrowly elliptical to broadly oblong; apex usually mucronulate. . . . 15. G. pilosum

GG. Leaves linear to lanceolate; apex obtuse or nearly acute but with rounded tips. . 4. G. boreale

FF. Fruits sessile or subsessile.

H. Leaves ovate or elliptical, minutely acuminate or the tips rounded. . . . . 5. G. circaezans

HH. Leaves lanceolate above and elliptical on the lower portion of the stem, narrowing to a rounded or obtuse tip. . . . . 8. G. lanceolatum

BB. Leaves in whorls of more than 4.

I. Margins of the leaves with retrorse hairs and the upper leaf surface with uncinate hairs. . . . . 1. G. aparine

II. Margins of the leaves with antrorse hairs, or if retrorse, the upper leaf surface not as above.

J. Midnerve on the lower leaf surface with vertical or apically directed hairs. . . . . 13. G. parisiense

JJ. Midnerve on the lower leaf surface glabrous or with retrorse hairs. . . . . 19. G. triflorum

AA. Fruits glabrous, glabrate, muriculate, tuberculate, roughened or papillate.

K. Leaves in whorls of 4.

L. Fruits fleshy, purplish-black.

M. Fruits a glabrate berry with scattered, appressed hairs seldom over 0.3 mm long; leaves mostly elliptical but varying from ovate to oblong to occasionally oblanceolate, acuminate; largest leaves mostly 8.3 - 13.2 mm long. . 7. G. hispidulum

MM. Fruits a glabrous berry; leaves mostly linear or narrowly elliptical to sometimes linear oblong, acute or slightly acuminate; largest leaves mostly 19.5 - 26.6 mm long. . . . . 20. G. uniflorum

LL. Fruits dry, not fleshy.

N. Angles of the stem with long, villous (0.6 - 1.6 mm long) and retrorse, flattened-hispid (0.1 - 0.4 mm long) hairs throughout, the hispid hairs often more abundant and dense on the upper stem angles; fruits glabrous on axillary, reflexed, long-villous peduncles. . . . . 14. G. pedemontanum

NN. Angles of the stem glabrous or pubescent, but not as in M above.

O. Fruits appearing glabrous, but roughened and often papillate, the projections with very minutely

scabrous hairs; leaves lanceolate to linear, acute with one prominent nerve, the lateral nerves absent or obscure. . . . . 2. *G. arkansanum*

OO. Fruits glabrous or glabrate.

P. Leaves 3-nerved, the lateral nerves sometimes less conspicuous than the midnerve.

Q. Fruits numerous in cymose panicles; leaves linear to lanceolate, obtuse or acute but rounded, the two lateral nerves usually less conspicuous than the midnerve. . . . . 4. *G. boreale*

QQ. Fruits in compound dichasia, bibracteate at each of the up to four branchings; leaves lanceolate, commonly broadly so, acute, the midnerve only occasionally more prominent than the lateral nerves. . 9. *G. latifolium*

PP. Leaves 1-nerved with no obscure lateral nerves.

R. Stems frequently with hairy nodes, otherwise glabrous or nearly so. . . . . 11. G. obtusum

RR. Stems with retrorse hairs, rarely nearly glabrous. . . . . 17. G. tinctorium

KK. Leaves in whorls of 5 or more, sometimes 4 and 5, 4 to 6, or rarely 4 and 6 on the same plant (sometimes with but 2 leaves at a node in G. obtusum and G. palustre).

S. Fruits tuberculate or muriculate.

T. Fruits muriculate; margins of the leaves antrorsely scabrous; leaves in whorls of mostly 6 or 7, sometimes 5 or 8. . . . . 13. G. parisiense

TT. Fruits tuberculate; margins of the leaves retrorsely scabrous throughout and also usually antrorsely scabrous distally; leaves in whorls of 6 to 10. . . . . 18. G. tricornutum

SS. Fruits not tuberculate or muriculate.

U. Leaves in whorls of 4 and 5, 4 to 6, or rarely 4 and 6 on the same plant (sometimes with but 2 leaves at a node in G. obtusum and G. palustre).

V. Leaf apices cuspidate; leaves in whorls of 4 (in the upper branches) and 6 on the same plant. . . . . 6. G. concinnum

VV. Leaf apices mostly obtuse, but not cuspidate.

W. Stems with frequently hairy nodes, otherwise glabrous or nearly so; leaves in whorls of 4 and 5 (rarely 6) on the same plant; side branches occasionally with 2 leaves/node. . . . . 11. G. obtusum

WW. Stems with retrorse hairs, rarely nearly glabrous.

X. Fruits numerous, usually borne 2 - 3 at the ends of several-times forked lateral and terminal peduncles; leaves in whorls of 4 to 6, sometimes opposite. . . . . 12. G. palustre

XX. Fruits usually borne 2 - 3 at the ends of simple, lateral and terminal peduncles; leaves in whorls of 4, 5, or 6. 17. G. tinctorium

UU. Leaves in whorls of 6 or more, without any whorls of 4 or 5 or opposite.

Y. Angles of the stem villosulous throughout or only in the inflorescence; leaves in whorls of 6 to 12, cuspidate. . 21. *G. verum*

YY. Angles of the stems glabrous or pubescent, but not villosulous.

Z. Angles of the stem retrorsely scabrous (sometimes sparsely so in *G. concinnum*); leaves in whorls of 6.

a. Margins of the leaves retrorsely scabrous. . . . . 3. *G. asprellum*

aa. Margins of the leaves usually antrorsely scabrous, occasionally glabrous, or retrorsely scabrous near the base. . . . . 6. *G. concinnum*

ZZ. Angles of the stem glabrous to densely pubescent on the lower angles and sides with straight, spreading or descending hairs (occasionally also pubescent on

the upper angles); leaves in whorls of 6 to 8, rarely 12; margins of the leaves antrorsely scabrous. . . 10. *G. mollugo*

CHAPTER IV

DESCRIPTIONS, DISTRIBUTIONS, ILLUSTRATIONS AND TAXONOMIC AND NOMENCLATURAL NOTES

1. GALIUM APARINE L., Sp. Pl. 1: 108. 1753.

G. vaillantii DC., Lam. & DC. Fl. Fr. ed. 3. 4: 263. 1805.

G. agreste var. echinospermum Wallr., Sched. Crit. 59. 1822.

G. aparine var. minor Hook., Fl. Bor. Am. 1: 290. 1833.

G. aparine var. vaillantii (DC.) Koch, Syn. Fl. Germ. 330. 1837.

G. spurium var. vaillantii (DC.) Gren. & Godr., Fl. Fr. 2: 44. 1851.

G. spurium var. vaillantii (DC.) Beck von Man., Fl. Nied. Österr. 2: 1122. 1893.

G. spurium var. echinospermum (Wallr.) Hayek, Fl. Steierm. 2: 393. 1912.

G. aparine var. echinospermum (Wallr.) Farw., Rep. Mich. Acad. Sci. 19: 260. 1917.

G. spurium forma vaillantii (DC.) R. J. Moore, Canad. J. Bot. 53: 882. 1975.

Erect or matted annual, up to 16.0 dm tall (mostly 5.7 - 9.4 dm); stems frequently simple or branching at the nodes, usually retrorsely scabrous (rarely only hispid) on the angles with hairs up to 0.4 mm long, at the nodes these often becoming spreading villous and up to 1.2 mm long; leaves in whorls of six to eight (rarely nine), linear to oblanceolate, mucronate or cuspidate, largest leaves (12.8) 21.7 - 42.5 (62.8) mm long and (1.2) 2.3 - 4.9 (10.1) mm wide, nerve one, prominent, upper leaf surface with slightly uncinate to uncinate hairs up to 0.5 mm long, lower leaf surface retrorsely scabrous (densely or sparsely so) on the midnerve with hairs up to 0.3 mm long, otherwise glabrous and lacking secretory glands, margins retrorsely scabrous with hairs up to 0.3 mm long; inflorescence cymose; flowers on glabrous or glabrate pedicels, borne 3 - 4 at the ends of lateral or terminal peduncles, the pedicels subtended by one or more reduced leaves; corollas four-lobed, white, lobes mostly acute, usually (0.5) 0.6 - 1 (1.2) mm long and (0.4) 0.5 - 0.7 (0.9) mm wide, glabrous; fruits pubescent with uncinate hairs seldom over 0.8 mm long, each mature carpel (1.2) 1.8 - 2.9 (4.8) mm long and (0.9) 1.4 - 2.3 (3.4) mm wide.—Fig. 3.

Type locality: "Habitat in Europae cultis & ruderatis."

Range: Circumpolar; present in most of temperate North America (Southeastern United States, Map 1; this

FIGURE 3

GALIUM APARINE: A, habit x 1; B, fruit x 10; C, upper leaf surface, margin, and apex x 12; D, flower x 24; E, stem at node x 10; F, leaf whorl x 1.5. A, B, C, E, F from C. A. Lawson & D. Dotts 1208 (OKL), and D from C. A. Lawson & D. Dotts 1210 (OKL).


A
B
C
D
E
F

species is known to occur in Delaware; however, no county localities could be determined for use on the distribution map).

Flowering - Fruiting time: March through June; rarely February in Louisiana.

Habitat: Frequent along roadsides, railroad tracks, and fence rows; in vacant lots, waste places, and open fields; and on moist wooded slopes, river and creek banks, and swamp margins.

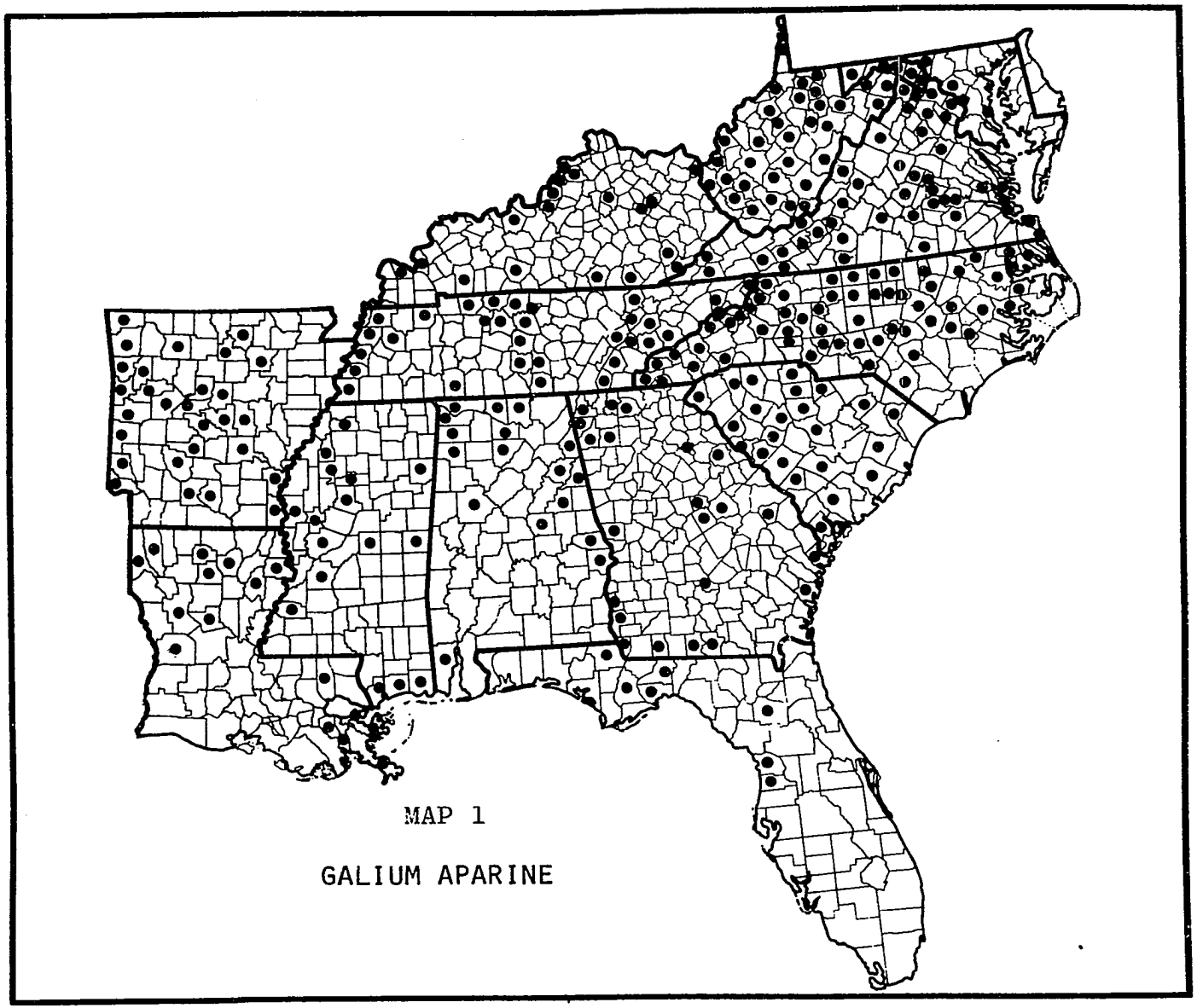
S.E. United States specimens examined: Six hundred and ninety-two sheets.

The upper leaf surface varies from sparsely to densely pubescent. Often these hairs are apically directed although at times there seems to be no uniform direction of growth.

No glabrous fruited material was found in the examination of material from the southeastern United States.

This species is frequently misidentified as G. triflorum. The differences between the two species are discussed under G. triflorum. Confusion is also frequently found between G. aparine and G. asprellum. Vegetatively, the major difference is found in the pubescence of the upper leaf surface. Once the plants have reached the flowering stage, differentiation may be made by the examination of the immature fruits.

In his recent work, R. J. Moore (1975) recognized both G. spurium and G. aparine in Canada. He presented



MAP 1

GALIUM APARINE

impressive evidence for such recognition. G. spurium was reported as 2n = 20 and with fruits, pollen grains, and flowers which were smaller than in G. aparine. Also, the leaves of G. spurium were reported to be more narrow than in G. aparine. Chromosome numbers for G. aparine were given as 2n = 22, 44, and 66. These same numbers (22, 44, and 66) are reported for G. aparine in portions of the southeastern United States (Radford, Ahles, and Bell, 1968). In this region measurements do not reveal a clear morphological division into a small-fruited - narrow-leaved group and a large-fruited - broad-leaved group. There are many morphological intermediates. Some specimens, however, fit Moore's description of G. spurium. Theoretically their chromosome number should be 2n = 20 although there is no report as such for the southeastern United States. Without a clear morphological separation and from a practical point of view, the supposed differences in chromosome numbers would not seem to be sufficient criteria to warrant separation into two or more taxa in this area.

Additional synonymy may be found in Moore (1975).

2. GALIUM ARKANSANUM Gray, Proc. Am. Acad. 19: 80. 1883.

G. latifolium var. β Torr. & Gray, Fl. N. Am. 2: 25. 1841.

Erect perennial, up to 6.3 dm tall (mostly 3 - 4.8 dm); stems diffuse, branching mostly at the upper nodes, glabrous

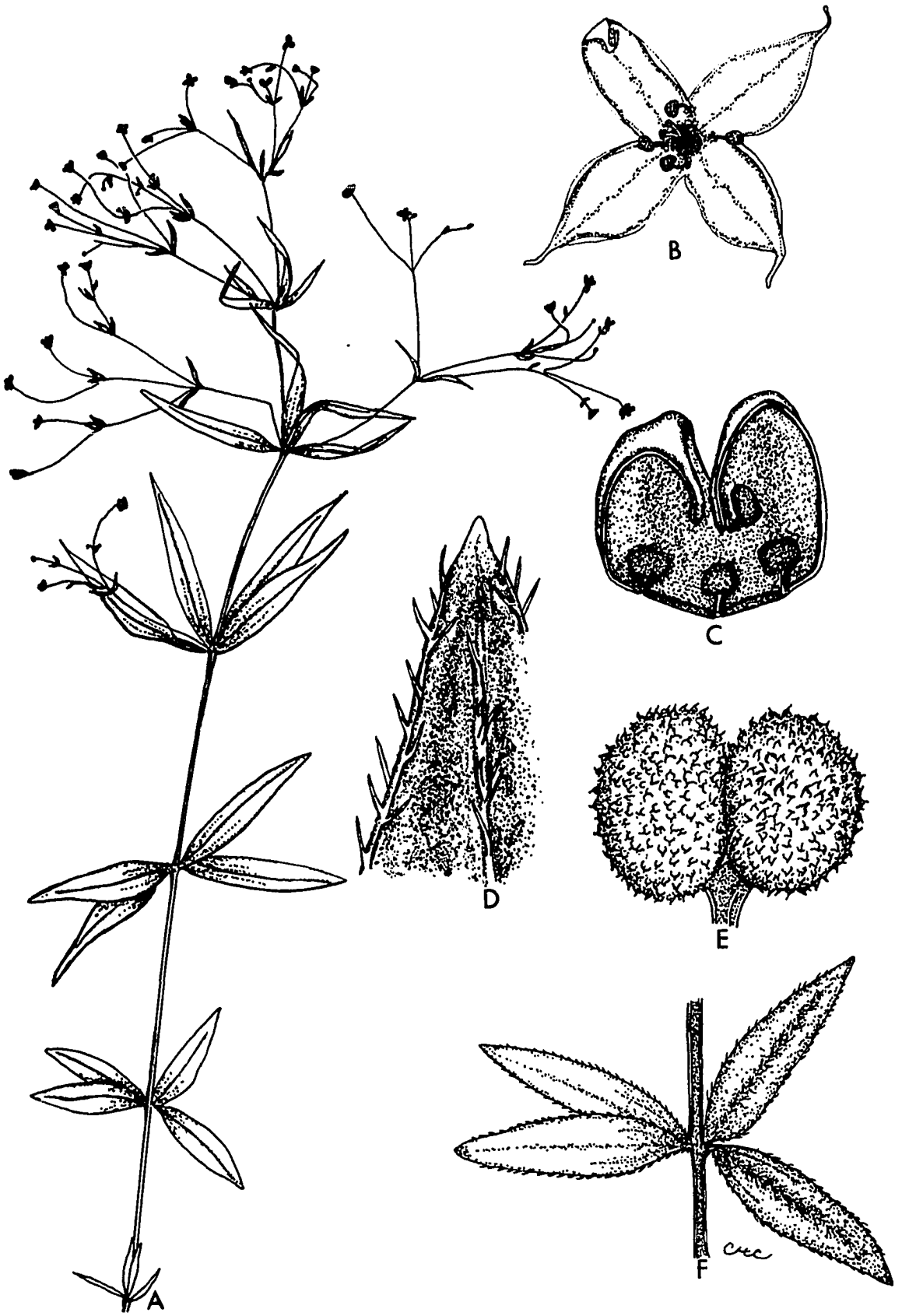
or with straight, spreading or ascending hairs up to 0.4 mm long on the angles; leaves in whorls of four, lanceolate to linear, acute, largest leaves (17.2) 26.2 - 37.8 (49.6) mm long and (2.2) 4.7 - 8.8 (10.4) mm wide, nerve one, prominent, lateral nerves absent or obscure, upper leaf surface with straight, ascending hairs up to 0.4 mm long on the midnerve (these hairs often appressed parallel to the midnerve), lower leaf surface glabrous or with straight, spreading or ascending hairs up to 0.6 mm long on the midnerve (these hairs sometimes curved rather than straight), secretory glands scattered over the lower surface, margins with straight, spreading or slightly ascending hairs up to 0.5 mm long; inflorescence a compound cyme, two or three times branched, mostly terminal, some lateral; flowers pedicellate, pedicels glabrous or with stiff, antrorse hairs up to 0.2 mm long; corollas four-lobed, usually purple, lobes narrowly and abruptly caudate (the appendage up to 0.8 mm long, often folded inside or broken off), usually (0.8) 1 - 1.3 (1.5) mm long excluding the appendage and (0.8) 0.9 - 1.1 (1.4) mm wide, outer surface glabrous or beset with stiff, straight hairs; fruits appearing glabrous, but roughened and papillate, the projections with very minute scabrous hairs mostly 0.05 mm long, each mature carpel (1.6) 2.1 - 2.7 (3.4) mm long and (1.6) 1.7 - 2.3 (2.6) mm wide.—Fig. 4.

Type: "Missouri (or Arkansas?) Dr. Engelmann!"

Range: Missouri, Arkansas, and Oklahoma (Southeastern United States, Map 2).

FIGURE 4

GALIUM ARKANSANUM: A, habit x 1; B, flower x 15; C, galled flower x 29; D, lower leaf surface, margin, and apex x 25; E, fruit x 13; F, leaf whorl x 2. A, B, F from P. L. Redfearn & D. M. Eggers 14900 (FSU), and C, D, E from D. Demaree 29910 (GH).


A
B
C
D
E
F

Flowering - Fruiting time: Mostly May through August, sometimes September and October.

Habitat: Frequent in dry, rocky, open hillsides and woods; sometimes along limestone ridges and rarely along creek banks.

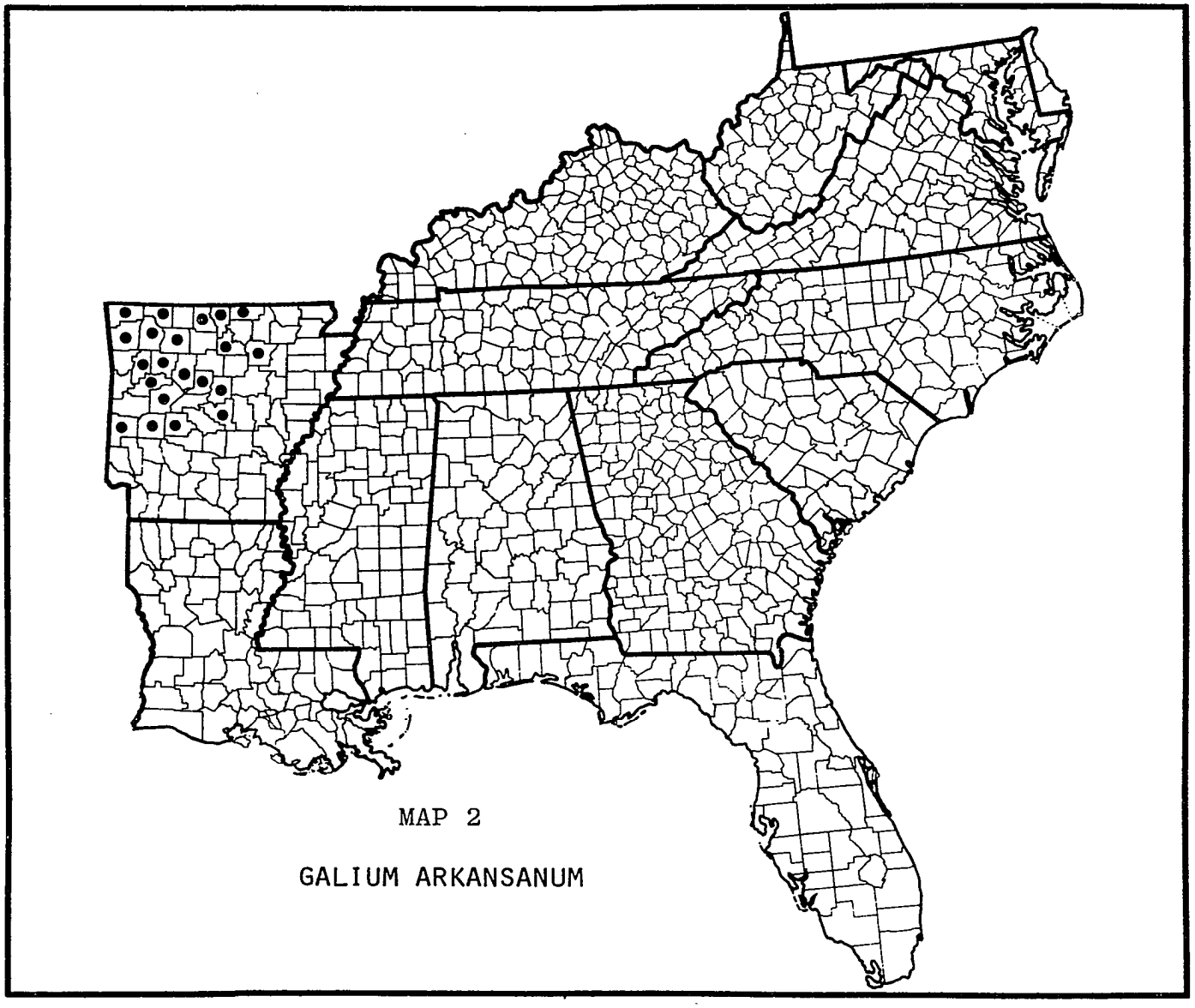
S.E. United States specimens examined: One hundred and sixty-two sheets.

In his description of G. arkansanum, Gray (1883) referred to "a linear-leaved form collected at the Hot Springs of Arkansas by Dr. Foreman of Washington." The variation in leaf width in this species does not accompany consistently and specifically other morphological characters or geographical distributions. In the Hot Springs area (Garland County) one can still find linear-leaved specimens, and these also have been found frequently in Montgomery, Johnson, and Carroll Counties.

The presence or absence of hairs on the outer surface of the corolla lobes is another character which, again, is not specifically associable with other characters; however, on any one plant, the flowers will have either all glabrous or all pubescent outer corolla lobes.

The lateral nerves are generally absent or obscure, but when they are present, they often have a pubescence similar to that on the midnerve.

This species resembles G. latifolium, which has generally longer and wider leaves than in this species.



MAP 2

GALIUM ARKANSANUM

As mentioned above, the lateral nerves in the leaves of G. arkansanum are generally absent or obscure, whereas they are present in G. latifolium. The fruits in G. latifolium are not roughened or papillate as in G. arkansanum. Also, the geographical ranges of the two species do not overlap.

Galled flowers may be found frequently in this species.

3. GALIUM ASPRELLUM Michx., Fl. Bor. Am. 1: 78. 1803.

Much branched, spreading perennial, up to 16.5 dm tall (mostly 6.2 - 13.7 dm); stems usually branching once or twice at a node, retrorsely scabrous on the angles with hairs 0.2 mm long or less; leaves in whorls of six, mostly oblanceolate, sometimes elliptical, cuspidate, largest leaves mostly (5.6) 10.2 - 15.2 (24.8) mm long and (2.2) 2.8 - 4.2 (5.4) mm wide, nerve one, prominent, upper leaf surface glabrous or with a few appressed, apically directed hairs near the margins and sometimes on the midnerve, lower leaf surface retrorsely scabrous on the midnerve, otherwise glabrous and lacking secretory glands, margins retrorsely scabrous (hairs on both the midnerve and margins 0.2 mm long or less); inflorescences primarily on the upper half of the plant, thus appearing terminal, the axillary inflorescences forming cymose panicles; flowers on glabrous pedicels; corollas four-lobed, white or yellowish, minute, lobes usually acute (if caudate the appendage not over 0.16 mm long), (0.6) 0.8 - 1 (1.2) mm long and (0.4) 0.5 - 0.8 (1.1) mm wide, glabrous; fruits glabrous, each mature carpel mostly (1.4) 1.6 - 1.9 (2.2) mm long and (0.9) 1.1 - 1.5 (1.8) mm wide.—Fig. 5.

FIGURE 5

GALIUM ASPRELLUM: A, habit x 1; B, galled flower x 27; C, flower x 22; D, fruit x 21; E, lower leaf surface, margin, and apex x 17; F, leaf whorl and stem x 3; G, inflorescence x 1. A from J. D. Smith s.n., Sept. 19, 1881 (US), B, C from E. S. Steele & Mrs. Steele 293 (GH), D from J. M. Greenman 308 (GH), and E, F, G from R. C. Spangler s.n., Sept. 15, 1923 (WVA).


A
B
C
D
E
F
G

Type locality: "Hab. in septentrionalibus Canadae."

Range: In Canada from Ontario east to Newfoundland and Nova Scotia; in the United States from New England south to North Carolina and Tennessee, north to Illinois, Iowa, and Minnesota (Southeastern United States, Map 3; this species is known to occur in Delaware; however, no county localities could be determined for use on the distribution map).

Flowering - Fruiting time: Rarely June, usually July through September.

Habitat: Frequent on banks of streams, creeks, and rivers; also in bogs, marshes, swamps, meadows, waste places, swales, and thickets; occasional in alluvial woods.

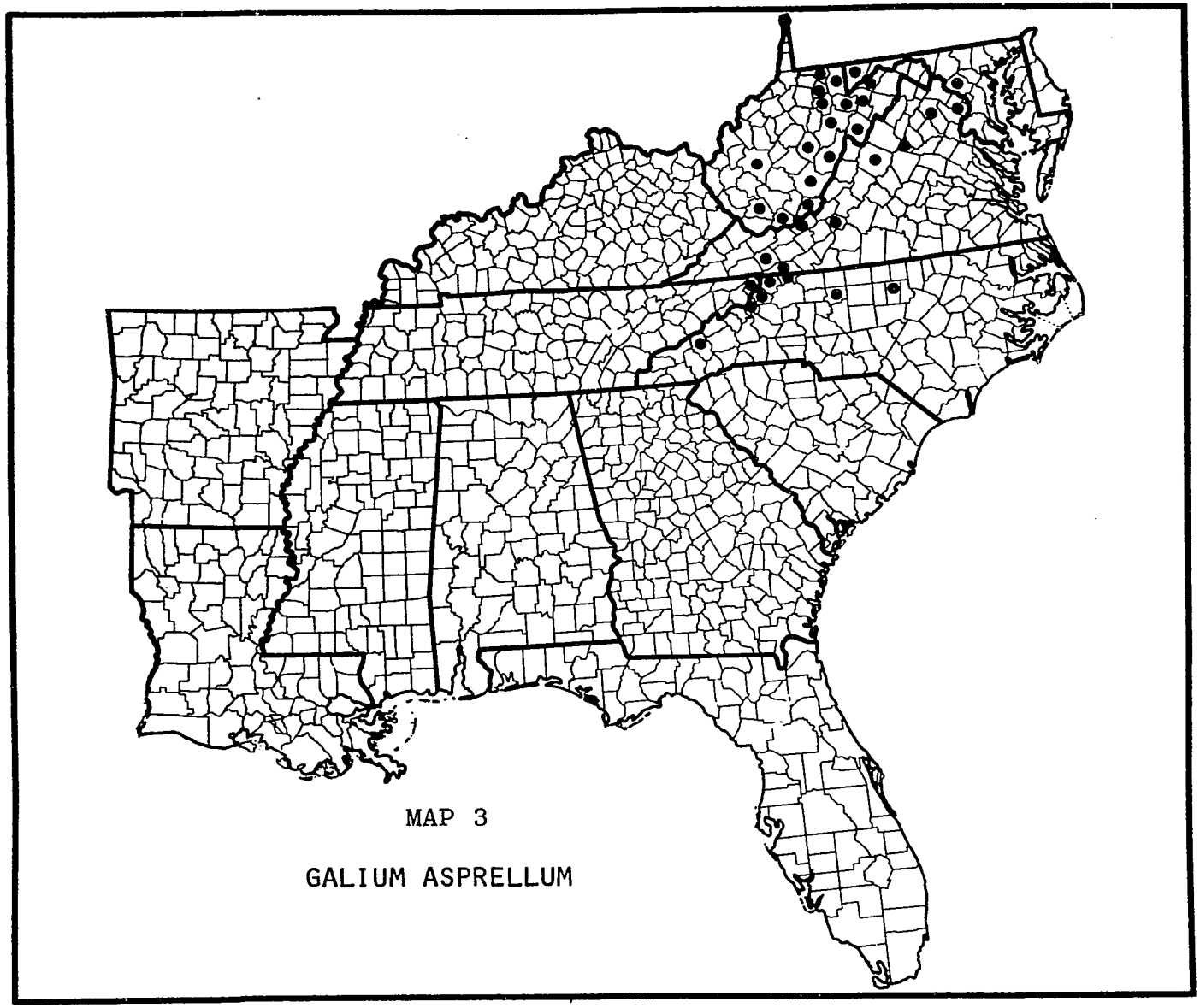
S.E. United States specimens examined: One hundred and nineteen sheets.

Due to the retrorse-scabrous condition of both the stems and leaves, this species is often found in tangled mats and climbing on other vegetation.

Rarely one or two short, stiff hairs, which can be detected only under magnification, may be found on the fruits.

This species has been misidentified as G. triflorum, G. mollugo, G. concinnum, and G. aparine. Under each of these four species the characters which differentiate them from G. asprellum are discussed.

Galled flowers are found frequently in this species.



MAP 3

GALIUM ASPRELLUM

4. GALIUM BOREALE L., Sp. Pl. 1: 108. 1753.

G. hyssopifolium Hoffm., Deutschl. Fl. ed. 2. 1: 71. 1800.

G. septentrionale Roem. & Schult., Syst. Veg. 3: 253. 1818.

G. strictum Torr., Cat. Pl. City N. Y. 23. 1819.

G. boreale α. hyssopifolium (Hoffm.) DC., Prodr. 4: 600. 1830.

G. boreale β. intermedium DC., Prodr. 4: 601. 1830.

G. boreale γ. scabrum DC., Prodr. 4: 601. 1830.

G. boreale α. typicum Beck von Man., Fl. Nied. Österr. 2: 1121. 1893.

G. boreale var. linearifolium Rydb., Mem. N. Y. Bot. Gard. 1: 375. 1900. Type: Rydberg 134, Pumpkin Seed Valley, Nebraska, 1891.

G. boreale ssp. septentrionale (R. & S.) Hara, J. Fac. Sci. Univ. Tokyo, Bot. 6: 378. 1956.

G. boreale ssp. septentrionale (R. & S.) Iltis, Rhodora 59: 40. 1957.

G. boreale f. hyssopifolium (Hoffm.) Boivin, Nat. Canad. 93: 433. 1966.

Upright perennial, up to 8.2 dm tall (mostly 3.8 - 6.3 dm); stems usually branching once or twice at a node, the leafy, frequently sterile, branches bearing leaves somewhat smaller than on the main stem, glabrous to pubescent on the angles and sometimes on the sides with retrorsely

scaberulous or straight, spreading or descending hairs (these hairs scarcely 0.05 mm long if scaberulous and up to 0.5 mm long when straight), glabrous or occasionally densely pubescent at the nodes; leaves in whorls of four, linear to lanceolate, obtuse or nearly acute but with rounded tips, largest leaves mostly (18.7) 22 - 39.8 (54.4) mm long and (2.2) 2.8 - 6.6 (9.4) mm wide, midnerve prominent, the two lateral nerves present but usually less conspicuously so, upper leaf surface usually glabrous or sometimes with short, appressed, apically directed hairs on the midnerve or the surface rarely minutely scabrous, lower leaf surface glabrous or pubescent on the nerves with short, scabrous or long, straight, spreading or ascending hairs (these hairs up to 0.4 mm long when straight), secretory glands scattered over the lower surface, margins frequently revolute and pubescent with mostly straight, spreading or ascending hairs up to 0.4 mm long (these hairs often slightly curved or sometimes scabrous and apically directed); inflorescences of numerous flowers primarily on the upper third of the plant, thus appearing terminal, the axillary inflorescences forming cymose panicles; flowers on glabrous pedicels, showy; corollas four-lobed, white, lobes slightly or broadly apiculate, usually (1.1) 1.3 - 1.6 (1.7) mm long and (0.7) 0.8 - 1 (1.1) mm wide, glabrous; fruits glabrous, glabrate, or pubescent with straight hairs up to 0.3 mm long or with short, curved hairs up to 0.2 mm long, each mature carpel

(0.7) 1.3 - 1.7 (1.8) mm long and (0.7) 0.8 - 1.1 (1.2) mm wide.—Fig. 6.

Type locality: "Habitat in Europae borealis pratis."

Range: Circumpolar; in the eastern United States south to Virginia, Kentucky and Missouri (Southeastern United States, Map 4; this species is known to occur in Kentucky; however, no county localities could be determined for use on the distribution map.).

Flowering - Fruiting time: Late May through July, occasionally August and September.

Habitat: In woods and along creeks and rivers; frequently associated with limestone and shale bluffs.

S.E. United States specimens examined: Forty-three sheets.

On one specimen from Virginia, the outer surface of some corolla lobes was pubescent. Except in this one instance, the glabrous corolla lobe was constant.

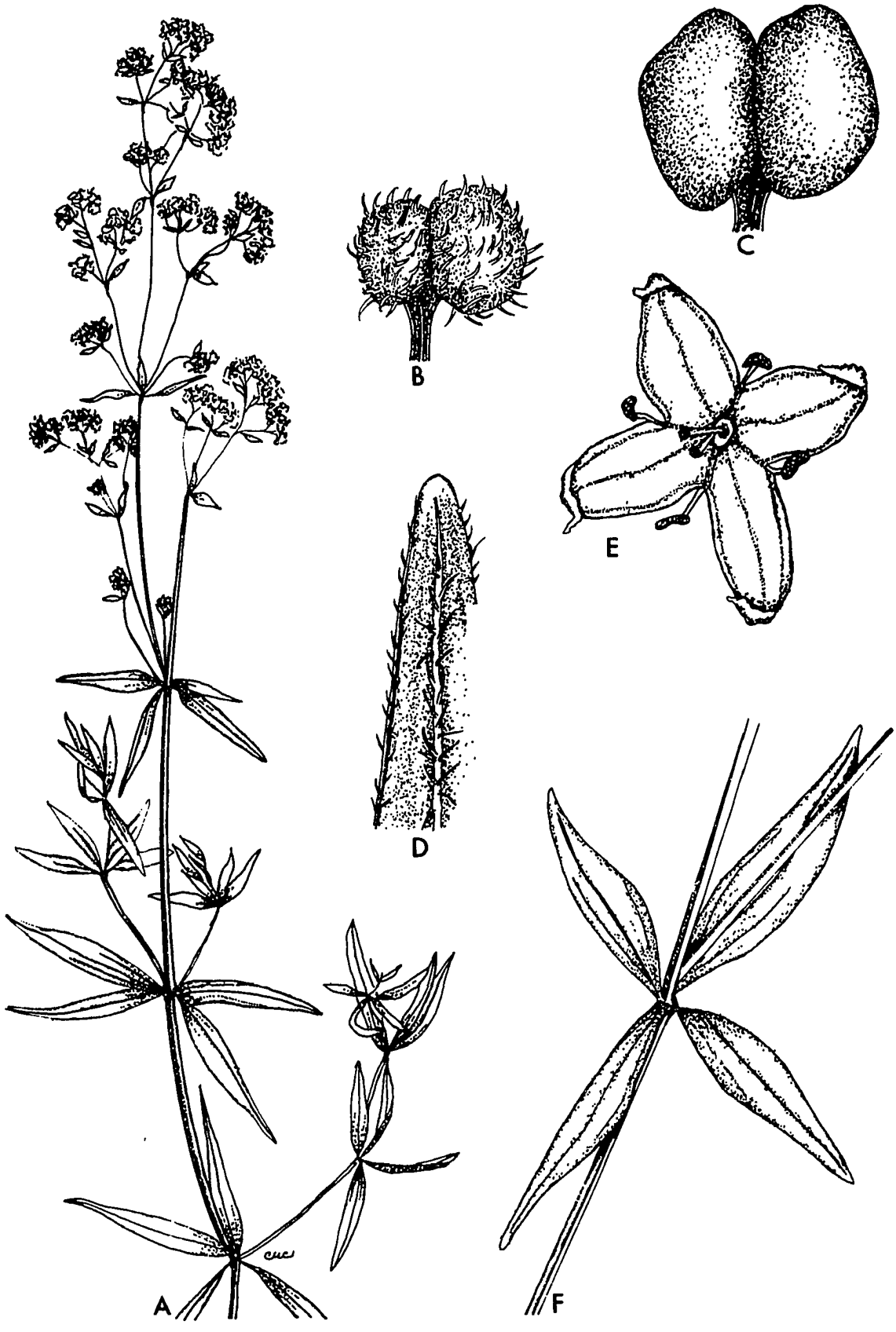
Galled flowers were found only on one specimen from West Virginia.

The pubescence of the fruit is perhaps the most difficult character to interpret in this highly variable species. Three varietal types based on fruit pubescence are recognized frequently in the European and American literature.

In the southeastern United States, it is sometimes difficult to distinguish with certainty between these types.

FIGURE 6

GALIUM BOREALE: A, habit x 1; B, pubescent fruit x 25; C, glabrous fruit x 25; D, lower leaf surface, margin, and apex x 17; E, flower x 16; F, leaf whorl x 4. A, D, E, F from C. A. Lawson & D. Dotts 1213 (OKL), B from C. E. Stevens 3876 (LONG), and C from H. A. Davis & Mrs. Davis 4740 (WVA).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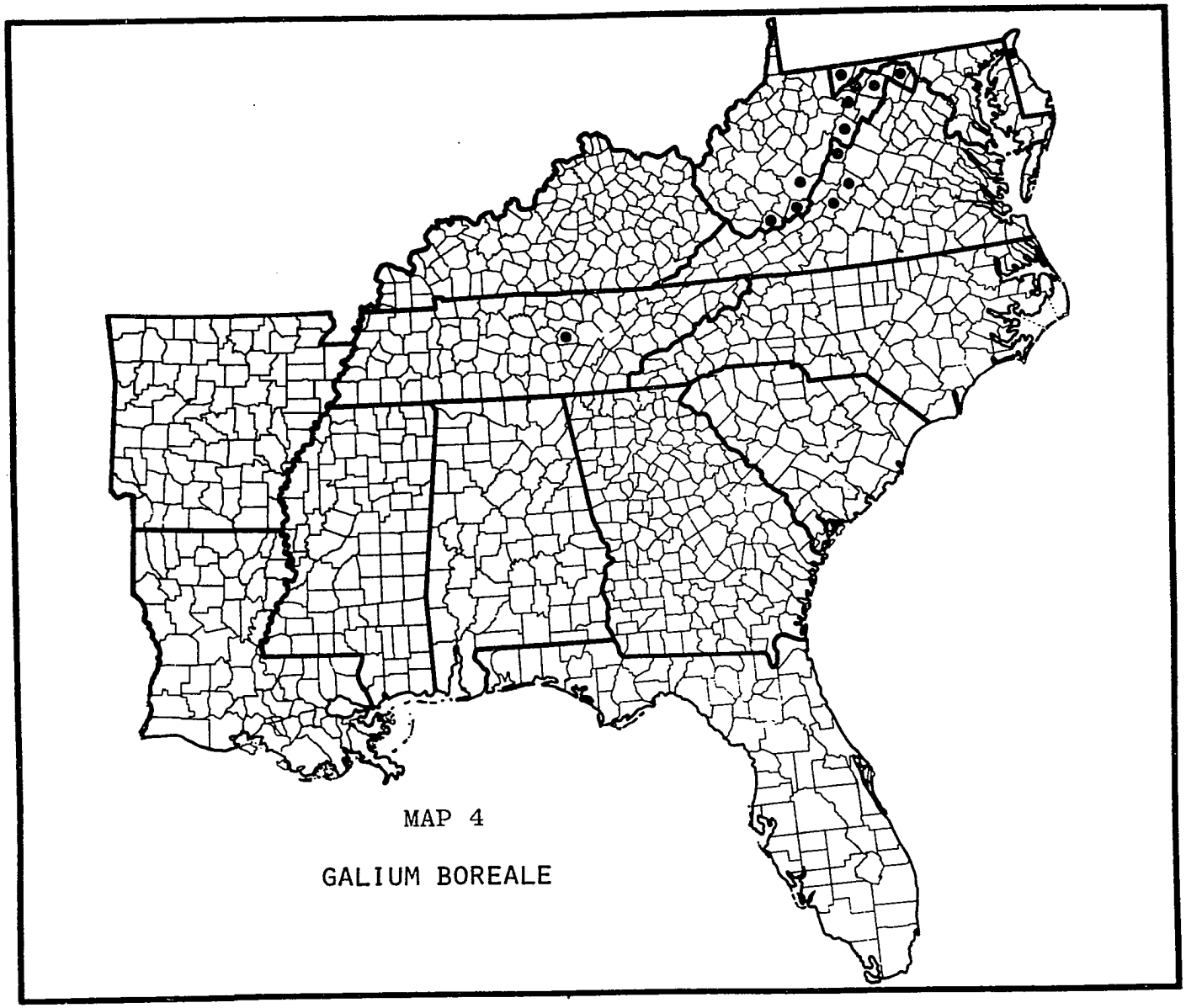
For example, there appears to be some gradation between a glabrate specimen of var. hyssopifolium and a sparsely pubescent specimen of var. intermedium. The same problem of interpretation may occur in separating some specimens of var. intermedium from var. boreale.

Where material has been collected abundantly in the Southeast in states such as West Virginia, all three types of fruit pubescence can be found. In Virginia plants with at least two types of fruit pubescence have been collected. There appears to be no distinct geographic range for these plants having differing fruit pubescence with sporadic occurrences of all three.

The lack of geographic separation, coupled with the gradation in fruit pubescence and the need to examine European material, brings about the decision to consider at present this taxon only at the species level.

Löve and Löve (1954) recommended, based on chromosome numbers and morphological differences, that the tetraploid (2n = 44), Eurasiatic type of G. boreale be segregated from the hexaploid (2n + 66), American - Asiatic type. While chromosome counts of plants from the southeastern United States support the counts given by Löve and Löve (2n = 66), there is no consistent agreement on morphological differences such as pubescence of the nodes, width of the corolla, and length of fruits. Since morphological differences between the Eurasiatic type and the southeastern



MAP 4

GALIUM BOREALE

United States type do not appear so clear-cut, no taxonomic segregation is proposed at this time.

Galium boreale is rarely misidentified. An occasional specimen has been confused as G. latifolium or G. circaezans.

5. GALIUM CIRCAEZANS Michx., Fl. Bor. Am. 1: 80. 1803.

Erect perennial, up to 5.2 dm tall (mostly 2.3 - 3.7 dm); stems simple, branching at the base, glabrous or with spreading hairs up to 0.7 mm long on the angles at least at the nodes; leaves in whorls of four, ovate or elliptical, minutely or inconspicuously acuminate or occasionally the tips rounded, largest leaves (11.8) 19.6 - 31.5 (44.4) mm long and (2.6) 9.6 - 15.1 (23.2) mm wide, nerves three, the lateral nerves usually prominent, upper leaf surface glabrous to pilose, the nerves with ascending or spreading hairs up to 0.5 mm long (these hairs sometimes appressed and parallel to the nerves), lower leaf surface glabrous to densely pilose, the nerves glabrous or with spreading hairs up to 0.7 mm long, secretory glands scattered over the lower surface, margins with stiff, straight ascending hairs up to 0.7 mm long; inflorescence a helicoid cyme; flowers sessile or subsessile, each subtended by one or two small bracts, remote; corollas four-lobed, light-green to light-yellow, lobes abruptly caudate (the appendage up to 0.4 mm long, often folded inside or broken off), usually (0.5) 0.6 - 0.9 (1.2) mm long excluding the appendage and (0.5) 0.6 - 0.8 (1) mm wide, glabrous or pubescent on the outer surface with hairs up to

0.4 mm long; fruits pubescent with uncinate hairs usually 0.8 - 1.2 mm long, each mature carpel (1.6) 1.9 - 2.5 (3.4) mm long and (1.2) 1.6 - 2.2 (3) mm wide.—Fig. 7.

Fernald (1937) described what he considered to be two well-defined geographic varieties of G. circaezans. The plants of the southern range, which proved to be the typical variety, were characterized by small leaves which were glabrous beneath or sparsely short-hispid on the nerves. Larger leaves with the nerves long-hirsute beneath described the northern variety. Plants with the latter characters were called by Fernald variety hypomalacum.

The southern extreme was reported to meet the northern in Virginia and locally elsewhere. The range now given in Fernald (1950) for the southern extreme is "Fla. to Tex., n. to Va. and locally to s. N.E., N.Y., Ky. and Mich." For the northern it is given as "s. Que. to Minn. and Neb., s. to s. N.E., Va., uplands of N.C., Ky., Mo. and Tex." The overlap in range occurs, then, in much of the northern half of the southeastern United States.

In examining specimens from Maryland, West Virginia, Virginia, Kentucky, North Carolina, Tennessee, and Arkansas material fitting both varieties was found. Material from South Carolina, Florida, Georgia, Alabama, Mississippi, and Louisiana mostly resembled the typical variety. Still an occasional plant of variety hypomalacum could be found.

Variety circaezans has been collected far more than

FIGURE 7

GALIUM CIRCAEZANS: A, habit x 1; B, flower x 18; C, fruit x 16; D, pubescent lower leaf surface, margin, and apex x 4; E, glabrous lower leaf surface, margin, and apex x 4; F, leaf whorl x 1.5. A, C, F from R. M. Harper 34 (US), B, E from C. A. Lawson & D. Dotts 1179 (OKL), and D from H. E. Ahles 42522 (NCU).

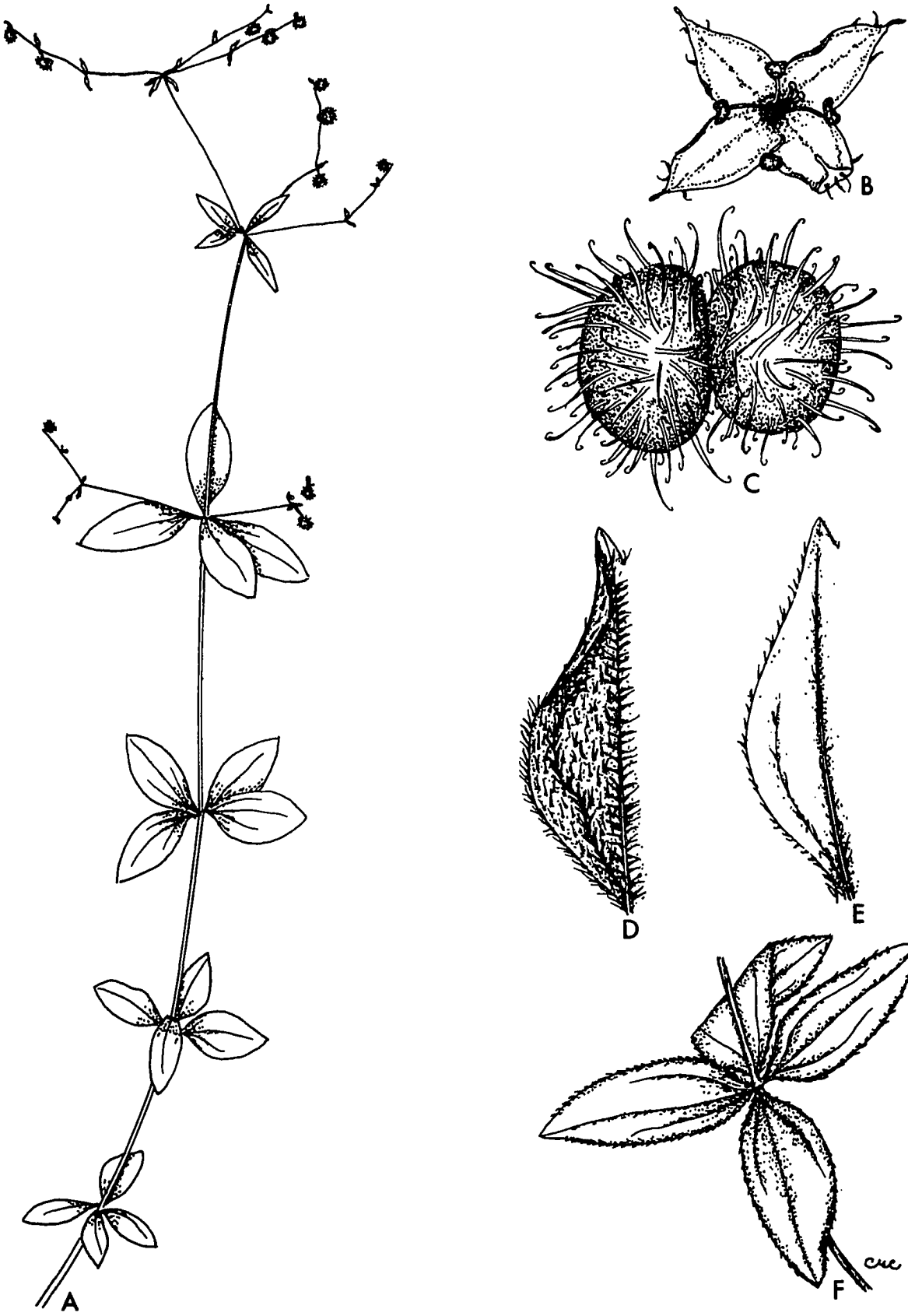

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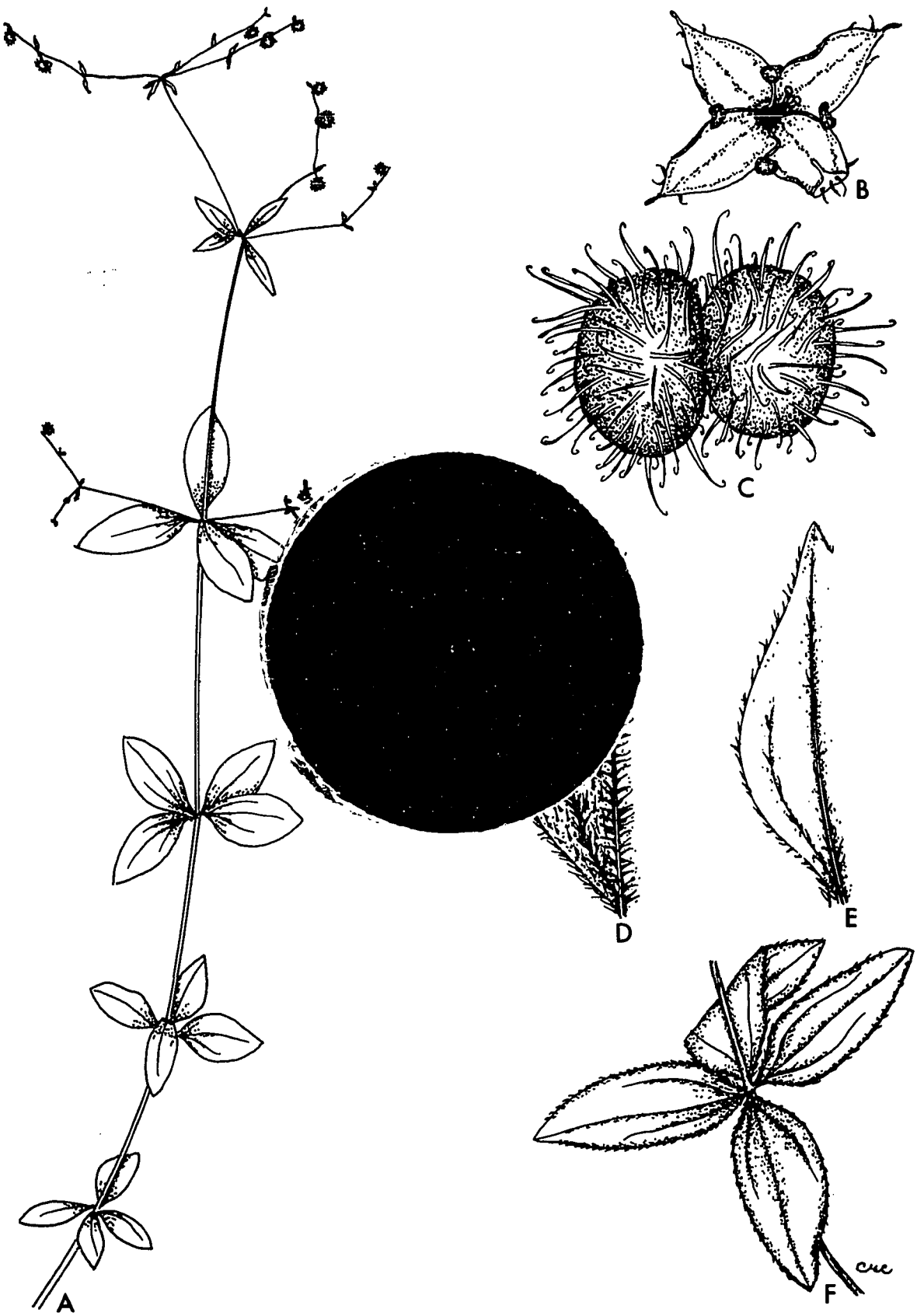
FIGURE 7

GALIUM CIRCAEZANS: A, habit x 1; B, flower x 18; C, fruit x 16; D, pubescent lower leaf surface, margin, and apex x 4; E, glabrous lower leaf surface, margin, and apex x 4; F. leaf whorl x 1.5. A, C, F from R. M. Harper 34 (US), B, E from C. A. Lawson & D. Dotts 1179 (OKL), and D from H. E. Ahles 42522 (NCU).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variety hypomalacum in the southeastern United States. The usual plants of variety circaezans have leaf undersurfaces which are sparsely short-hispid on the nerves (Fig. 8 A) or glabrous (Fig. 8 B). Plants with leaves as in Fig. 8 A are referred to below as the "usual variation." There are, however, variations from the usual plants, and while the following variations are not abundant, they may be found occasionally in the northern half of the southeastern United States.

1) Leaf undersurface short-hispid on the nerves but slightly pubsecent on the surface (Fig. 8 C).

2) Leaf undersurface short-hispid on the nerves and pubescent on the surface near the apex (Fig. 8 D).

3) The usual variation and variation #1 on the same plant (Fig. 8 A & C).

4) The usual variation and variation #2 on the same plant (Fig. 8 A & D).

5) Leaf undersurface short-hispid on the nerves or glabrous on the same plant (Fig. 8 A & B).

All these variations, except for plants with completely glabrous leaves, have as a common denominator leaf undersurfaces which are short-hispid on the nerves. When emphasis is placed on the length of the hairs on the nerves of the lower leaf surface rather than on the pubescence of this surface, the usual variation and the variations mentioned above, for the most part, segregate geographically from variety hypomalacum as variety circaezans.

Variety hypomalacum with its leaves long-hirsute on the nerves of the lower leaf surface is usually also appressed pubescent on this surface (Fig. 8 E). Occasionally the following variations were found:

1) Leaf undersurface long-hirsute on the nerves but the surface glabrous (Fig. 8 F).

2) Leaf undersurface long-hirsute on the nerves with the surface glabrous or appressed pubescent on the same plant (Fig. 8 E & F).

Again, the constant character is the type of pubescence on the nerves of the leaf undersurface.

Mixed collections of both varieties have been made in the southeastern United States. These collections are not abundant, however.

The hairs on the stem angles and nerves on both the lower and upper leaf surfaces are straight to slightly curved.

Specimens of this species are occasionally misidentified as G. pilosum. Differentiation is possible by comparing, for example, the inflorescence types, leaf apices, or leaf pubescence. More frequently, however, in areas where their ranges overlap, G. circaezans and G. lanceolatum are confused. This confusion arises most easily in vegetative material when the leaf undersurface of G. circaezans is glabrous or sparsely pilose and/or sparsely short-hispid on the nerves. The other variations in leaf pubescence found in G. circaezans are not so similar to those found in

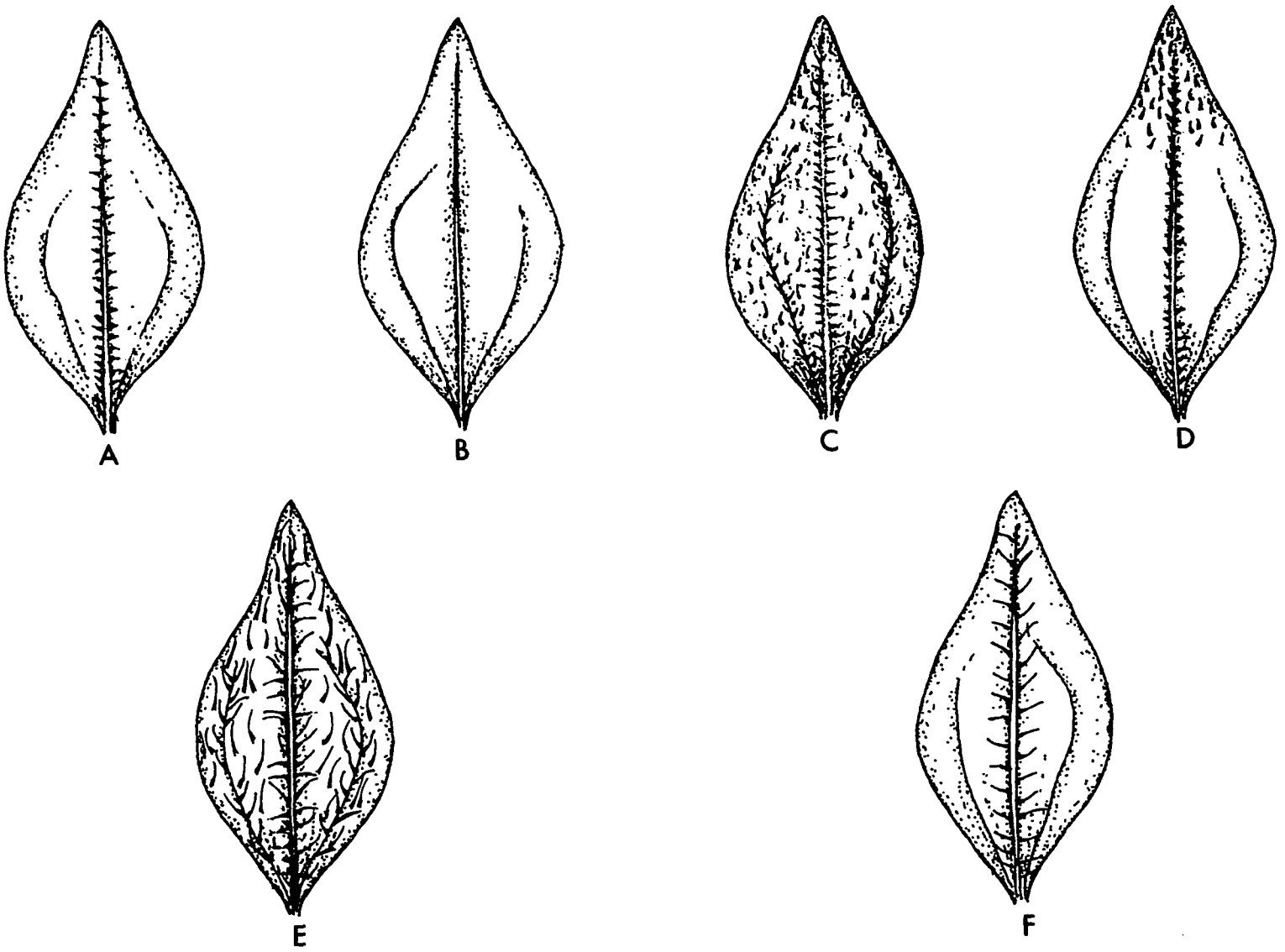
FIGURE 8

VARIATIONS IN PUBESCENCE

ON LOWER LEAF SURFACE

A - D *Galium circaezans* var. *circaezans*

E - F *Galium circaezans* var. *hypomalacum*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G. lanceolatum. Further comparisons and differentiation of these two species are discussed under G. lanceolatum.

KEY TO VARIETIES

Nerves on lower leaf surface glabrous or short-hispid with hairs 0.3 mm or less long; lower leaf surface usually glabrous. . . . 5a. G. circaezans var. circaezans

Nerves on lower leaf surface long-hirsute with longest hairs more than 0.3 mm and up to 0.7 mm long; lower leaf surface usually appressed pilose. . . . . 5b. G. circaezans var. hypomalacum

5a. G. CIRCAEZANS VAR. CIRCAEZANS

G. circaezans Michx., Fl. Bor. Am. 1: 80. 1803.

G. bermudense L., Sp. Pl. 1: 105. 1753, pro parte. For explanation of this being a nomen confusum, see Weatherby and Blake (1916).

G. boreale sensu Walt., Fl. Carol. 87. 1788, not L.

G. brachiatum sensu Muhl., Cat. ed. 1. 16. 1813, not Pursh.

G. circaeoides R. & S., Syst. 3: 256. 1818.

G. rotundifolium δ. circaezans (Michx.) O. Ktze., Rev. Gen. 1: 282. 1891.

G. circaezans var. glabrum Britt., Bull. Torr. Bot. Cl. 21: 32. 1894. Type: C. H. Peck, near Whitehall, N. Y., July, 1892 (NY).

G. circaezans var. glabellum Britt., Mem. Torr. Bot. Cl. 5: 303. 1894 (substitute name for G. circaezans var. glabrum Britt.).

Nerves on lower leaf surface glabrous or short-hispid with hairs 0.3 mm or less long; lower leaf surface usually glabrous, but occasionally variably pubescent.

Type locality: "Hab. in Carolina."

Range: Mostly southeastern and central eastern United States, west to Missouri, Kansas, Oklahoma, and Texas (Southeastern United States, Map 5; this variety is known to occur in Delaware; however, no county localities could be determined for use on the distribution map).

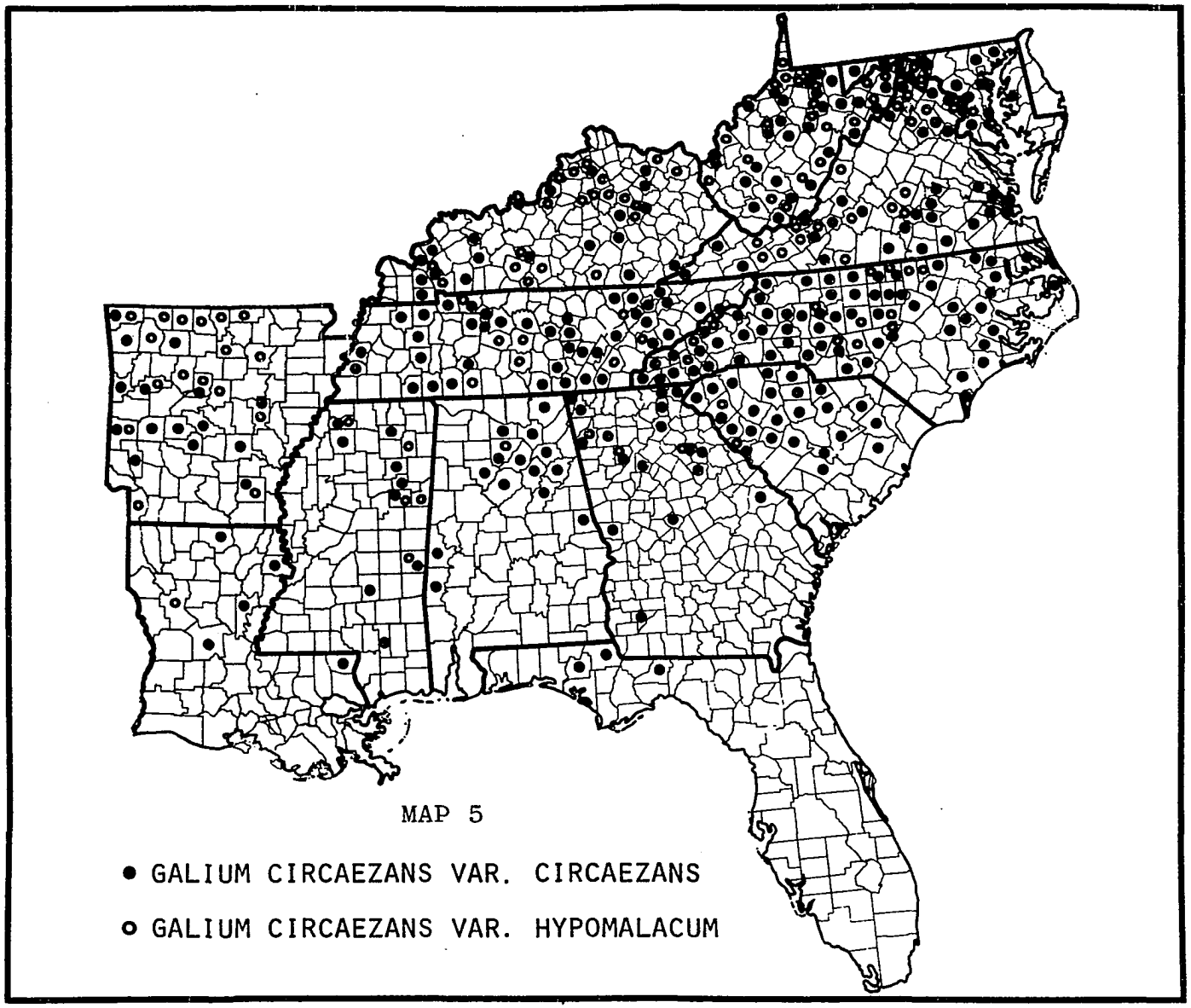
Flowering - Fruiting time: Mostly May through August, occasionally September.

Habitat: Frequent in rich, deciduous woods or pine-hardwood forests; occasionally along creeks and river bluffs; infrequent in roadside ditches, wet meadows, and swamps. Often associated with rocky soil of sandstone, shale, or limestone.

S.E. United States specimens examined: Five hundred and eighty-seven sheets.

5b. G. CIRCAEZANS VAR. HYPOMALACUM Fern., Rhodora 39: 450. 1937.

Nerves on lower leaf surface long-hirsute with hairs more than 0.3 mm and up to 0.7 mm long; lower leaf surface usually appressed pilose, but occasionally glabrous.



MAP 5

● GALIUM CIRCAEZANS VAR. CIRCAEZANS

o GALIUM CIRCAEZANS VAR. HYPOMALACUM

Type: F. E. McDonald, open dry woods, Peoria, Illinois, July, 1903 (GH).

Range: Quebec, mostly northeastern and central eastern United States, west to Minnesota, Nebraska, Oklahoma, and Texas (Southeastern United States, Map 5; this variety is also known to occur in Delaware; however, no county localities could be determined for use on the distribution map).

Flowering - Fruiting time: Mostly May through August, rarely April, occasionally September.

Habitat: Similar to that of variety circaezans.

S.E. United States specimens examined: Two hundred and eighty-eight sheets.

6. GALIUM CONCINNUM Torr. & Gray, Fl. N. Am. 2: 23. 1841.

Erect or ascending, much branched perennial, up to 4.6 dm tall (mostly 2.4 - 3.8 dm); stems commonly branching once at a node, nearly glabrous or sparsely retrorse-scabrous on the angles (these hairs minute, 0.1 mm or less long); leaves in whorls of six or occasionally reduced to four in the upper branches, linear to narrowly oblong, elliptical, or oblanceolate, cuspidate, largest leaves mostly (7.8) 11.3 - 15.9 (21) mm long and (1) 1.6 - 2.4 (3.4) mm wide, nerve one, prominent, leaf surfaces glabrous or rarely with an occasional hair on the midnerve, secretory glands absent on the lower surface, margins sometimes revolute, glabrous or antrorsely scabrous (these hairs 0.1 mm or less long and

occasionally retrorsely scabrous near the base of the leaf); inflorescence a compound cyme, two or three times branched, mostly terminal, some lateral; flowers on glabrous pedicels; corollas minute, four-lobed, white, lobes acute or caudate (the appendage up to 0.2 mm long), usually (0.6) 0.7 - 1 (1.2) mm long and (0.5) 0.6 - 0.8 (1) mm wide, glabrous; fruits glabrous, each mature carpel mostly (1.2) 1.6 - 2.3 (2.4) mm long and (0.8) 1.2 - 1.8 (2) mm wide.—Fig. 9.

Type: "Dry open woods and hill-sides, Michigan, abundant near Ann Arbor! Blue Lick, Kentucky, Dr. Short!"

Range: Pennsylvania south to Kentucky, west to Arkansas, Oklahoma, Kansas, and Missouri, and north to Minnesota (Southeastern United States, Map 6).

Flowering - Fruiting time: Late May through August, sometimes September.

Habitat: Frequent in deciduous and pine woods, along creek banks, and occasionally along open roadsides. Often associated with shale, limestone, and sandstone.

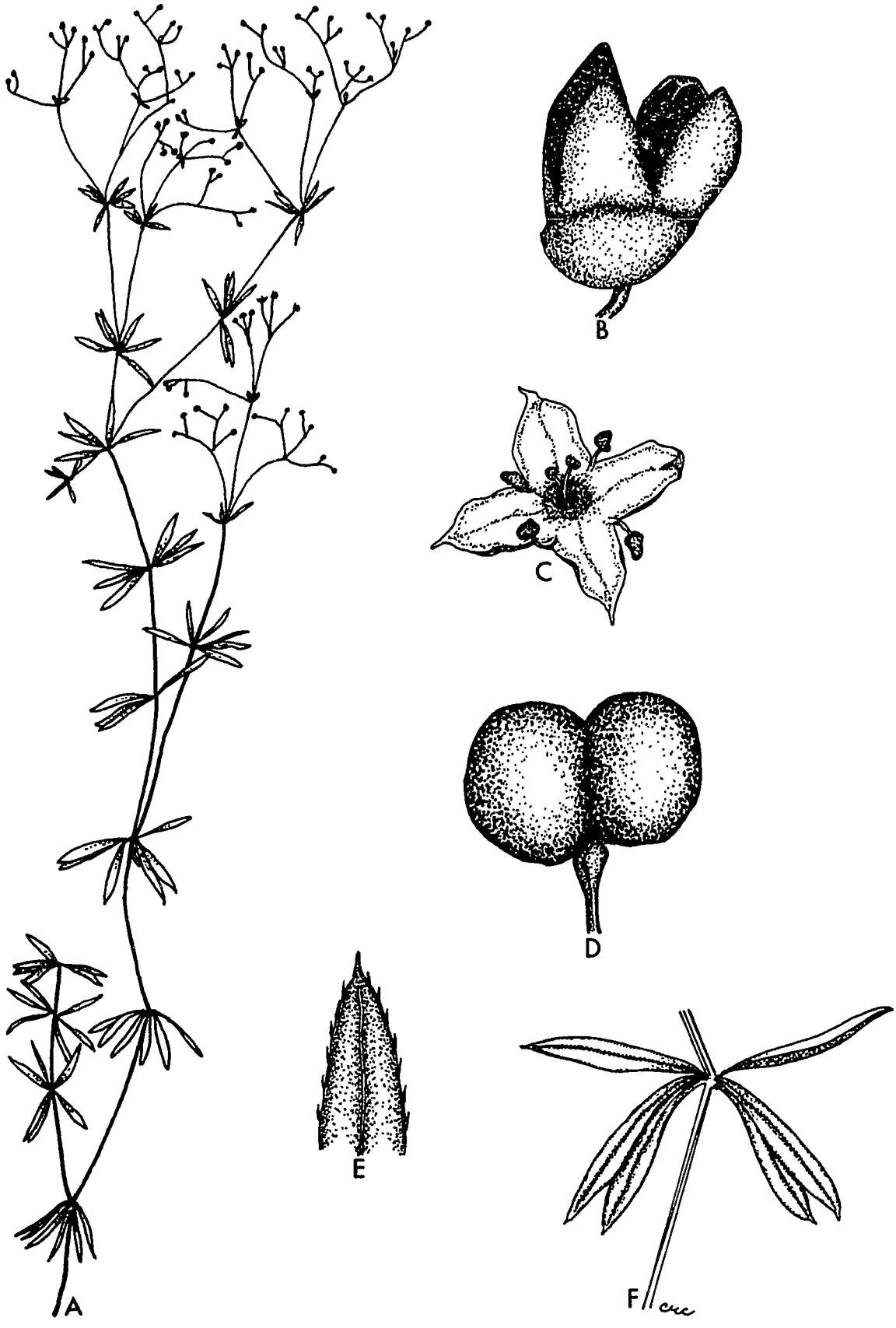
S.E. United States specimens examined: One hundred and fifty-eight sheets.

There is a tendency for the margins on the lower part of the leaf to be less scabrous than those on the upper part of the leaf.

The corolla lobes were originally described as "white" (Torrey and Gray, 1841) and are also stated to be white on many labels; however, no flowering material was examined in this study.

FIGURE 9

GALIUM CONCINNUM: A, habit x 1; B, galled flower x 18; C, flower x 18; D, fruit x 17; E, upper leaf surface, margin, and apex x 17; F, leaf whorl x 4. A, E, F from O. W. Gupton 4045 (NCU), B, C from F. W. Hunnewell 5337 (GH), and D from Wm. M. Canby s.n., Aug. 1858 (NY).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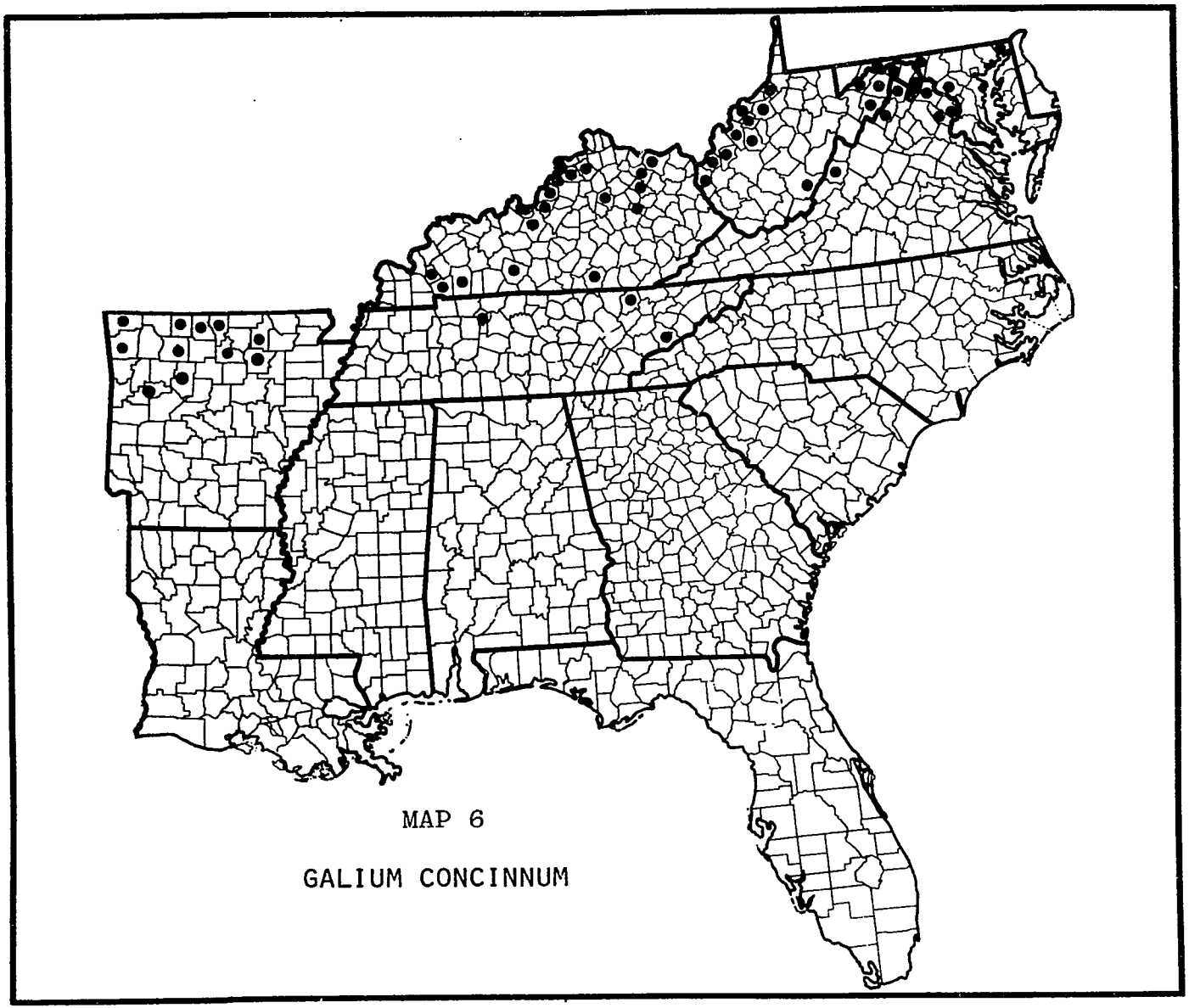
Galium concinnum resembles G. mollugo in the vegetative state. A comparison of these two species is presented under G. mollugo. Similarity may also be seen between G. concinnum and four other species: G. tinctorium, G. obtusum, G. asprellum, and G. parisiense. The obtuse leaf apices of G. tinctorium and G. obtusum may be used to distinguish them from G. concinnum with cuspidate leaf apices. The leaves in G. concinnum are usually longer and wider than in G. parisiense. Glabrous fruits are found in G. concinnum, while G. parisiense has muriculate or uncinate fruits. The leaf margins in G. asprellum are retrorse-scabrous throughout, while those in G. concinnum are usually antrorsely scabrous with only occasional retrorse-scabrous hairs near the base of the leaf.

There was one specimen stated to have been collected in South Carolina, but this is doubtless a mistaken locality. The state "Missouri" has been lined through on the label and replaced by "South Carolina" even though the collector, Rev. John Davis, is known to have been living in Missouri the year this specimen was collected. Although I can find no certain proof that the specimen was collected in Missouri rather than South Carolina, the known range of the species indicates Missouri to be a much more likely locality than the disjunct one created if South Carolina were correct.

Galled flowers are found frequently in this species.



MAP 6

GALIUM CONCINNUM

7. GALIUM HISPIDULUM Michx., Fl. Bor. Am. 1: 79. 1803.

Valantia hypocarpia L., Syst. ed. 10. 2: 1307. 1759, excl. Browne's Jamaican plant.

Rubia peregrina sensu Walt., Fl. Car. 86. 1788, not L.

Rubia brownei Michx., Fl. Bor. Am. 1: 81. 1803, excl. Browne's Jamaican plant.

G. hispidum Pursh, Fl. Am. Sept. 1: 104. 1814, ? error for G. hispidulum Michx.

Rubia walteri DC., Prodr. 4: 590. 1830.

G. peregrina (sensu Walt.) B. S. P., Prel. Cat. N. Y. 24. 1888.

Bataprine hispidula (Michx.) Niewl., Am. Midl. Nat. 1: 264. 1910.

G. carolinianum F. G. Dietr., Vollst. Lexic. Gärtn. u. Bot. Nachtr. 3: 429. 1817.

Ascending to diffuse, stoloniferous perennial, up to 7 dm tall (mostly 1.6 - 3.9 dm); stems branching near the base and commonly once, sometimes twice, at the lower nodes, glabrous to densely pubescent on the angles and side with stiff, spreading straight, descending, or retrorsely curved hairs mostly 0.2 - 0.4 mm long; leaves in whorls of four, mostly elliptical but varying from ovate to oblong to occasionally oblanceolate, acuminate, largest leaves mostly (6) 8.3 - 13.2 (20.4) mm long and (2.1) 3.5 - 5.3 (7.6) mm wide, nerve one, prominent, lateral nerves rarely visible, upper leaf surface muriculate, glabrous or with stiff,

vertical or slightly curved, ascending hairs, lower leaf surface glabrous or with stiff, vertical and variously divergent, often curved, hairs (hairs on both surfaces 0.14 - 0.4 mm long), secretory glands scattered over the lower surface, margins sometimes revolute, glabrous to densely hispid with hairs 0.2 - 0.4 mm long; inflorescence a simple dichasium; flowers pedicellate, borne 2 - 3 at the ends of axillary, naked peduncles, one flower often subtended by a small bract, pedicels glabrate or with pubescence similar to that of the stems; corollas four-lobed, yellow-green to light yellow, lobes caudate (the appendage up to 0.4 mm long, often broken off), usually (0.6) 0.8 - 1.2 (1.6) mm long excluding the appendage and (0.6) 0.7 - 1 (1.6) mm wide, glabrous to densely hispid on the outer surface with hairs seldom over 0.25 mm long; fruit a purplish-black, glabrate berry with scattered, appressed hairs seldom over 0.3 mm long, each mature carpel (2) 2.5 - 3.3 (4) mm long and (1.6) 1.9 - 2.6 (3.2) mm wide.—Fig. 10.

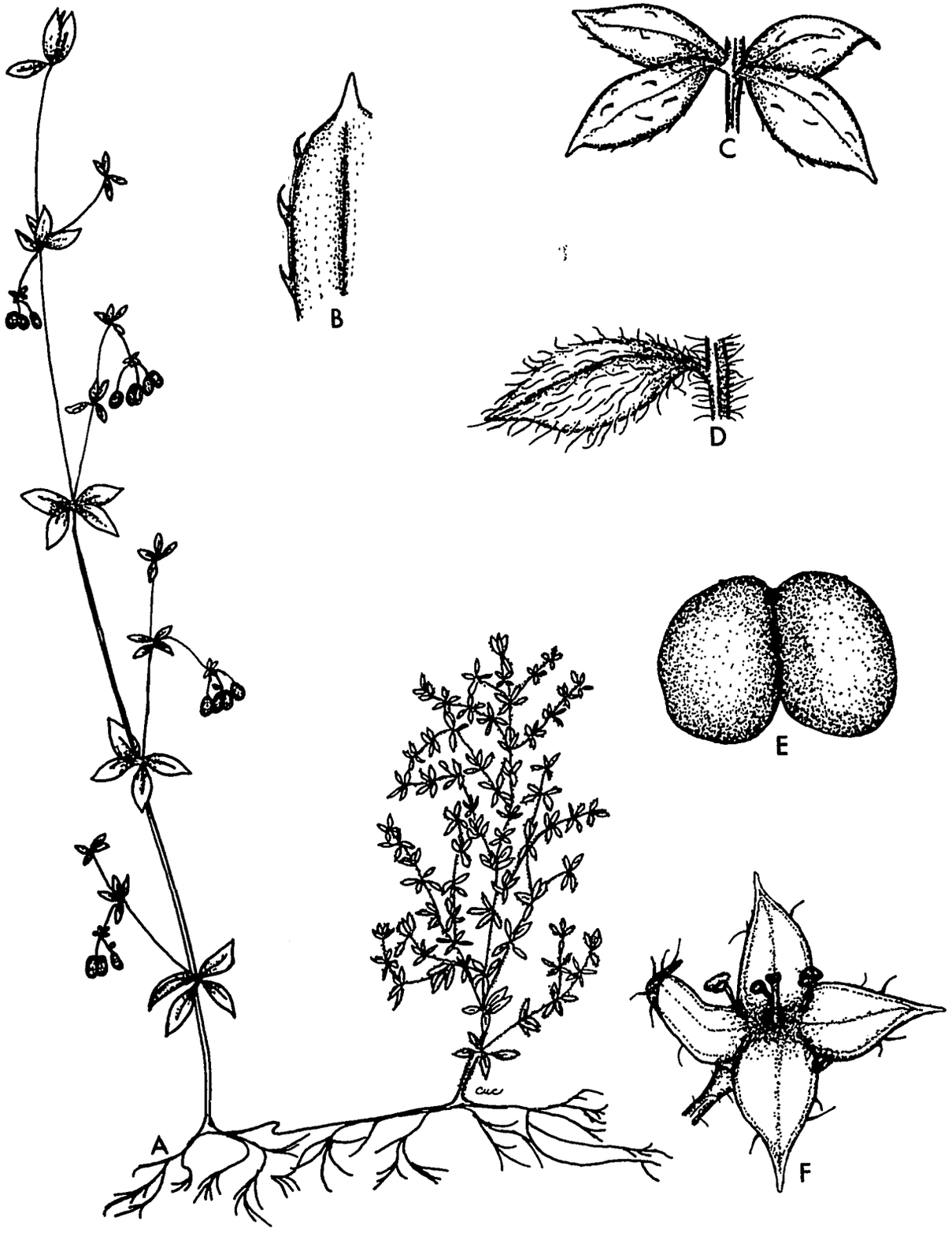
Type locality: "Hab. in Carolina inferiore."

Range: New Jersey south to Florida and west to Louisiana (Southeastern United States, Map 7).

Flowering - Fruiting time: April to December; some fruits have been found to persist on the plants as late as March of the year after flowering. In the more southern states, the plants appear to be practically evergreen.

FIGURE 10

GALIUM HISPIDULUM: A, habit showing two growth forms x 1; B, leaf margin and apex x 50; C, slightly pubescent upper leaf surface and glabrous stem x 5; D, densely pubescent upper leaf surface and stem x 5; E, fruit x 5; F, flower x 19. A, B, C from C. A. Lawson & D. Dotts 1116 (OKL), and D, E, F from C. A. Lawson & D. Dotts 854 (OKL).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Habitat: Sandy, often dry, soil of pine and oak woods, dunes, beaches, maritime forests, coastal islands, marshes, wooded river bluffs, and disturbed or vacant lots.

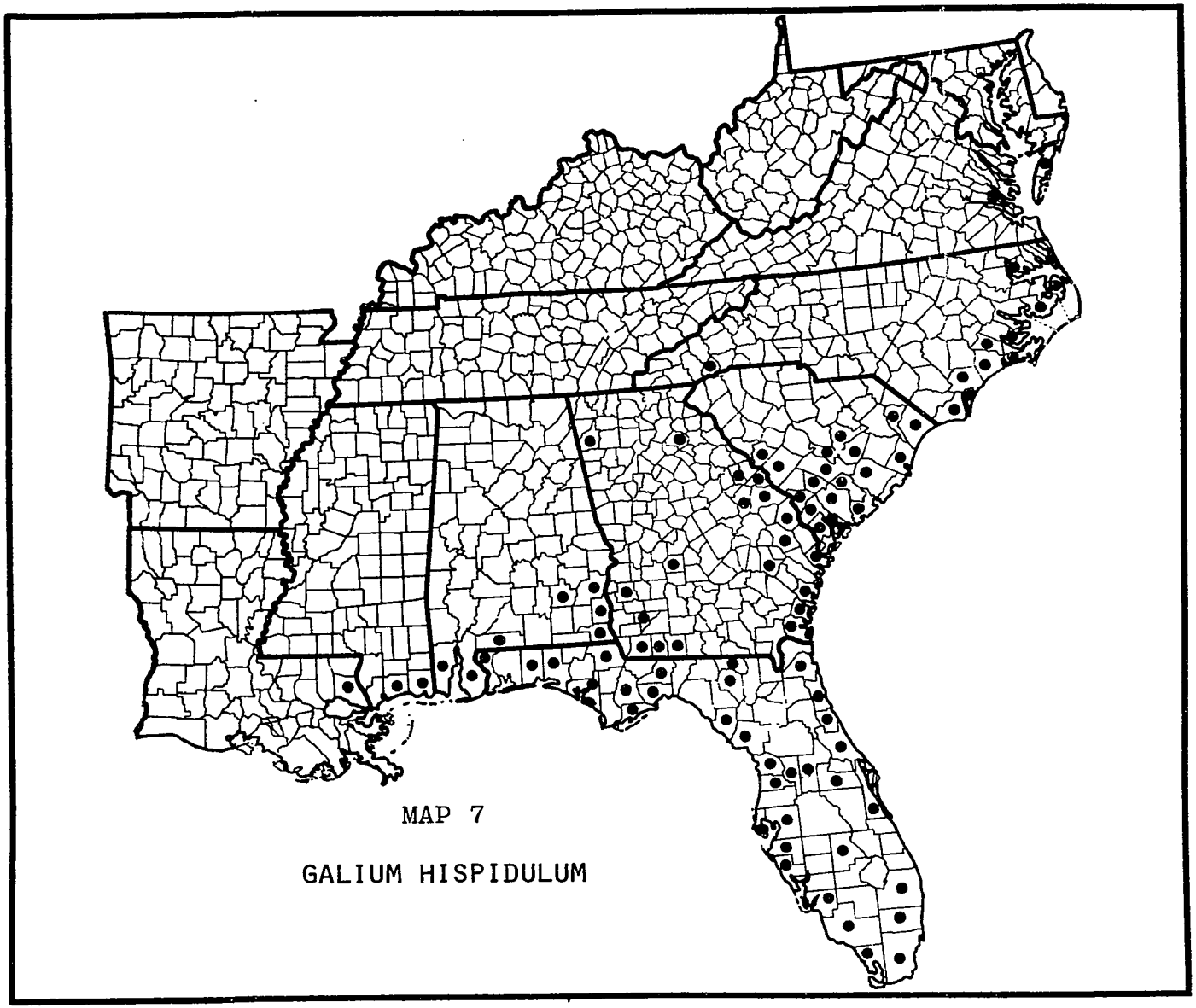
S.E. United States specimens examined: Five hundred and ninety-five sheets.

The earliest specific epithet for this species is hypocarpia L. which included more than one species when described. Since this name is confused and clearly refers to more than one species, I am continuing to use the later name, G. hispidulum Michx., for which the application seems clear.

Throughout the range of this species, the pubescence is highly variable. Glabrate specimens to densely hispid ones with every intermediate can be found in each state where G. hispidulum occurs in the southeastern United States.

There are essentially two growth forms which occur in this species. One has expanded internodes and rather large leaves on definite main stems. The other has shortened internodes, small leaves, and no definite main stem. There is a general tendency for the plants with expanded internodes to be glabrate or only moderately pubescent and for the plants with shortened internodes to be densely hispid; however, both forms can be found in single populations as revealed in the populational studies in the summer of 1973.

In early vegetative condition glabrate specimens with expanded internodes and glabrate ones of G. pilosum



MAP 7

GALIUM HISPIDULUM

are difficult to differentiate. In areas where these species are found growing together, collections may contain mixed vegetative material. The most helpful character in distinguishing these two species is the leaf apex. In G. hispidulum the apex is acuminate, while in G. pilosum it is mostly mucronulate.

One specimen, J. A. Duke 0205 (NCU) from South Carolina has all the characters of G. hispidulum except one. The fruits are densely covered with uncinate hairs - a characteristic unlike the typical glabrate fruit having only a few scattered, appressed hairs.

8. GALIUM LANCEOLATUM Torr., Fl. N. & Mid. U. S. 168. 1824.

G. circaezans var. ? lanceolatum Torr., Cat. Pl. City N. Y. 23. 1819 (nomen provisiorum).

G. torreyi Bigel., Fl. Bost. ed. 2. 56. 1824.

G. rotundifolium ε. lanceolatum (Torr.) O. Ktze. Rev. Gen. 1: 283. 1891.

Erect perennial, up to 7 dm tall (mostly 3.1 - 4.9 dm); stems simple, branching at the base, mostly glabrous or with a few straight, spreading hairs up to 0.3 mm long scattered on the angles and sides or at the nodes; leaves in whorls of four, lanceolate above and elliptical on the lower portion of the stem, narrowing to a rounded or obtuse tip, largest leaves (35.2) 42.6 - 55.3 (63.2) mm long and (10.6) 12.7 - 17.8 (26) mm wide, midnerve prominent, the lateral

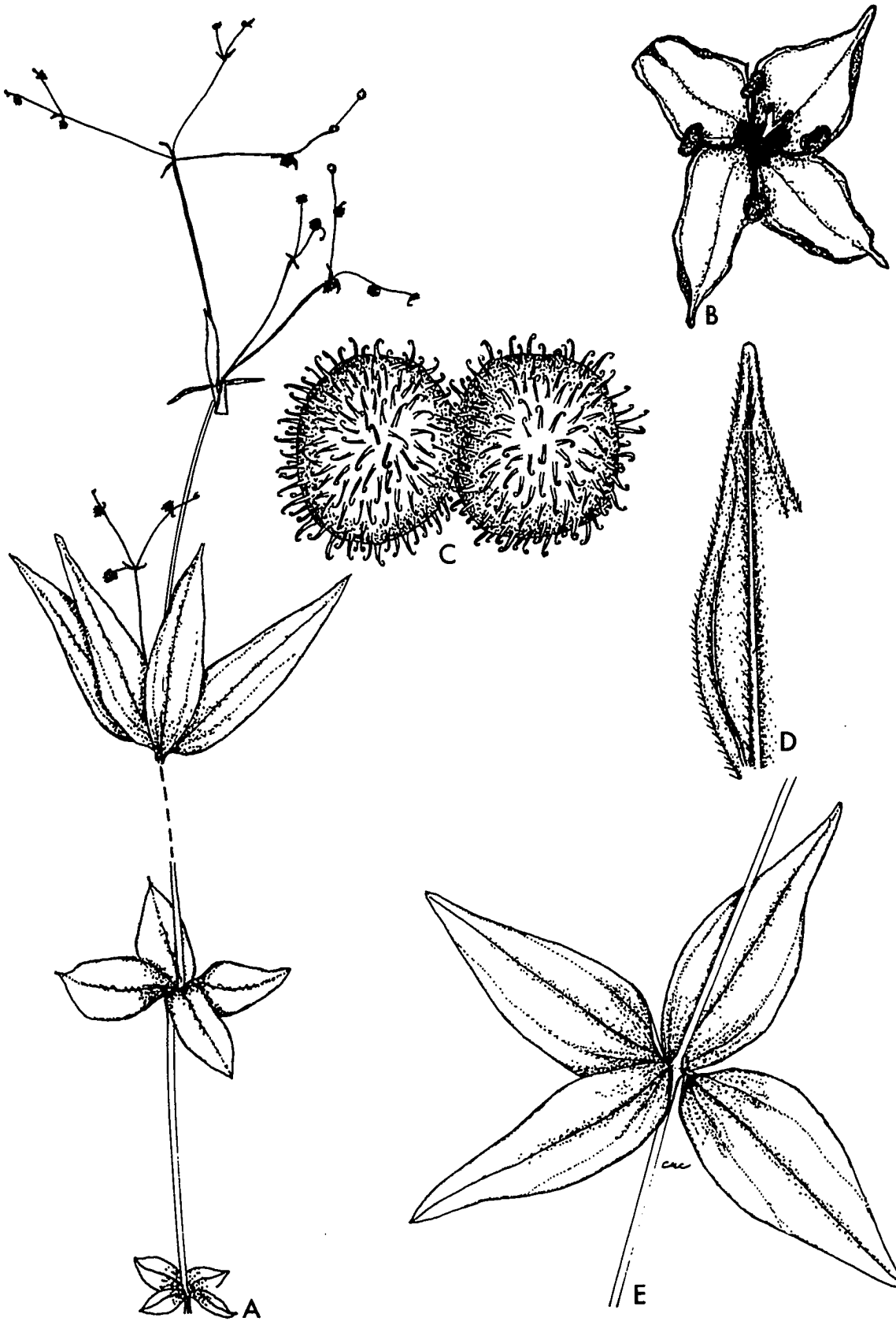
nerves present but usally less conspicuously so, upper leaf surface appearing glabrous but with a few stiff, straight, spreading or ascending hairs up to 0.2 mm long on the veins (these hairs sometimes appressed and parallel to the veins) or rarely also with a few appressed, apically directed hairs scattered over the surface, lower leaf surface glabrous or with pubescence as on the upper surface except the hairs up to 0.4 mm long and not appressed and parallel to the veins, secretory glands scattered over the lower surface, margins with stiff, straight, ascending hairs up to 0.5 mm long; inflorescence a helicoid cyme; flowers sessile or subsessile, each subtended by one or two small bracts, remote; corollas four-lobed, purple when dry, lobes slightly or narrowly caudate (the appendage up to 0.6 mm long), usually (0.9) 1.2 - 1.5 (1.6) mm long excluding the appendage and (0.8) 0.9 - 1.2 (1.3) mm wide, glabrous; fruits pubescent with uncinate hairs up to 1 mm long, each mature carpel (1.7) 2.1 - 2.7 (2.8) mm long and (1.2) 1.6 - 2.4 (2.8) mm wide.—Fig. 11.

Type locality: "In stony woods, Bloomingdale, &c., New-York. Litchfield, Connecticut. Brace. Williamstown, Massachusetts. Dewey."

Range: Quebec and Ontario to Minnesota, south to Tennessee and North Carolina (Southeastern United States, Map 8; this species is known to occur in Delaware and Kentucky; however, no county localities could be determined for use on the distribution map).

FIGURE 11

GALIUM LANCEOLATUM: A, habit showing leaves from upper and lower portions of the stem x 1; B, flower x 14; C, fruit x 12; D, lower leaf surface, margin, and apex x 2; E, leaf whorl x 1. A from E. Balters 1834 (LONG) for upper portion of stem and J. M. Greenman 311 (GH) for lower portion of stem, B from H. E. Ahles 43630 (NCU), C, E from J. M. Greenman 311 (GH), and D from E. Balters 1834 (LONG).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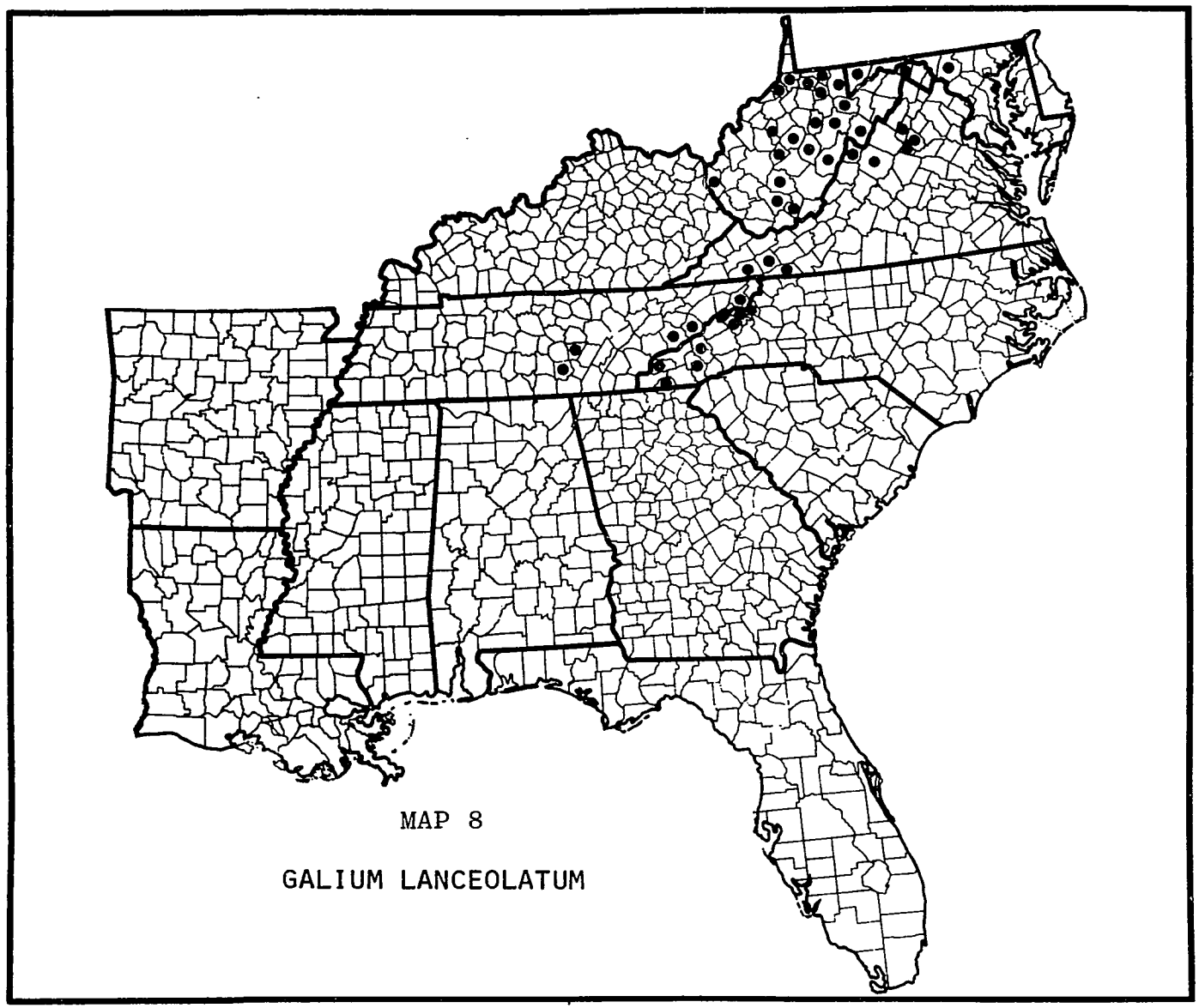
Flowering - Fruiting time: May through August, occasionally September, rarely October.

Habitat: Frequent in woodlands, on hillsides, and on mountain slopes in rich, rocky, or mesic areas; sometimes associated with shales and limestones.

S.E. United States specimens examined: Eighty-six sheets.

This species in the immature stages is frequently misidentified and confused with G. latifolium and G. circaezans.

On the upper portion of the stems, the leaves in both G. latifolium and G. lanceolatum are lanceolate; however, in G. lanceolatum the leaves on the lower portion of the stems are elliptical. Also, there is a slight, but not always easily discernible, difference in leaf apices in these two species. Once the plants have reached young flowering stage, minute hairs are noticeable along the outer edge of each carpel of G. lanceolatum. The hairs at this stage are tightly appressed and are slightly yellow in color. The young fruits of G. latifolium appear light green and glabrous. As the plants mature, differentiation is possible by examing the inflorescence types. A helicoid cyme characterizes G. lanceolatum, while a compound dichasium type inflorescence is found in G. latifolium. Also, the branches of the inflorescence in G. lanceolatum usually have a few scattered hairs, whereas the peduncles in G. latifolium are glabrous.



MAP 8

GALIUM LANCEOLATUM

As stated above, the leaf shape of G. lanceolatum is lanceolate on the upper portion of the stem. In G. circaezans the leaves are elliptical throughout. The helicoid inflorescence and pubescent fruits are alike in these two species; however, the flowers of G. circaezans are usually pubescent on the outer surface of the corolla lobes, while they are glabrous in G. lanceolatum. In G. circaezans the flower color is light green or light yellow. No live flowering material of G. lanceolatum was examined in this study, but the flowers are reported to be yellowish, turning dull purple (Fernald, 1950). The purple color is retained in pressed, dried material.

It is known that the second part (which includes page 168) of Torrey's (1824) A Flora of the Northern and Middle Sections of the United States was published in February, 1824. Bigelow's (1824) second edition of Florula Bostoniensis was also published in this same year, but the exact date of publication has not been determined. For Bigelow's G. torreyi to be an older specific epithet than Torrey's G. lanceolatum, the date of publication would have to precede February, 1824.

Galled flowers are found frequently in this species.

9. GALIUM LATIFOLIUM Michx., Fl. Bor. Am. 1: 79. 1803.

G. latifolium var. hispidum Small, Mem. Torr. Bot. Cl. 4: 126. 1894.

G. latifolium var. hispidifolium Small, Mem. Torr. Bot. Cl. 5: 303. 1894 (superfluous name based on var. hispidum Small).

Erect perennial, up to 6 dm tall (mostly 3 - 4.5 dm); stems simple, branching at the base, mostly glabrous or glabrate with a few straight, spreading hairs up to 0.3 mm long scattered on the angles especially near the nodes, rarely densely pubescent on the angles and sides; leaves in whorls of four, lanceolate, commonly broadly so, acute but with rounded tips, largest leaves (21.2) 33 - 46.5 (55.6) mm long and (7.2) 10.8 - 16 (20) mm wide, nerves three, the midnerve occasionally more prominent than the lateral nerves, leaf surfaces glabrous or with straight, stiff, spreading or slightly ascending hairs on the veins (up to 0.2 mm long on the upper surface and up to 0.5 mm long on the lower surface), rarely also with appressed, apically directed hairs on the surfaces, secretory glands scattered over the lower surface, margins with stiff, straight, slightly ascending hairs up to 0.5 mm long; inflorescence a compound dichasium, bibracteate at each of the up to four branchings; flowers on glabrous pedicels; corollas four-lobed, purple at least on the inner surface, lobes caudate (the appendage up to 0.8 mm long), usually (0.8) 1.1 - 1.5 (1.7) mm long excluding the appendage

and (0.7) 0.8 - 1.1 (1.3) mm wide, glabrous; fruits glabrous, each mature carpel (2) 2.4 - 2.9 (3.4) mm long and (1.4) 1.8 - 2.5 (3.2) mm wide.—Fig. 12.

Type locality: "In altis montibus utriusque Carolinae."

Range: Eastern United States from Pennsylvania south to Georgia and west to Kentucky, Tennessee, and Alabama (Southeastern United States, Map 9).

Flowering - Fruiting time: May through September, occasionally October.

Habitat: Mountainous areas along roadsides, wooded slopes, ridges, and hillsides; in deciduous woods; and on shale and limestone embankments.

S.E. United States specimens examined: Four hundred and sixty-one sheets.

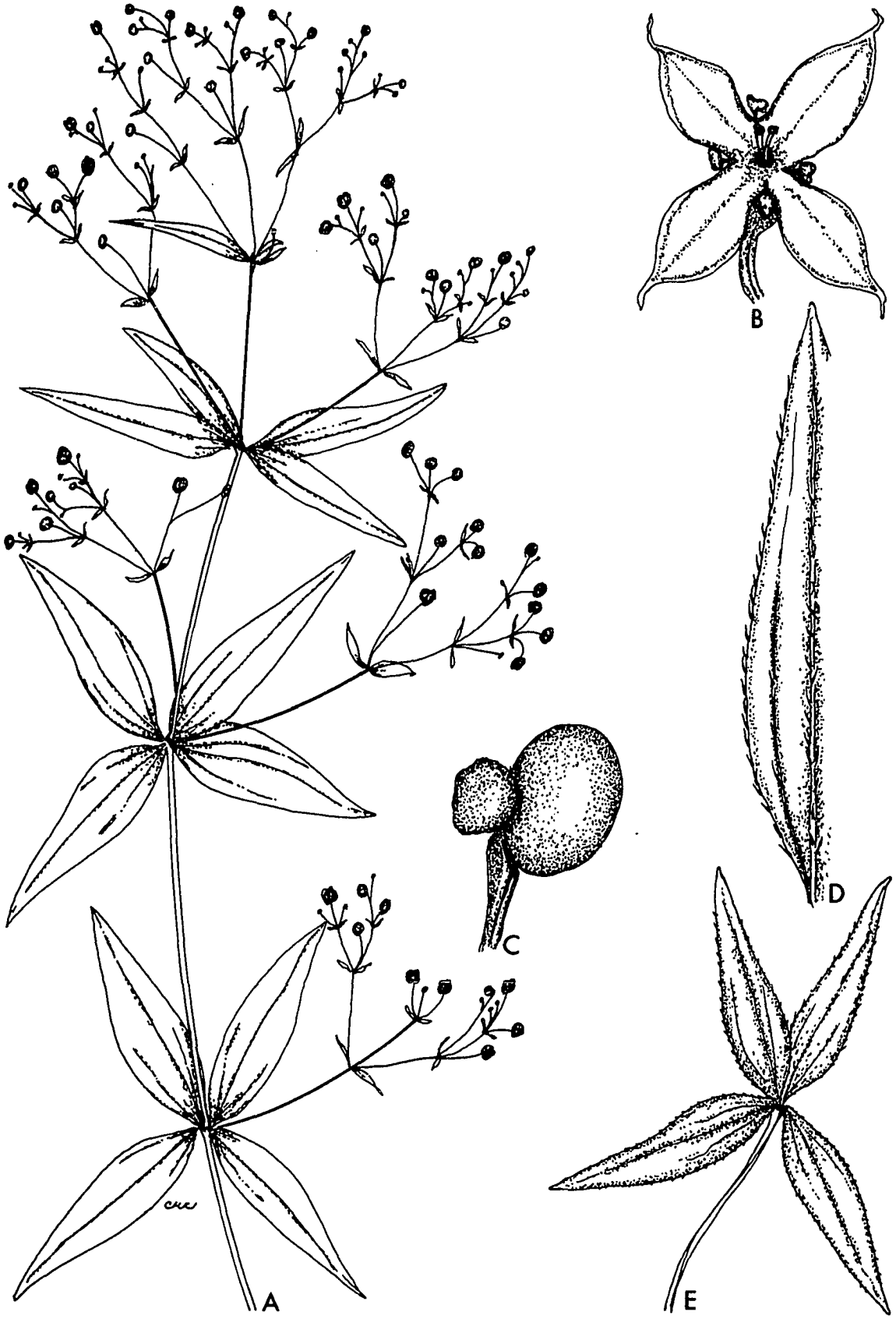
This species and G. lanceolatum are remarkably similar in the immature states. Their differences are enumerated in the discussion of G. lanceolatum. Likewise, the similarity of G. latifolium to G. arkansanum is discussed under the latter species.

A few specimens from scattered localities in Virginia and West Virginia are densely pubescent on the leaves and stems. Differing degrees of leaf and stem pubescence occur throughout the species range, however, and no sub-specific division seems warranted.

Enlarged, galled flowers are also present in this species.

FIGURE 12

GALIUM LATIFOLIUM: A, habit x 1; B, flower x 25; C, fruit with one abortive carpel x 10; D, lower leaf surface, margin, and apex x 3; E, leaf whorl x 2. A from H. A. Allard 2117 (VPI), B from F. W. Hunnewell 2 (GH), and C, D, E from J. R. Massey & H. Massey 3760 (NCU).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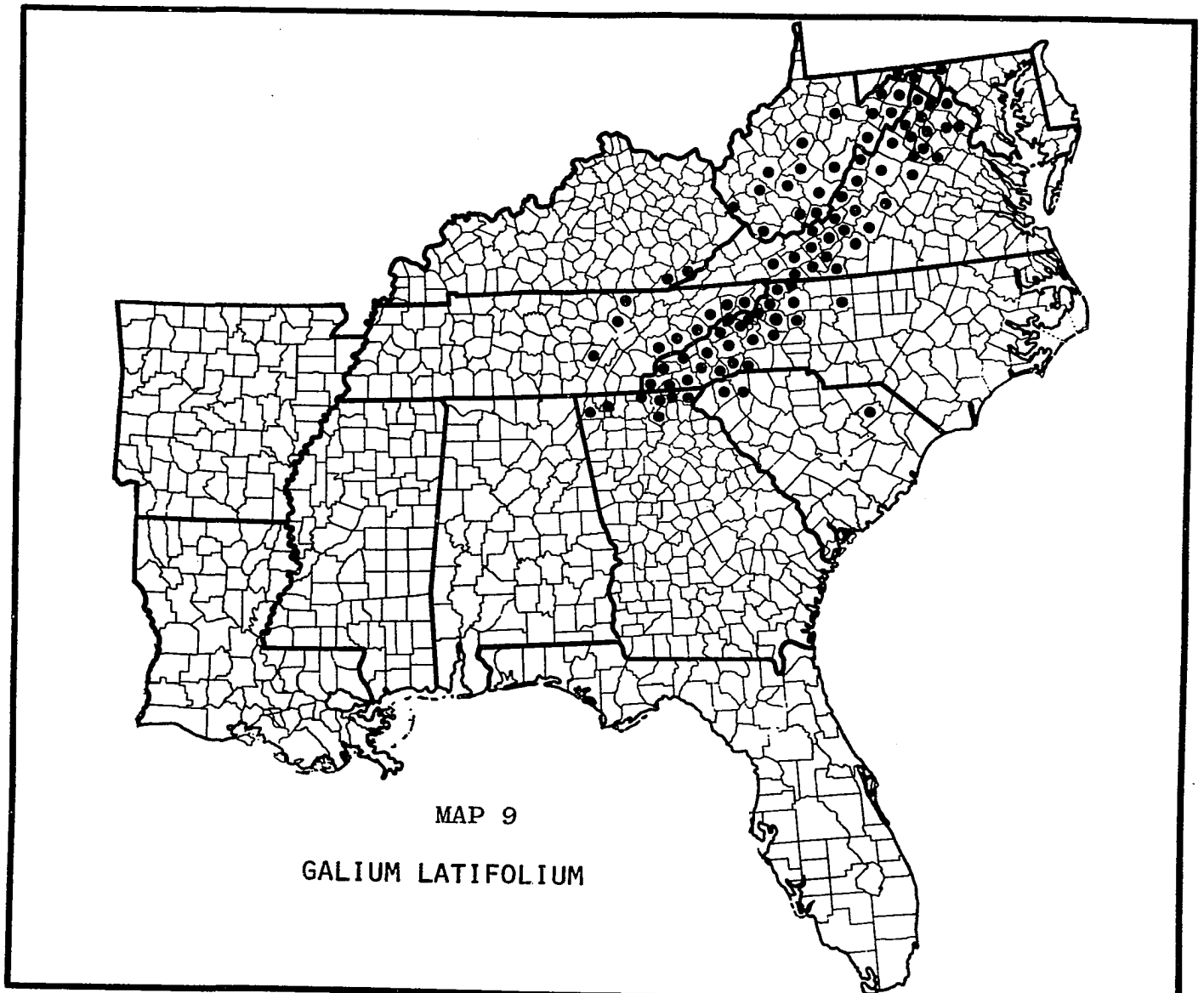


MAP 9

GALIUM LATIFOLIUM

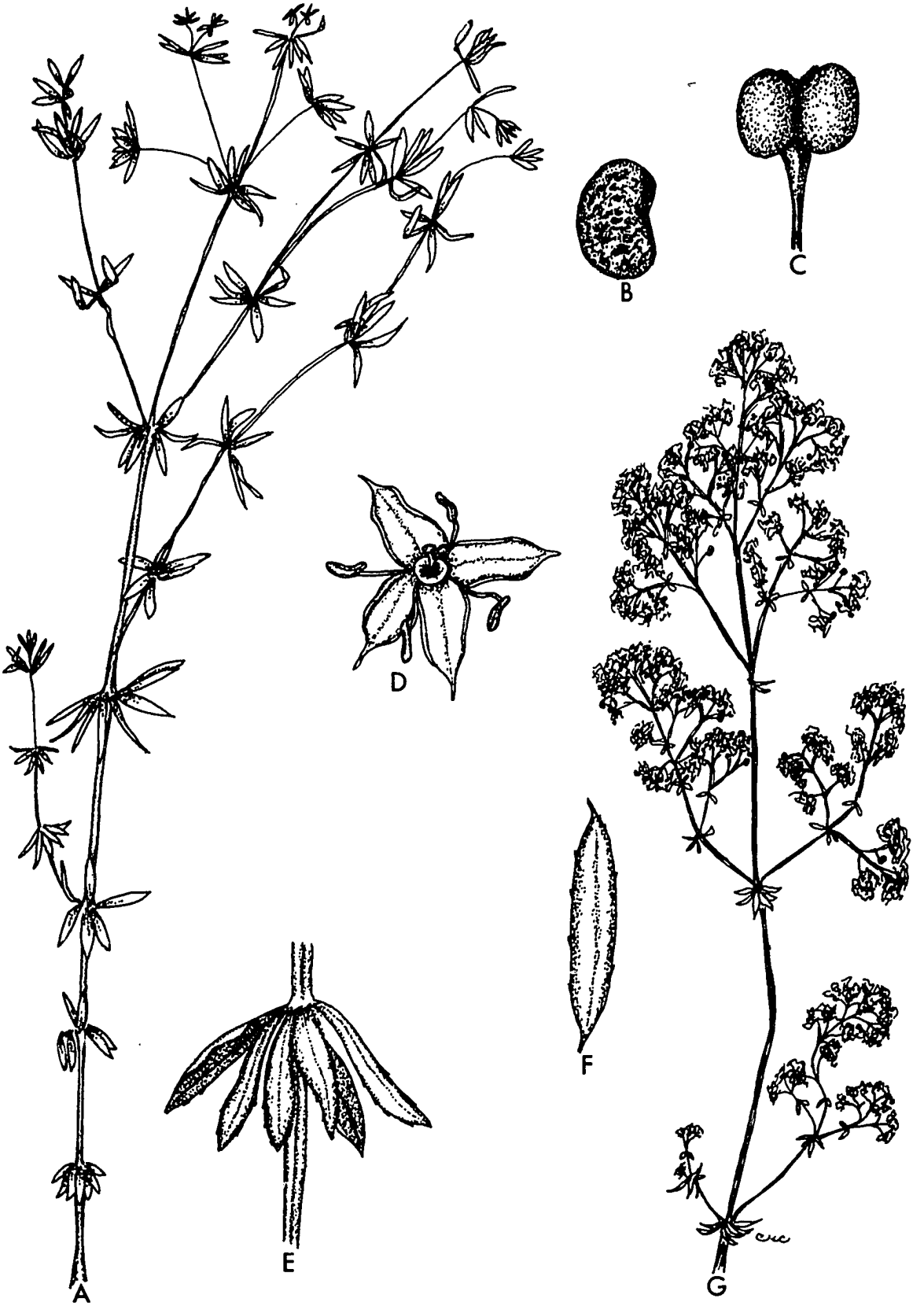
10. GALIUM MOLLUGO L., Sp. Pl. 1: 107. 1753.

Erect, rhizomatous perennial, up to 10.6 dm tall (mostly 5.3 - 8.6 dm); stems branching near the base and commonly once or twice at the often enlarged nodes, glabrous to densely pubescent on the lower angles and sides with straight, spreading or descending hairs mostly 0.2 - 0.4 mm long (occasionally also pubescent on the upper angles); leaves in whorls of six to eight, rarely twelve, obovate to oblanceolate to linear, cuspidate, largest leaves (8) 10.5 - 15.2 (18.8) mm long and (1.4) 1.9 - 3.3 (4.8) mm wide, midnerve prominent, leaf surfaces glabrous or the lower surface pubescent throughout or only on the midnerve, secretory glands rarely visible on the lower surface, margins antrorsely scabrous with hairs mostly 0.06 - 0.1 mm long; inflorescences primarily on the upper half of the plant, thus frequently appearing terminal, the axillary inflorescences forming cymose panicles; flowers on glabrous pedicels, showy, fragrant; corollas four-lobed, white, lobes caudate (the appendage up to 0.3 mm long), usually (0.6) 0.7 - 1.2 (1.6) mm long excluding the appendage and (0.4) 0.5 - 0.8 (1.2) mm wide, glabrous; fruits glabrous, globose or sometimes reniform, wrinkling in drying, each mature carpel mostly (0.9) 1 - 1.5 (1.8) mm long and (0.6) 0.7 - 1.1 (1.2) mm wide.—Fig. 13.

Type locality: "Habitat in Europa mediterranea."

FIGURE 13

GALIUM MOLLUGO: A, habit x 1; B, reniform fruit x 14; C, globose fruit x 9; D, flower x 11; E, leaf whorl x 3.5; F, upper leaf surface, margin, and apex x 7; G, inflorescence x 1. A, D, E, F, G from C. A. Lawson & D. Dotts 1215 (OKL), and B, C from H. E. Ahles 43942 (NCU).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Range: Eurasian; rare in Oregon and California; introduced in the northeastern United States, west to Indiana and south to North Carolina and Tennessee (Southeastern United States, Map 10).

Flowering - Fruiting time: May to October, but usually only through September.

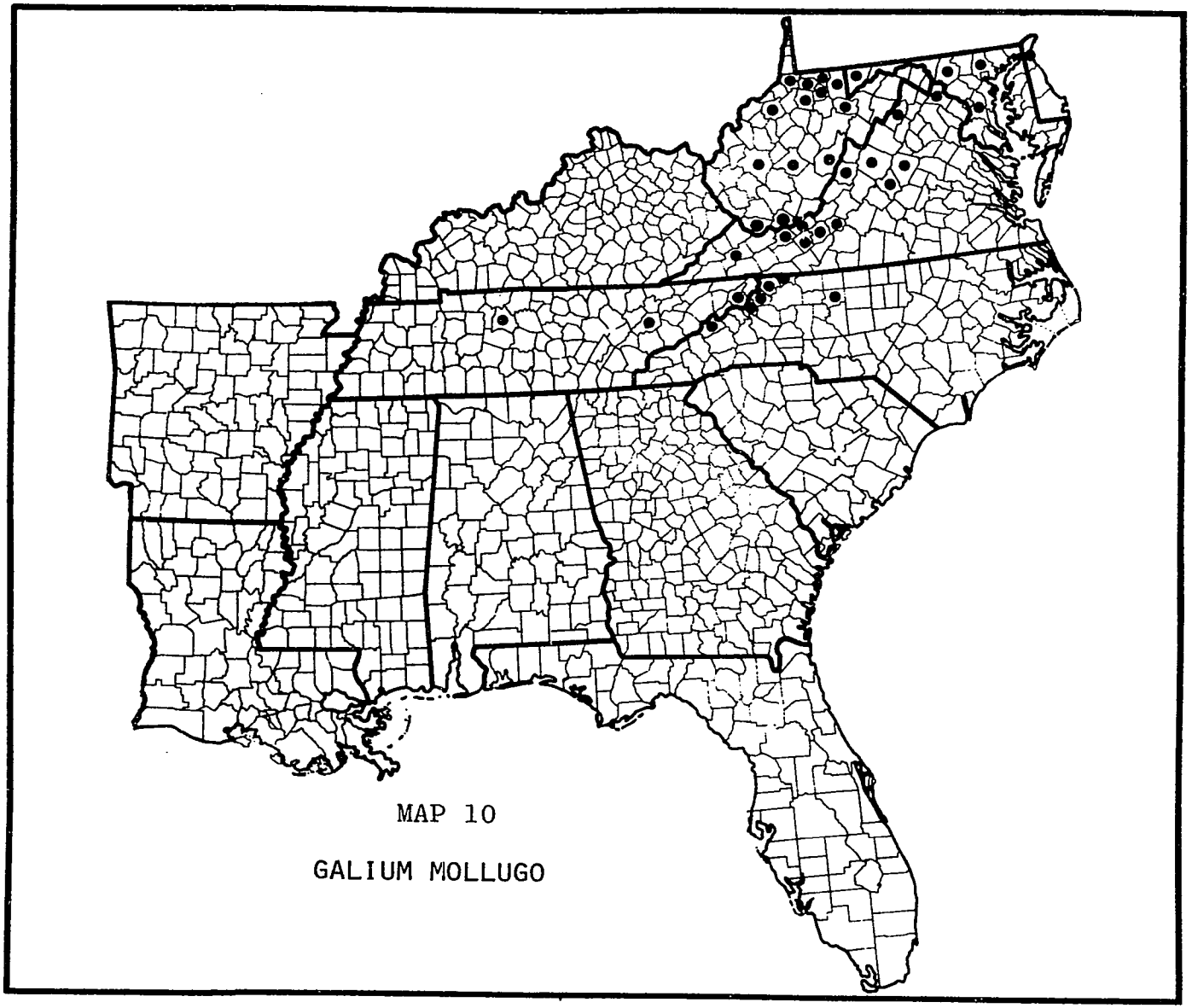
Habitat: Mostly in disturbed areas along roadsides, railroad tracks, river and creek banks, and margins of pastures; occasionally in fields, rich woods, clearings, marshy areas, and dry woods.

S.E. United States specimens examined: One hundred and sixty-two sheets.

This species is highly variable as witnessed by the many named European subspecies, varieties, and subvarieties. Taxa differentiation is often based on pubescence of the stem, abundance and size of the flowers, and shape, length, width, and pubescence of the leaves.

The specimens of G. mollugo from the southeastern United States are equally as variable. For the most part, the stems are glabrous. Of the specimens seen from Maryland, Delaware, the District of Columbia, and Tennessee all had glabrous stems. Both pubescent- and glabrous-stemmed material was examined from Virginia, West Virginia, and North Carolina; however, only in North Carolina were the pubescent-stemmed specimens more frequent than the glabrous ones.

At one site in Virginia, a populational study revealed



MAP 10

GALIUM MOLLUGO

the presence of both glabrous- and pubescent-stemmed plants. Of the thirty-three specimens collected from this population, thirteen were pubescent on the lower stem angles and sides - tweleve of these abundantly so. The other twenty specimens were glabrous and ranged from immature to mature plants. Duplicate specimens from collections made in West Virginia also revealed this same variation. It seems doubtful that two different types of plants could have been introduced in the same or nearly the same location. How to explain the lack of pubescent material from Maryland, Delaware, the District of Columbia, and Tennessee is unresolved. There is the remote chance that coincidentally only glabrous specimens were collected from these populations. This, however, seems unlikely. It should be pointed out that many subvarietal names have been proposed in Europe to correspond to the variation in stem pubescence.

Flower size shows another particularly noticeable variation. Corolla lobe length varied from 0.6 - 1.6 mm, and lobe width ranged from 0.4 - 1.2 mm. The large corollas were found frequently on specimens from North Carolina, Virginia, Delaware, and the District of Columbia and were often less densely flowered and narrow leaved. Plants with these character variations have been distinguished at times as G. erectum Hudson, G. mollugo subsp. erectum (Huds.) Briquet, or G. mollugo var. erectum (Huds.) Domin.

Populational studies by the author revealed both

small, densely flowered specimens and large, less densely flowered specimens in the same populations. Both flowering types had narrow leaves. Again, it seems unlikely that two different types of plants could have been introduced in the same small area.

Because of the populational variation, further division below the species level based on stem pubescence, flower size and abundance, or leaf shape seem uncertain and is not now attempted.

Immature, vegetative G. mollugo is often misidentified as either G. asprellum or G. concinnum. Both G. asprellum and G. concinnum have retrorse-scabrous stems as opposed to the glabrous or straight, spreading or descending pilose stems of G. mollugo. The leaf margins of G. mollugo are antrorse-scabrous. This same marginal pubescence usually can be found in G. concinnum, or the leaf margins may be glabrous. In G. asprellum the leaf margins are retrorse-scabrous.

The carpels of the mature fruits are frequently reniform in shape and show a small, acute bract between them. When the fruits are globose, this bract-like protrusion is less conspicuous.

11. GALIUM OBTUSUM Bigel., Fl. Bost. ed. 2. 55. 1824.

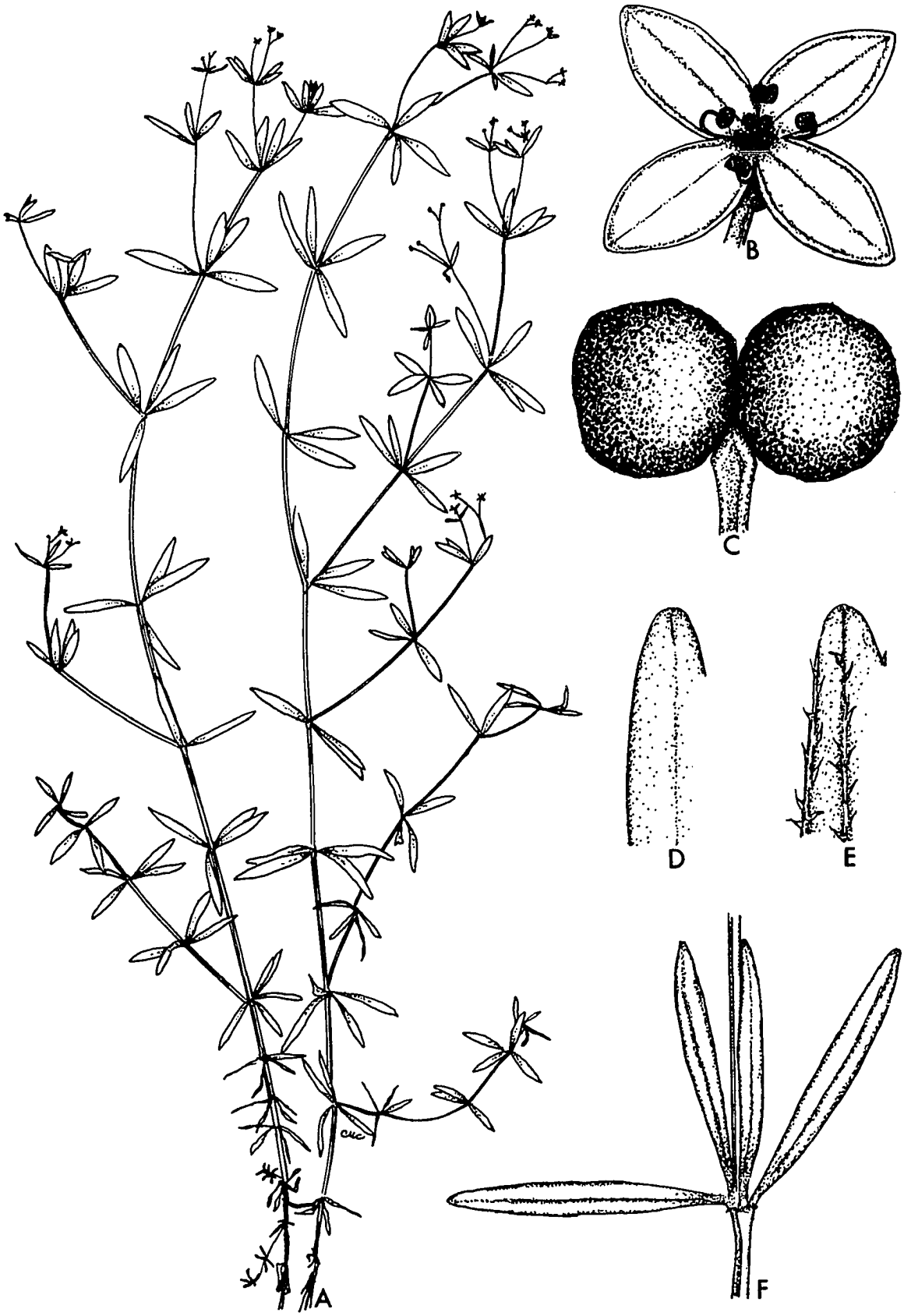
Erect or reclining perennial, up to 8.1 dm tall (mostly 2.6 - 4.8 dm); stems usually branching once at each of the frequently hairy nodes, otherwise glabrous or nearly

so; leaves mostly in whorls of four, sometimes five (rarely six), linear, lanceolate, elliptical, or oblanceolate, mostly obtuse, largest leaves (8.4) 11 - 18 (30.4) mm long and (0.8) 1.2 - 2.4 (4.1) mm wide, nerve one, leaf surfaces completely glabrous or with flattened-hispid or scabrous hairs along the margins and midnerve beneath (these hairs up to 0.2 mm long), secretory glands absent on the lower surface, margins often revolute; inflorescence cymose; flowers on glabrous pedicels, usually borne 2 - 3 at the ends of lateral or terminal peduncles, the pedicels occasionally subtended by one or more reduced leaves; corollas four-lobed, white, lobes mostly acute, usually (0.8) 0.9 - 1.3 (1.6) mm long and (0.5) 0.7 - 0.9 (1) mm wide, glabrous; fruits glabrous, each mature carpel (1.4) 1.7 - 2.4 (2.8) mm long and (1.2) 1.6 - 2.2 (2.4) mm wide.—Fig. 14.

Galium obtusum is a very polymorphic species. Plants in the Atlantic Coastal Plain and Piedmont Plateau of Virginia, North Carolina, and South Carolina (sometimes Georgia) have, for the most part, very narrow, linear leaves, elongated internodes, and a flaccid habit. Also, the peduncles are usually long and slender, and frequently there are only two leaves to a whorl on the side branches (Fig. 15 A). To these plants the name G. obtusum var. filifolium (Wieg.) Fern. may be applied. Westward, the plants have much stiffer, broader leaves than the coastal ones (up to 4 mm wide as compared to 2 mm). These leaves are elliptical to oblanceolate,

FIGURE 14

GALIUM OBTUSUM: A, habit x 1; B, flower x 22; C, fruit x 15; D, glabrous lower leaf surface, margin, and apex x 10; E, lower leaf surface with apex, pubescent midnerve, and margin x 10; F, leaf whorl x 3. A, B, D, F from L. Donavan 281 (AUA), C from D. M. Moore 51-425 (UARK), and E from D. Demaree 60156 (NCU).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and the internodes are shortened. Two major type of habits are displayed by these plants. One is erect with ascending leaves and ascending inflorescences. The other has spreading leaves and generally spreading inflorescences with a slightly more loose habit (Fig. 15 B). Geographically and morphologically these two type are difficult to separate from one another as well as from the plants which Gleason (1952) called G. obtusum var. ramosum. All three type plants seem best treated as variations within G. obtusum var. obtusum. All are easily differentiated and separated from the coastal type, however.

There seems to be no consistent differences in the pubescence of these variants. Other characters such as flower and fruit size do not show appreciable degrees of difference.

Separation into varieties on the basis of morphological characters is difficult with some of the available material. A few plants, nearly all from the Coastal Plain, approach the coastal variety except for a leaf width up to 3.7 mm. Because thse plants show a more close affinity for the coastal variety than the westward group, they are at the present time being placed with the other coastal plants.

It seems desirable to subdivide this species in which there is such great polymorphism and in which there is some morphological - geographical correlation. The morphological peculiarities could be in direct response

FIGURE 15

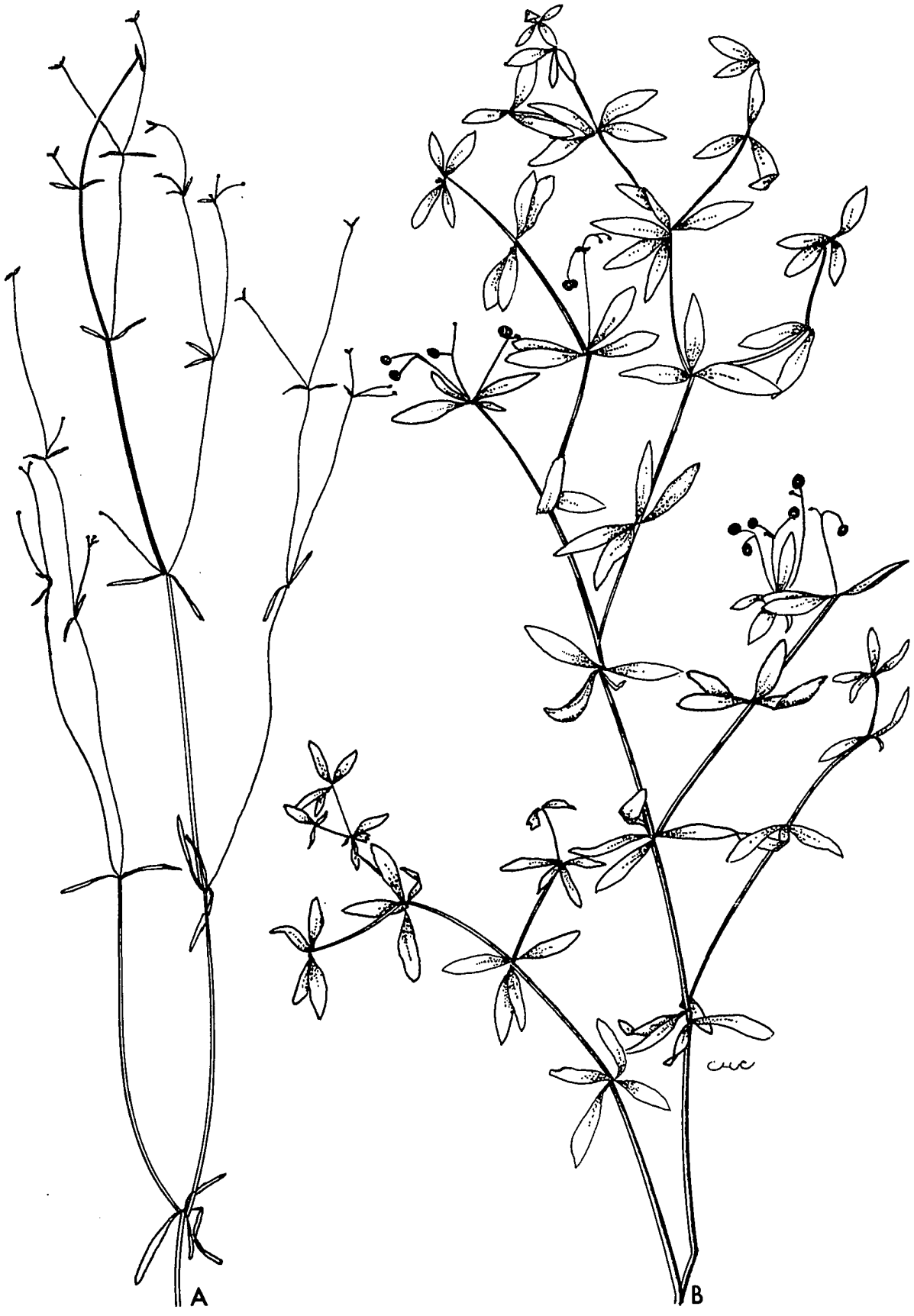
VARIATIONS IN HABIT IN

GALIUM OBTUSUM

A - flaccid habit with very narrow, linear leaves, elongated internodes, and two leaves to a whorl on the side branches (G. obtusum var. filifolium) x 1.

B - loose habit with spreading leaves and generally spreading inflorescences (variant of var. obtusum) x 1.

A from C. A. Lawson & D. Dotts 1176 (OKL), and B from F. Brown & A. Clebsch s.n., June 10, 1950 (NCU).


A
B

to ecological factors as has been suggested by Steyermark (1963) for the inland plants of this species. It is possible that selection for adaptation to different ecological settings has taken place within the species, but no firm hypothesis has yet been established.

As discussed under G. concinnum, the similarity between this species and G. obtusum has caused confusion at times. G. obtusum is also frequently confused with G. tinctorium as noted under the latter species.

The hairs on the margins and midnerve beneath are often abundant and may be ascending, descending, or spreading.

Galled flowers are found frequently in this species.

KEY TO VARIETIES

Leaves up to 4 mm wide and lanceolate, elliptical, or oblanceolate; internodes not elongated; habit erect or loose. . . . 11a. G. obtusum var. obtusum

Leaves seldom over 2 mm wide and usually linear; internodes elongated; habit flaccid. . . . . 11b. G. obtusum var. filifolium

11a. G. OBTUSUM VAR. OBTUSUM

G. obtusum Bigel., Fl. Bost. ed. 2. 55. 1824.

G. trifidum β. latifolium Torr., Fl. N. & Mid. U. S. 1: 165. 1824.

G. obtusum var. ramosum Gl., Phytologia 4: 24. 1952. Type: Gleason 9128, wet prairie along railway, just west of Seymour, Champaign Co., Ill., July 3, 1940 (NY). v.s.—Fig. 16.

FIGURE 16

PHOTOTYPE OF

GALIUM OBTUSUM VAR. RAMOSUM

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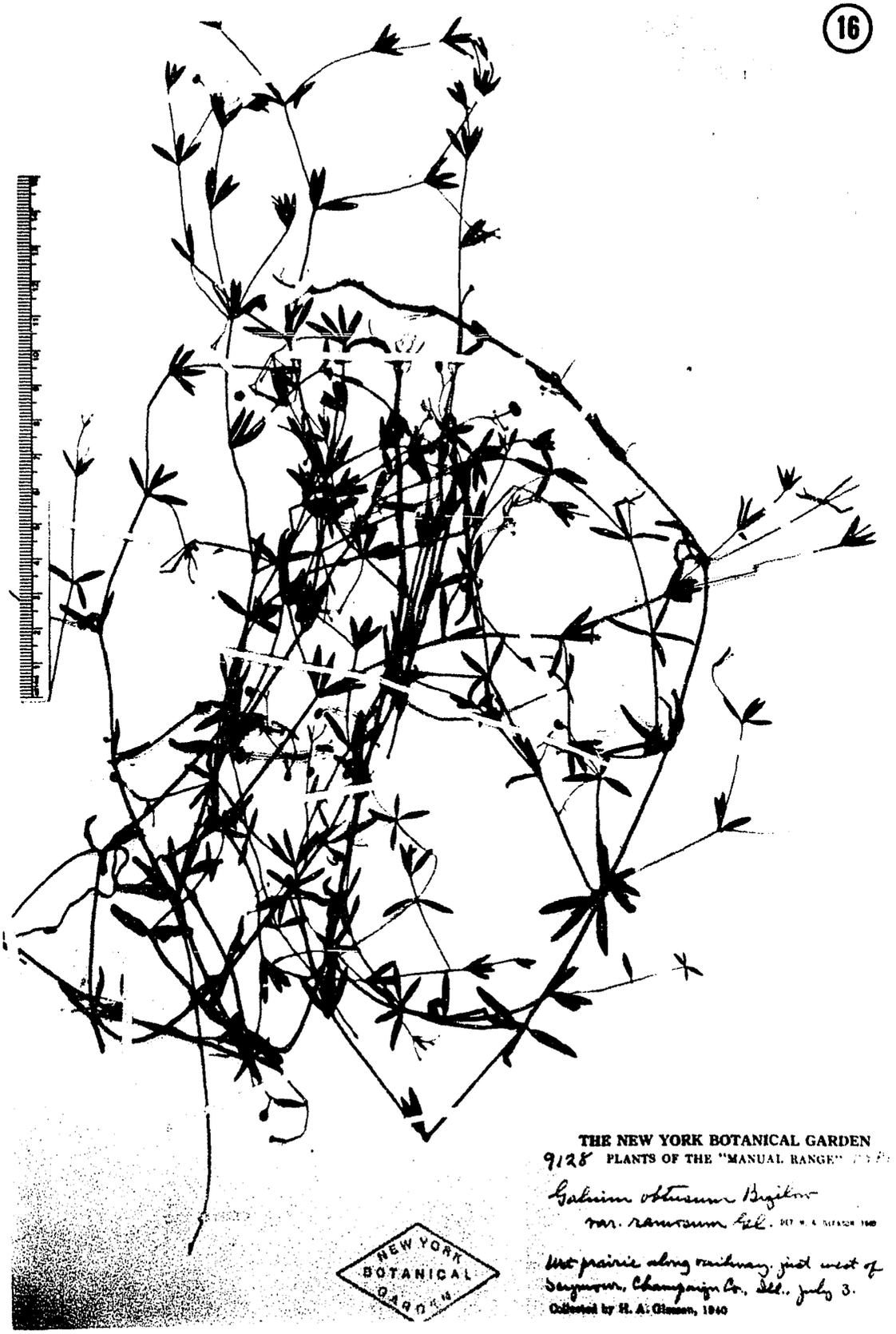


THE NEW YORK BOTANICAL GARDEN

9128 PLANTS OF THE "MANUAL RANGE"

Galium obtusum Bigelow
var. ramosum Gl. DET. H. A. GLEASON 1940

Wet prairie along railway, just west of Seymour, Champaign Co., Ill., July 3.

Collected by H. A. Gleason, 1940

NEW YORK BOTANICAL GARDEN

Leaves lanceolate, elliptical, or oblanceolate; largest leaves (8.4) 10 - 17.8 (26.4) mm long and (1.3) 1.6 - 3.6 (4) mm wide.

Type locality: "On the banks of Muddy brook, Roxbury."

Range: Eastern U.S. and adjacent Canada, west to Kansas, Oklahoma, and Texas (Southeastern United States, Map 11).

Flowering - Fruiting time: May through July, sometimes August.

Habitat: Frequent in wooded areas, wet meadows, and ditches; also along pond and creek margins and roadsides; occasionally in swampy, boggy areas.

S.E. United States specimens examined: One hundred and ninety-six sheets.

11b. G. OBTUSUM VAR. FILIFOLIUM (Wieg.) Fern., Rhodora 37: 443. 1935.

G. tinctorium var. filifolium Wieg., Bull. Torr. Bot. Cl. 24: 397. 1897.

G. filifolium (Wieg.) Small, Man. S.E. 1208. 1933.

G. obtusum subsp. filifolium (Wieg.) Puff, Beitr. Biol. Pfl. 51:

Leaves mostly linear; largest leaves typically (9.8) 12.4 - 18.7 (24) mm long and (0.8) 1 - 1.7 (2.4) mm wide, occasionally leaves (9.8) 12.2 - 19.7 (30.4) mm long and (0.8) 0.9 - 1.9 (3.7) mm wide.

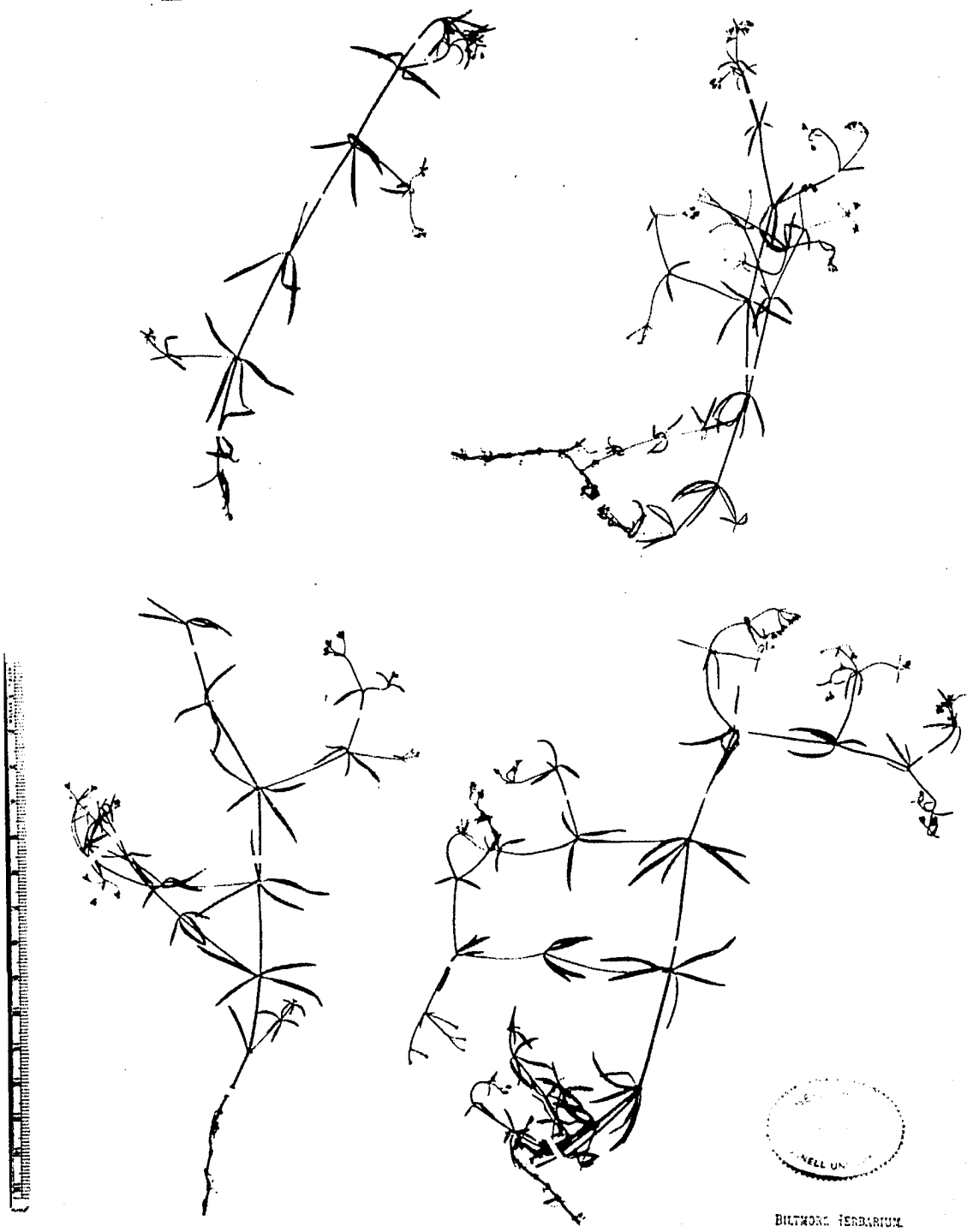
Type: Beadle 479, Bladen Co., North Carolina, 1896 (CU).—Fig. 17.

FIGURE 17

PHOTOTYPE OF

GALIUM OBTUSUM VAR. FILIFOLIUM

17



BILTMORE HERBARIUM

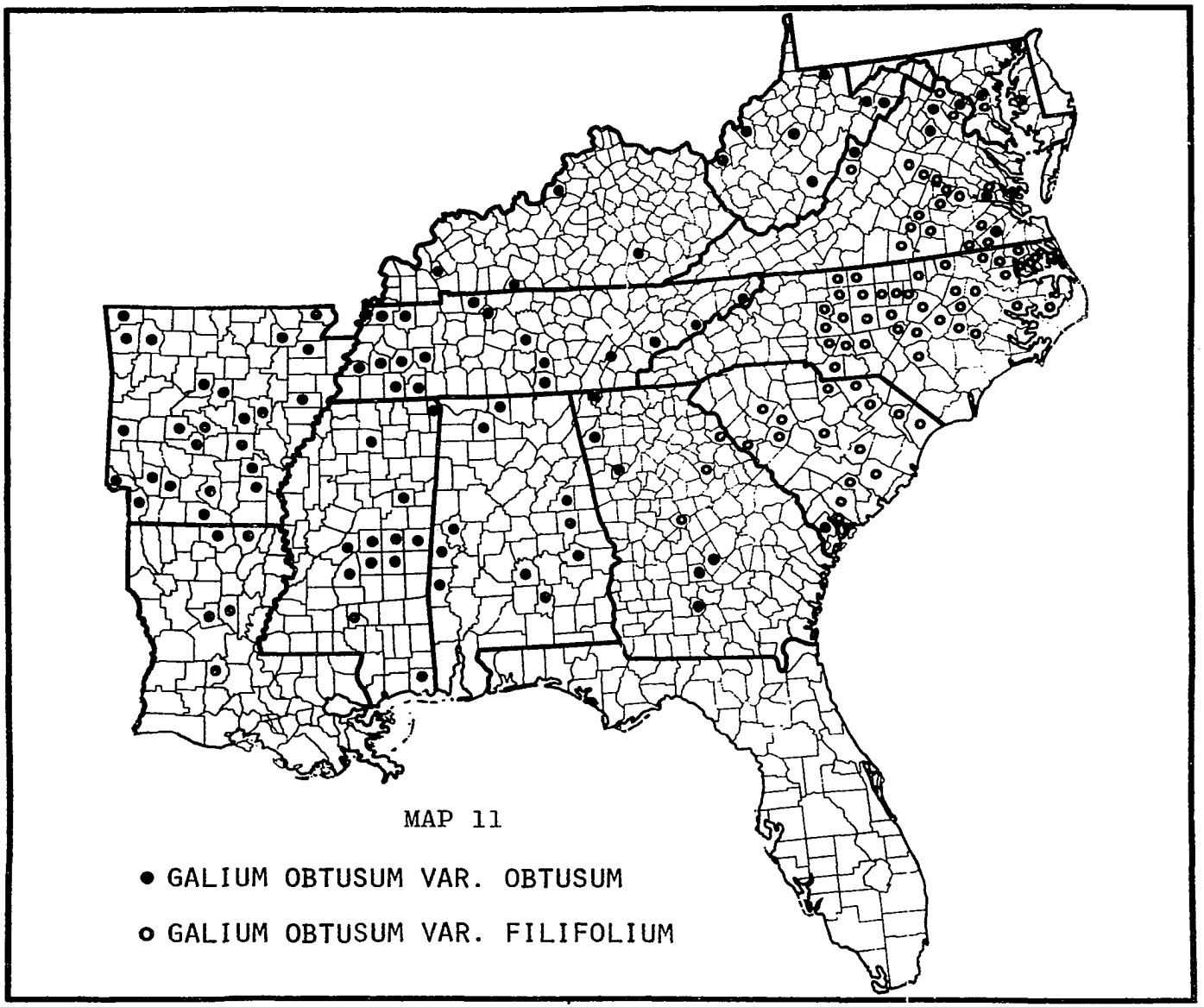
Galium tinctorium filifolium, Wiegand
Type specimen
Bull. Jow. Cl. 24, 389 (1897)

No. 479.

Galium trifidum L.

Scudhills, Bladen Co., N.C.

May 11th, 1896.



MAP 11

● GALIUM OBTUSUM VAR. OBTUSUM

o GALIUM OBTUSUM VAR. FILIFOLIUM

Range: Virginia south to Georgia (Southeastern United States, Map 11). Wiegand (1897) cited Rugel, collected in Florida in 1843, as belonging to this variety. I do not have any specimens of variety filifolium from Florida, but according to the literature, it can occur there.

Flowering - Fruiting time: Sometimes April, mostly May through August.

Habitat: Frequent in swamps, marshes, swales, alluvial bottomlands, damp thickets, floodplains, and low meadows; also along creek banks and occasionally along roadsides and woodland margins.

S.E. United States specimens examined: Two hundred and one sheets.

12. GALIUM PALUSTRE L., Sp. Pl. 1: 105. 1753.

Perennial, up to 5 dm tall; stems sometimes branching once, rarely twice, at the nodes, retrorsely hispid on the angles with hairs up to 0.1 mm long; leaves in whorls of four to six (sometimes opposite in the species), narrowly elliptical to oblanceolate, mostly obtuse, largest leaves 6 - 11 mm long and 1.6 - 2.3 mm wide, nerve one, leaf surfaces pubescent along the margins and usually on the midnerve beneath with scabrous or flattened-hispid hairs up to 0.1 mm long, secretory glands absent on the lower surface, margins often revolute; inflorescence cymose; flowers on glabrous pedicels, usually borne 2 - 3 at the ends of the several-times forked lateral and terminal peduncles; corollas showy, four-lobed,

white or rose-tinged, lobes obtuse or acute, 0.9 - 1.1 mm long and up to 0.8 mm wide, muriculate at least on the inner surface; fruits glabrous.—Fig. 18.

Type locality: "Habitat in Europae rivulis limosis."

Range: Eurasian; introduced in the United States from New England south to Pennsylvania and West Virginia and west to Michigan and Wisconsin (Southeastern United States, Map 12).

Flowering - Fruiting time: The one known collection from the southeastern United States was collected in June and is in flower.

Habitat: The specimen from West Virginia was collected in a wet ditch.

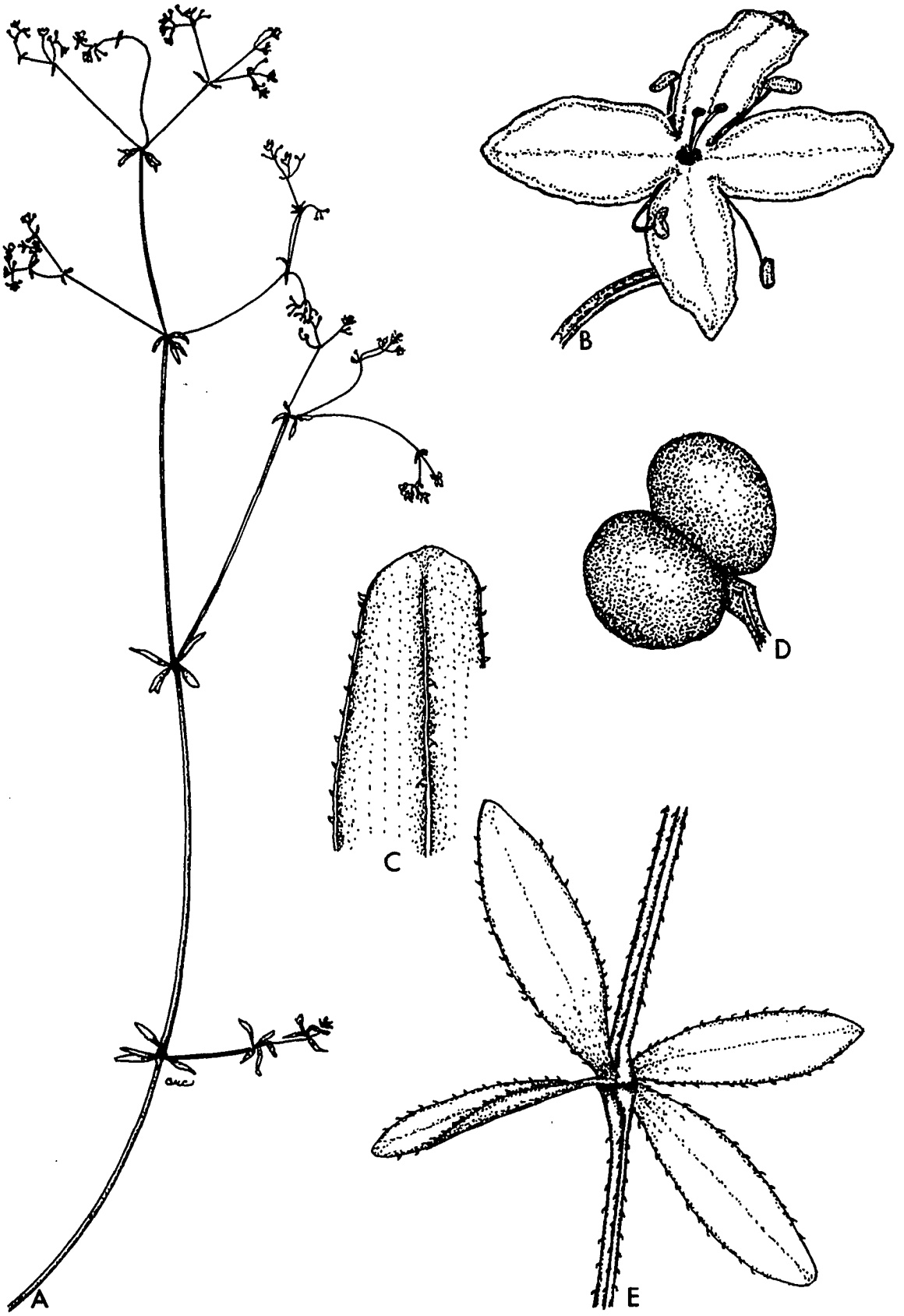
S.E. United States specimens examined: One sheet representing one collection.

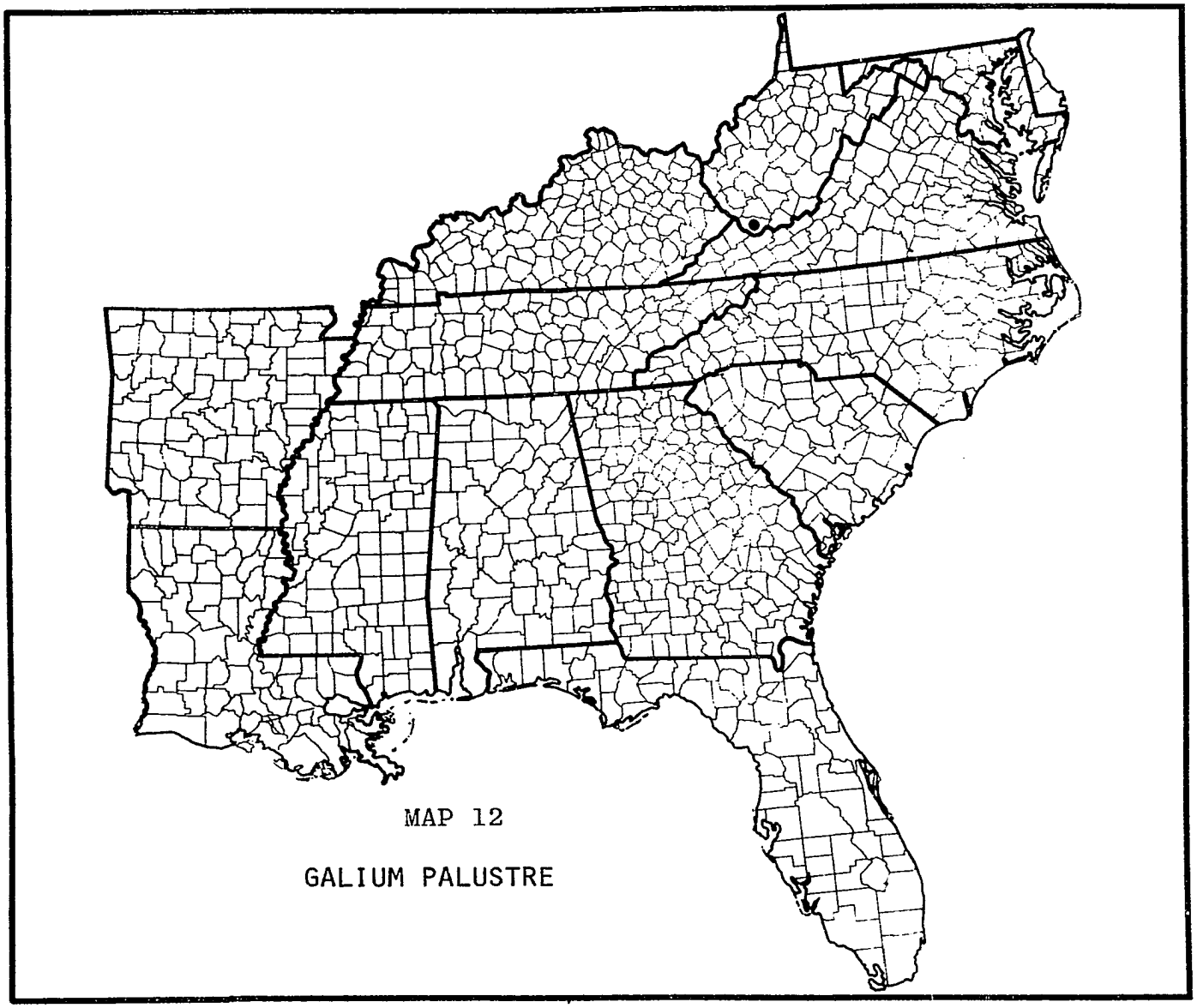
This Eurasian introduction is known in the southeastern United States by only one collection made in Anawalt, West Virginia in 1969. Presently, it is unknown whether this species is established in the area of collection or merely a waif.

The height and flower color data given in the description above were taken from Fernald (1950) since the available dried fragments were not helpful in obtaining this information. Also, there were no mature fruits on the specimen, but Gleason and Cronquist (1963) give the fruit size as 2 mm.

FIGURE 18

GALIUM PALUSTRE: A, habit x 1; B, flower x 23; C, lower leaf surface, margin, and apex x 13; D, fruit x 19; E, leaf whorl and stem x 8. A - E from D. J. Music s.n., June 17, 1969 (WVA).


A
B
C
D
E



MAP 12

GALIUM PALUSTRE

Galium palustre very closely resembles G. tinctorium. The former species has somewhat larger and broader corolla lobes, more elongated internodes, and the inflorescence is forked and, thus, more floriferous than in the latter species. The peduncles in G. palustre may branch up to three or four times. Usually there are three corolla lobes/flower in G. tinctorium, while there are four in G. palustre.

Wiegand (1897) pointed out that the stems may be glabrous in this species, but this was not the case in the specimen available.

13. GALIUM PARISIENSE L., Sp. Pl. 1: 108. 1753.

Erect, much branched annual, up to 6.4 dm tall (mostly 1.4 - 3.6 dm); stems branching near the base and diffusely throughout at maturity, retrorsely scabrous on the angles with hairs 0.1 mm long or less; leaves in whorls of mostly six or seven, sometimes five or eight, linear, elliptical to narrowly oblanceolate, mucronate or sometimes cuspidate, largest leaves mostly (3.6) 4.6 - 7.9 (11.4) mm long and (0.7) 0.8 - 1.3 (2) mm wide, nerve one, prominent, upper leaf surface with appressed, apically directed, scabrous hairs (these hairs sometimes only on the midnerve) or the surface rarely glabrous, lower leaf surface with vertically or apically directed, scabrous hairs on the midnerve, otherwise glabrous and lacking secretory glands, margins antrorsely scabrous (hairs on both surfaces and margins 0.1 mm or less long); inflorescence of compound

cymes; flowers on glabrous pedicels; corollas minute, four-lobed, greenish-white, lobes acute or rarely caudate, usually 0.4 - 0.6 mm long and 0.2 - 0.3 mm wide, glabrous; fruits muriculate or with unicinate hairs 0.3 mm or less long, each mature carpel (0.5) 0.7 - 0.9 (1.1) mm long and (0.4) 0.5 - 0.6 (0.8) mm wide.—Fig. 19.

The leaf margins are frequently revolute giving the appearance of an even narrower leaf. Leaf width measurements were taken only on leaves whose margins were not revolute. Also, in mature specimens, the leaves are obscured by the numerous flowering branches.

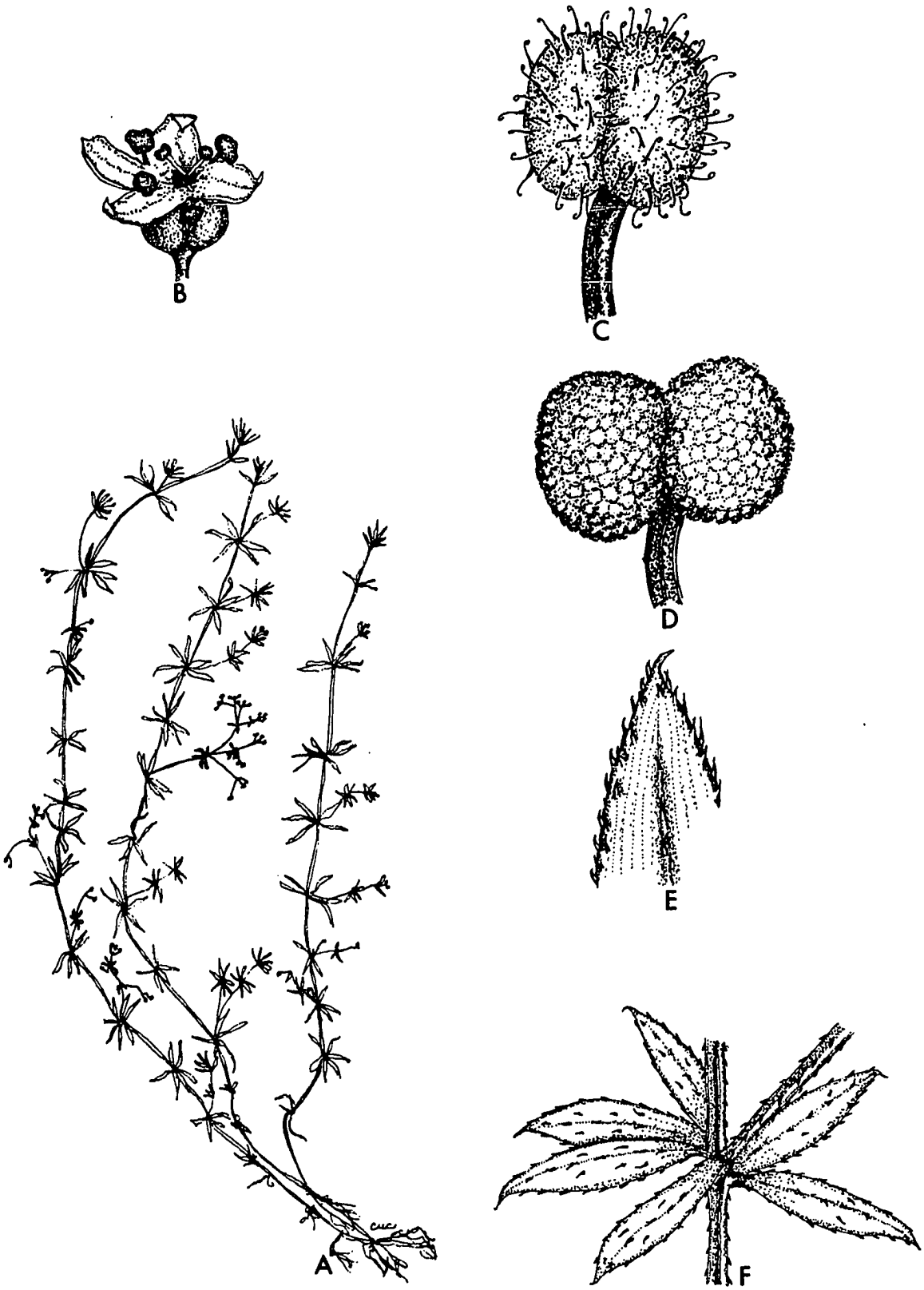
Flower color for this species has been reported as greenish-white (Fernald, 1950); however, no living material was examined in this study.

Only in Louisiana have specimens been found whose fruits are uncinate hairy. The Louisiana specimens represent six duplicates of one collection. Presently no material with tuberculate fruits has been examined from Louisiana even though the tuberculate phase is the only one found in all other southeastern states. These two phases have been recognized as varieties of G. parisiense. The typical variety has uncinate hairs on the fruits, while variety leiocarpum Tausch has muriculate fruits.

C. L. Hitchcock et al. (1959) pointed out that G. anglicum var. parvifolium (Gaud. ex R. & S.) DC. may provide an earlier varietal epithet than G. parisiense var. leiocarpum

FIGURE 19

GALIUM PARISIENSE: A, habit x 1; B, flower x 25; C, fruit with uncinate hairs x 42; D, muriculate fruit x 42; E, lower leaf surface, margin, and apex x 25; F, leaf whorl and stem x 7. A from S. W. Leonard 3435 (NCU), B, D from O. W. Gupton 4066 (NCU), C from J. W. Thieret 29393 (NCU), and E, F from C. E. Wood, Jr. 6130 (GH).


B
C
D
E
A
F

Tausch but that no proper nomenclatural combination appears to have been made. He did not propose a new combination since a thorough search of the European lieterature might provide an even earlier varietal epithet. A search of such literature is not within the scope of this study, so I, too, will not at this time propose a new combination.

This species and G. concinnum have been confused occasionally. Their differences are discussed under G. concinnum.

KEY TO VARIETIES

Fruits uncinate hairy. . 13a. G. parisiense var. parisiense
Fruits muriculate. . . . 13b. G. parisiense var. leiocarpum

13a. G. PARISIENSE VAR. PARISIENSE

G. parisiense L., Sp. Pl. 1: 108. 1753.

G. litigiosum DC., in Lam. & DC. Fl. Fran. 4: 263. 1805.

G. litigiosum β. nanum DC., in Lam. & DC. Fl. Fran. 4: 263. 1805.

G. parisiense ssp. litigiosum (DC.) Gaud., Fl. Helvet. 1: 438. 1828.

G. parisiense var. trichocarpum Tausch, Flora 18: 354. 1835.

G. parisiense α. typicum Beck von Man., Fl. Nied. Österr. 2: 1122. 1893.

Fruits with uncinate hairs 0.3 mm or less long.

Type locality: "Habitat in Anglia, Gallia."

Range: European; introduced in the United States in California and Louisiana (Southeastern United States, Map 13).

Flowering - Fruiting time: June for the one known collection from the Southeast. The plants are mostly in fruit.

Habitat: This one collection was made along a railroad.

S.E. United States specimens examined: Six sheets representing one collection.

13b. G. PARISIENSE VAR. LEIOCARPUM Tausch, Flora 18: 354. 1835.

G. anglicum Huds., Fl. Angl. ed. 2. 69. 1778.

G. divaricatum Lam., Encyc. Meth. 2: 580. 1788.

G. parvifolium Gaud. ex. Roem. & Schult., Syst. Veg. 3: 246. 1818.

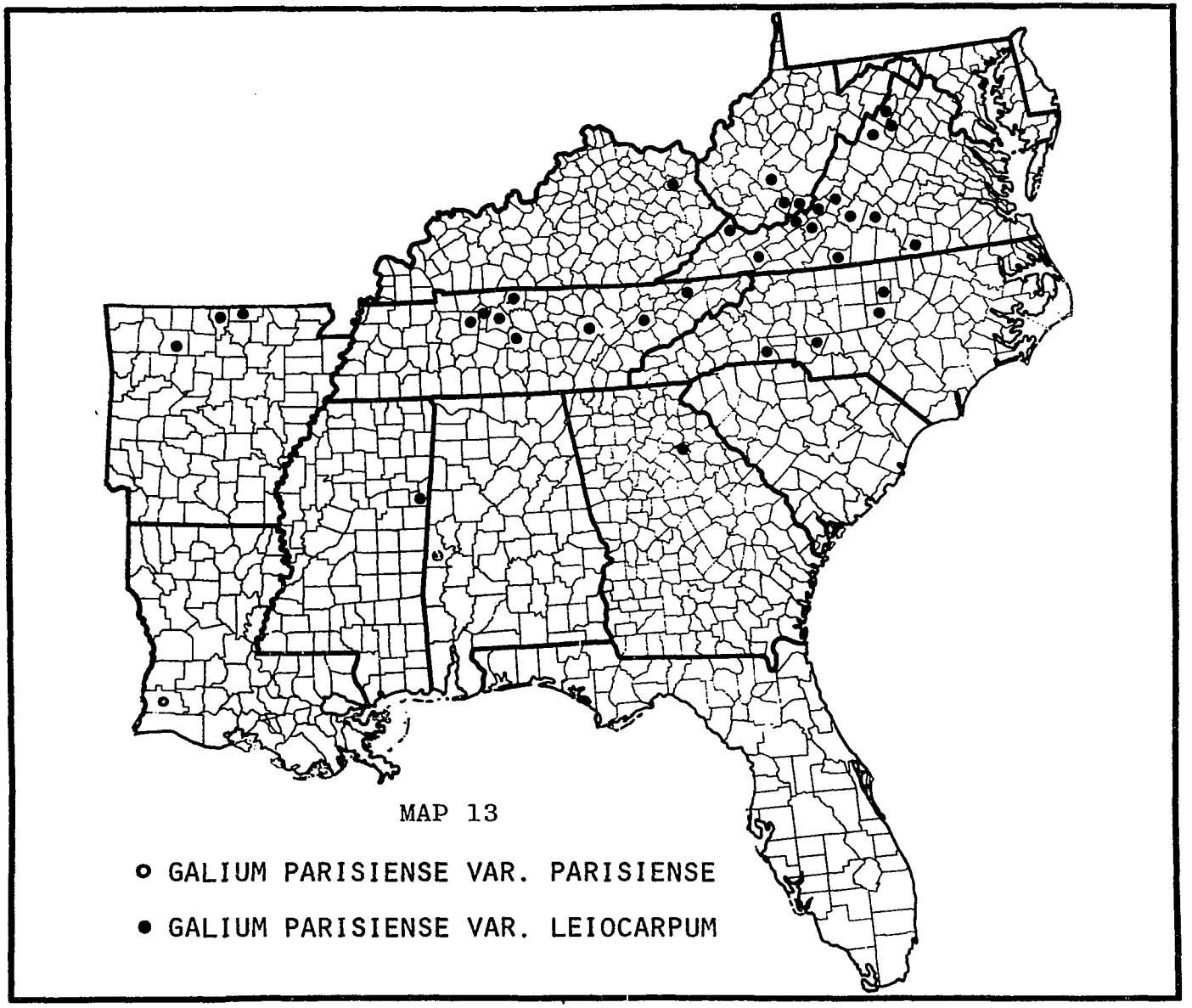
G. parisiense ssp. anglicum (Huds.) Gaud., Fl. Helvet. 1: 438. 1828.

G. parisiense ssp. parvifolium (Gaud. ex. R. & S.) Gaud., Fl. Helvet. 1: 439. 1828.

G. anglicum var. parvifolium (Gaud. ex R. & S.) DC., Prodr. 4: 607. 1830.

G. parisiense var. divaricatum (Lam.) Devis., Fl. Dalmat. 3: 8. 1852.

G. parisiense β. anglicum (Huds.) Beck von Man., Fl. Nied. Österr. 2: 1122. 1893.



MAP 13

○ GALIUM PARISIENSE VAR. PARISIENSE

● GALIUM PARISIENSE VAR. LEIOCARPUM

Fruits muriculate.

Type locality: Europe.

Range: European; introduced in the United States from Ohio and West Virginia south to Georgia and west to Arkansas; also in California and Oregon (Southeastern United States, Map 13).

Flowering - Fruiting time: Rarely May, mostly June through August.

Habitat: Introduced in lawns, fields, pastures, meadows, and waste places; along railroads, roadsides, and fence rows; and rarely along creeks and rivers. Occasionally found in rocky glades and foothills and on rocky ledges and outcrops.

S.E. United States specimens examined: One hundred and three sheets.

14. GALIUM PEDEMONTANUM All., Auct. Fl. Pedem. 2. 1789, not Bieb.

Vaillantia pedemontana (All.) Bell., Mem. Acad. Sci. Turin, 1790 - 91. 5: 252. t. 7, p. 286. 1793, not Waldst. & Kit.

Erect annual, up to 5 dm tall (mostly 1.3 - 3.6 dm); stems simple or branching near the base, rarely with a short branch at a node, angles of the stem with long, villous and retrorse, flattened-hispid hairs throughout, the hispid hairs often more abundant and dense on the upper stem angles (0.6 - 1.6 mm long if villous and 0.1 - 0.4 mm long if hispid);

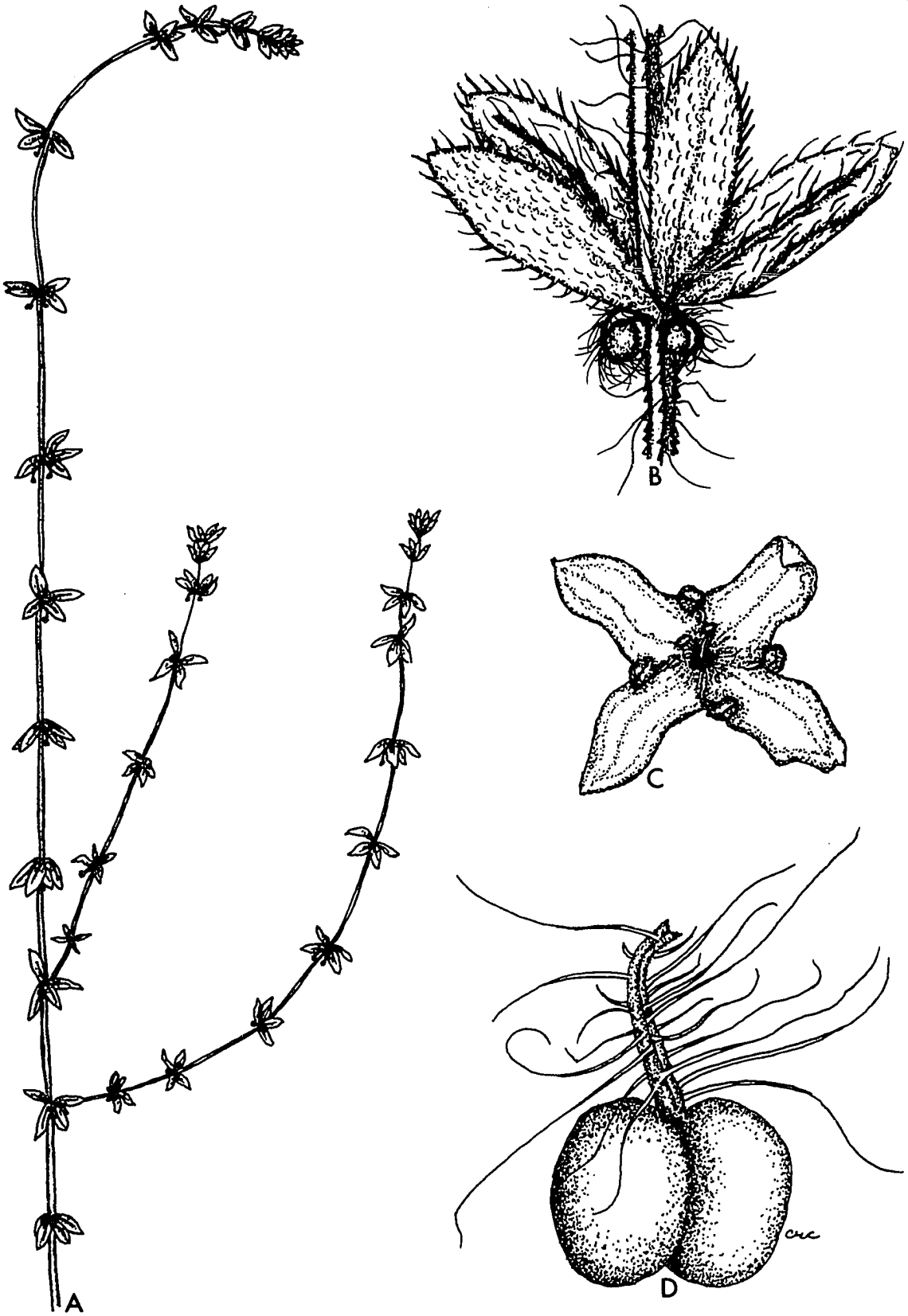
leaves in whorls of four, elliptical, acute to slightly rounded, largest leaves mostly (4) 5.5 - 8.3 (10) mm long and 2.2 - 3.1 mm wide, nerve one, prominent, lateral nerves obscure when present, leaf surfaces, margins, and midnerve with equally abundant, long, straight hairs 0.2 - 1.2 mm long (hairs on the upper surface sometimes slightly shorter, somewhat appressed, and apically directed), secretory glands present only near the apex on the lower surface; inflorescence cymose; flowers usually pedicellate, borne 1 - 3 at the ends of short, axillary peduncles (these occurring four at a node and mostly 1.5 - 2.2 mm long), the pedicels and peduncles long villous, reflexed in fruit, often hidden by the leaves; corollas four-lobed, pale yellow to white, lobes acute to slightly rounded, usually 0.3 - 0.4 mm long and 0.2 - 0.3 mm wide, glabrous (rarely with one or two hairs); fruits glabrous, each mature carpel mostly (0.7) 0.8 - 1 (1.2) mm long and (0.5) 0.6 - 0.8 (0.9) mm wide.—Fig. 20.

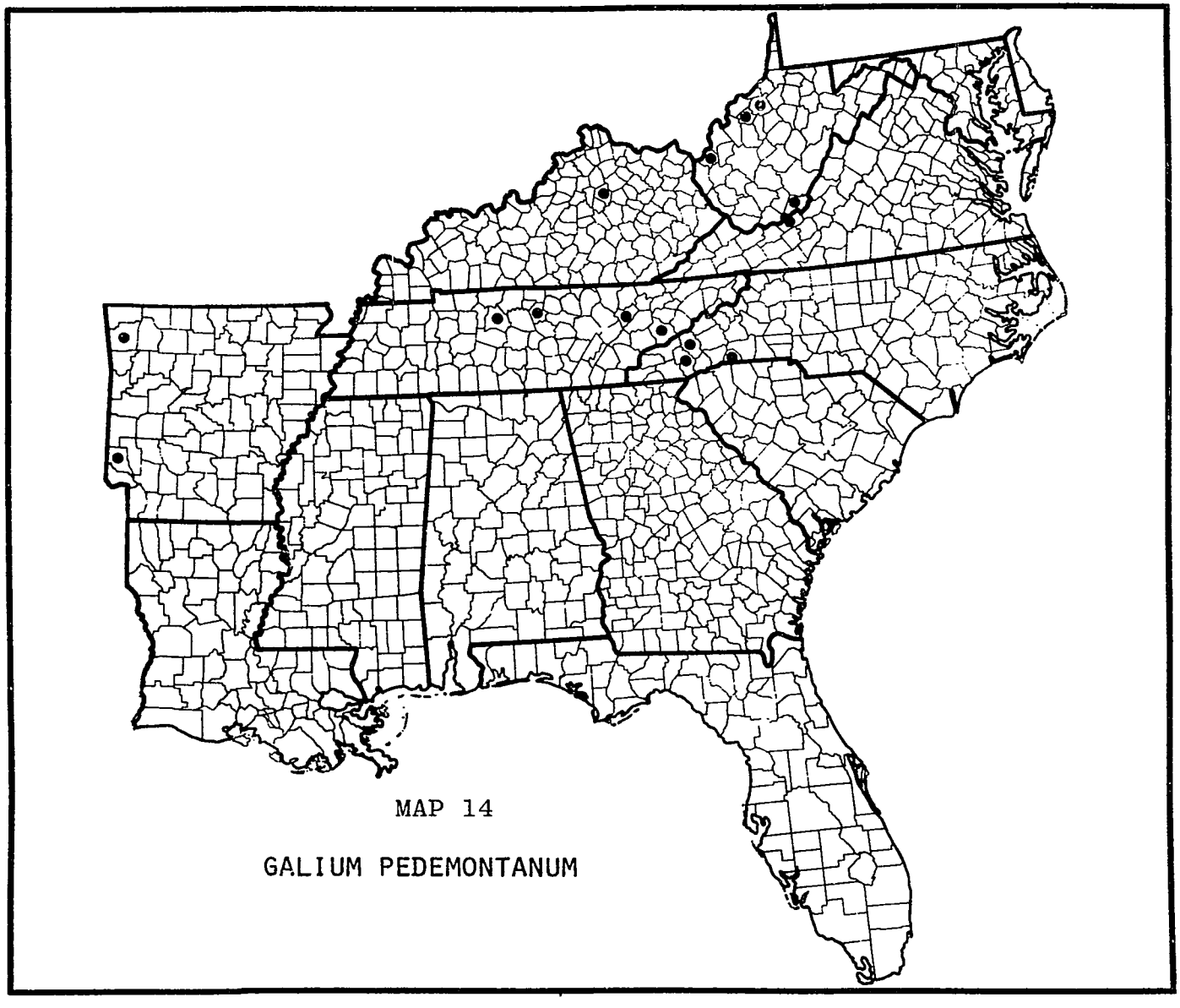
Type locality: Europe.

Range: European; introduced in the United States from Ohio south to North Carolina and Tennessee, west to Arkansas and Oklahoma, and north to Missouri and Illinois (Southeastern United States, Map 14). This species has spread considerably westward since its first report from West Virginia and Kentucky (Bartholomew, 1941). Just recently I annotated a specimen of G. pedemontanum which had been collected in Montana.

FIGURE 20

GALIUM PEDEMONTANUM: A, habit x 1; B, leaf whorl, stem, and reflexed fruits at node x 8; C, flower x 62; D, fruit and pedicel x 37. A - D from D. Pittillo 3567 (OKL).


A
B
C
D
orc



MAP 14

GALIUM PEDEMONTANUM

Flowering - Fruiting time: April through August.

Habitat: Introduced in lawns, pastures, fields, and grassy thickets, and along road and creek banks.

S.E. United States specimens examined: Forty-five sheets.

This species is seldom misidentified but has on occasion been confused with G. virgatum.

15. GALIUM PILOSUM Ait., Hort. Kew. 1: 145. 1789.

Erect, tufted perennial, up to 12.6 dm tall (mostly 3.5 - 7.7 dm); stems simple or branching, glabrous to glabrate or spreading pilose or with uncinate hairs on the angles (these hairs up to 0.7 mm long when spreading pilose), sides rarely pubescent; leaves in whorls of four, broadly to narrowly elliptical to broadly oblong, usually mucronulate, largest leaves (8.6) 13.5 - 21.4 (32.4) mm long and (1.8) 5.4 - 9.4 (16.9) mm wide, midnerve prominent, lateral nerves obscure or absent, surfaces of leaves and midnerve glabrous to densely pilose with hairs up to 0.6 mm long, secretory glands scattered over the lower leaf surface, margins ciliate or with a few uncinate hairs; inflorescence of simple and compound cymes, lateral and terminal; flowers on glabrous or pubescent pedicels; corollas four-lobed, usually greenish on the outer surface and purple on the inner surface, lobes narrowly and abruptly caudate (the appendage up to 0.4 mm long, often folded inside or broken off), usually 0.7 - 0.9 (1) mm long excluding the appendage and 0.6 - 0.9 (1) mm wide,

glabrous or pubescent on the undersurface with hairs up to 0.2 mm long; fruits pubescent with uncinate hairs seldom over 0.7 mm long, each mature carpel (1.5) 1.6 - 2 (2.2) mm long and 1.3 - 1.6 (1.7) mm wide.—Fig. 21.

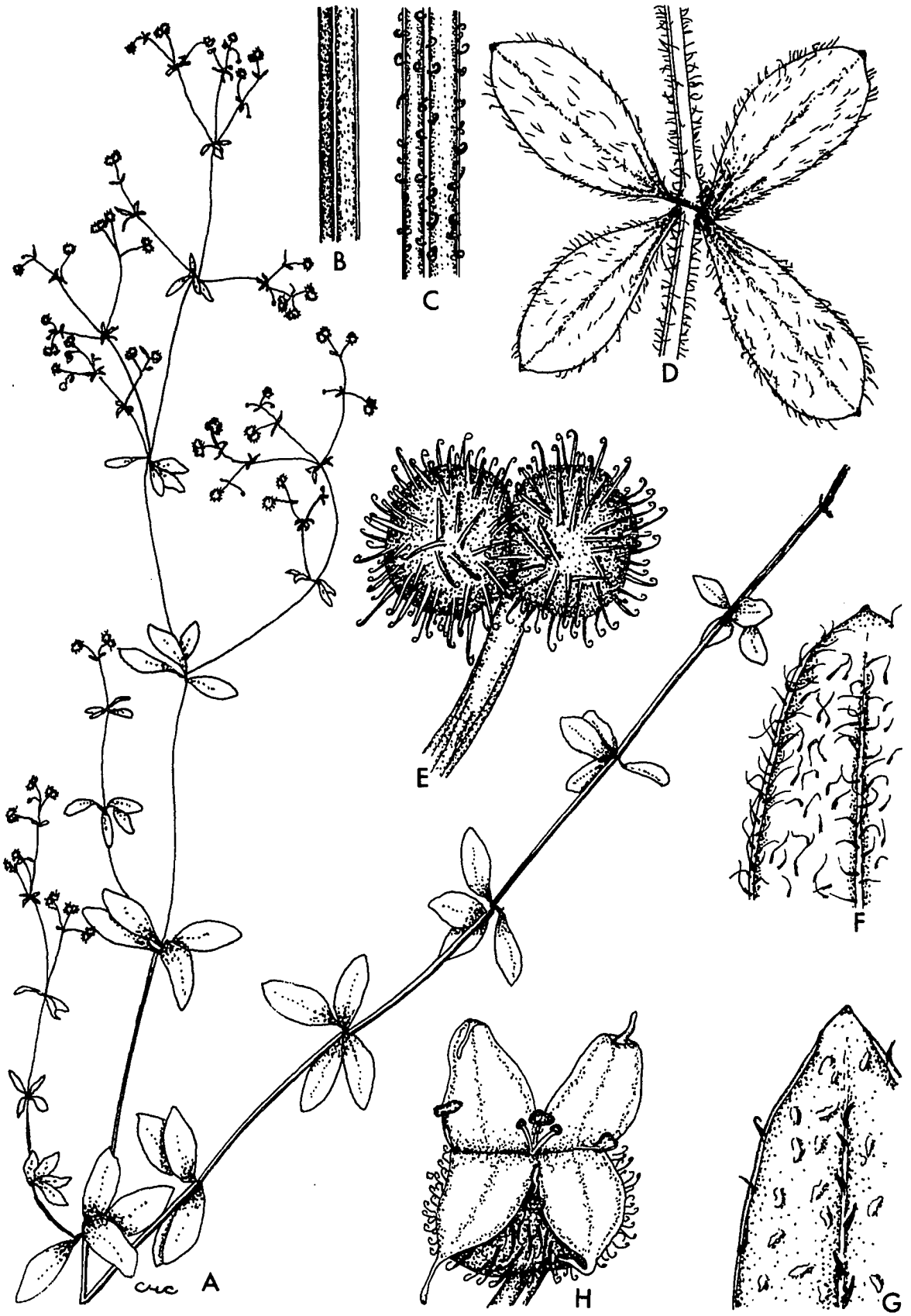
Weatherby and Blake (1916) recognized three varieties of this species and pointed out an occasional intermediate. Their separation of varieties was dependent, for the most part, upon the degree of hair curvature present on the angles of the lower stem or the absence of such hairs. Variety pilosum was described as "Stem from densely pilose all over to sparsely spreading-pilose or spreading-hispid-pilose on the angles below." The description, "Stem finely and usually densely incurved-uncinate on the angles, at least below; ..." was given for variety puncticulosum. "Stem glabrous throughout; ..." described variety laevicaule.

The recognition of all three varieties in the southeastern United States seems warranted with slight amendments of the varietal circumscriptions of two of the varieties.

As noted previously for Oklahoma material of this species (Lawson, 1973), most Oklahoma specimens had straight-spreading hairs on the angles of the lower stem with a noticeable change in hair curvature upward along the stem angles. The pubescence on at least the upper one-third of these stem angles was of antrorsely or retrorsely uncinate hairs. This same variation occurs in all states in the

FIGURE 21

GALIUM PILOSUM: A, habit x 1; B, glabrous stem x 5; C, stem with uncinate hairs x 8; D, leaf whorl with stem spreading pilose x 3; E, fruit x 13; F, densely pilose lower leaf surface, margin, and apex x 23; G, glabrous lower leaf surface with scattered secretory glands, margin, and apex x 23; H, flower x 25. A, E, F from C. A. Lawson & D. Dotts 773 (OKL), B from A. H. Curtiss 6420 (MO), C from C. A. Lawson & D. Dotts 876 (OKL), D from C. A. Lawson & D. Dotts 790 (OKL), G from O. Lakela, R. & J. A. Lassiter 26038 (USF), and H from D. M. E. Ware 3249 (VDB).


A
B
C
D
E
F
G
H

southeastern United States, but only rarely in West Virginia and Florida. In Arkansas the majority of specimens examined varied in this manner. After examining specimens annotated by Weatherby and Blake, it is now known that they considered this variation to be an intermediate between variety pilosum and variety puncticulosum; however, the abundance of this so-called "intermediate" is now far greater than they seemed to indicate. Variety puncticulosum is amended in this study to include these plants.

Weatherby and Blake (1916) cited C. R. Ball 514 (GH) as being intermediate between variety pilosum and variety laevicaule. In my opinion, all but one of the plants on the sheet have a noticeable change in hair curvature upward along the stem, and, thus, are called here variety puncticulosum. The remaining plant on this sheet has a few straight-spreading hairs scattered on the stem angles and could probably best be described as "glabrate." This glabrate condition, intermediate between variety pilosum and variety laevicaule is also found on one isotype, A. H. Curtiss 6420 (US). Variety laevicaule is amended in this study to include both glabrous and glabrate specimens of G. pilosum.

Narrowly elliptical leaves do not seem to correlate consistently with the glabrous or glabrate stems of variety laevicaule. Only in Florida can this correlation be made frequently. Likewise, broadly elliptical and broadly oblong leaves are not always restricted to plants whose stem pubescence fit varieties pilosum or puncticulosum.

Frequently, the type of pubescence on the leaves will be similar to that on the stem angles. This, however, is not always true, making a positive correlation of leaf to stem pubescence difficult. When present on the leaf surfaces, the pubescence is highly variable, ranging from appressed, straight or curved hairs to vertical, straight or curved hairs. Any of these variations may occur with any of the variations in stem pubescence.

The variation in stem pubescence correlates well with geographic distribution. Variety pilosum is most abundant in the northern portion of the southeastern United States, while variety puncticulosum is found most frequently in the southern portion. Variety laevicaule is most abundant in Florida, but it may be found occasionally in much of the southern portion. Mixed varietal collections were found infrequently in the examination of available material. It is unknown whether these plants were taken from the same or different populations, but of the 36 actual field populations examined in this study, only two from North Carolina were mixed.

This species is frequently misidentified as G. circaezans and G. hispidulum. The differences between G. pilosum and the latter two species are discussed individually under G. circaezans and G. hispidulum.

KEY TO VARIETIES

A. Angles of upper stem glabrous or nearly so.

B. Angles of lower stem pubescent.

C. Hairs on angles of lower stem spreading to widely spreading, straight to curved. . . . . 15a. G. pilosum var. pilosum

CC. Hairs on angles of lower stem antrorsely or retrorsely uncinate. . . . . 15b. G. pilosum var. puncticulosum

BB. Angles of lower stem glabrous or nearly so. . . . 15c. G. pilosum var. laevicaule

AA. Angles of upper stem pubescent.

D. Hairs on angles of upper stem spreading to widely spreading, straight to curved. . . . . 15a. G. pilosum var. pilosum

DD. Hairs on angles of upper stem antrorsely or retrorsely uncinate. . . . . 15b. G. pilosum var. puncticulosum

15a. G. PILOSUM VAR. PILOSUM

G. pilosum Ait., Hort. Kew. 1: 145. 1789.

G. bermudense L., Sp. Pl. 1: 105. 1753, pro parte. For explanation of this being a nomen confusum, see Weatherby and Blake (1916).

G. puncticulosum β. pilosum (Ait.) DC., Prod. 4: 601. 1830.

G. rotundifolium θ. bermudense f. pilosum (Ait.) Ktze. Rev. Gen. 1: 282. 1891.

Angles of upper stem glabrous or with spreading to widely spreading, straight to curved hairs.

Type: "New York, Dr. Martin."

Range: Eastern United States and adjacent Canada, west to Kansas, Oklahoma, and Texas (Southeastern United States, Map 15; this variety is known to occur in Delaware and Florida; however, no county localities could be determined for use on the distribution map).

Flowering - Fruiting time: Frequent in pine, pine-oak, and oak-hickory forests; also along margins of woods, roadsides, and aquatic areas and on rocky bluffs and ridges; occasional in fields, meadows, and thickets.

S.E. United States specimens examined: Four hundred and eighty-seven sheets.

15b. G. PILOSUM VAR. PUNCTICULOSUM (Michx.) T. & G., Fl. N. Am. 2: 24. 1841.

G. puncticulosum Michx., Fl. Bor. Am. 1: 80. 1803.

G. purpureum Walt., Fl. Car. 87. 1788, not L.

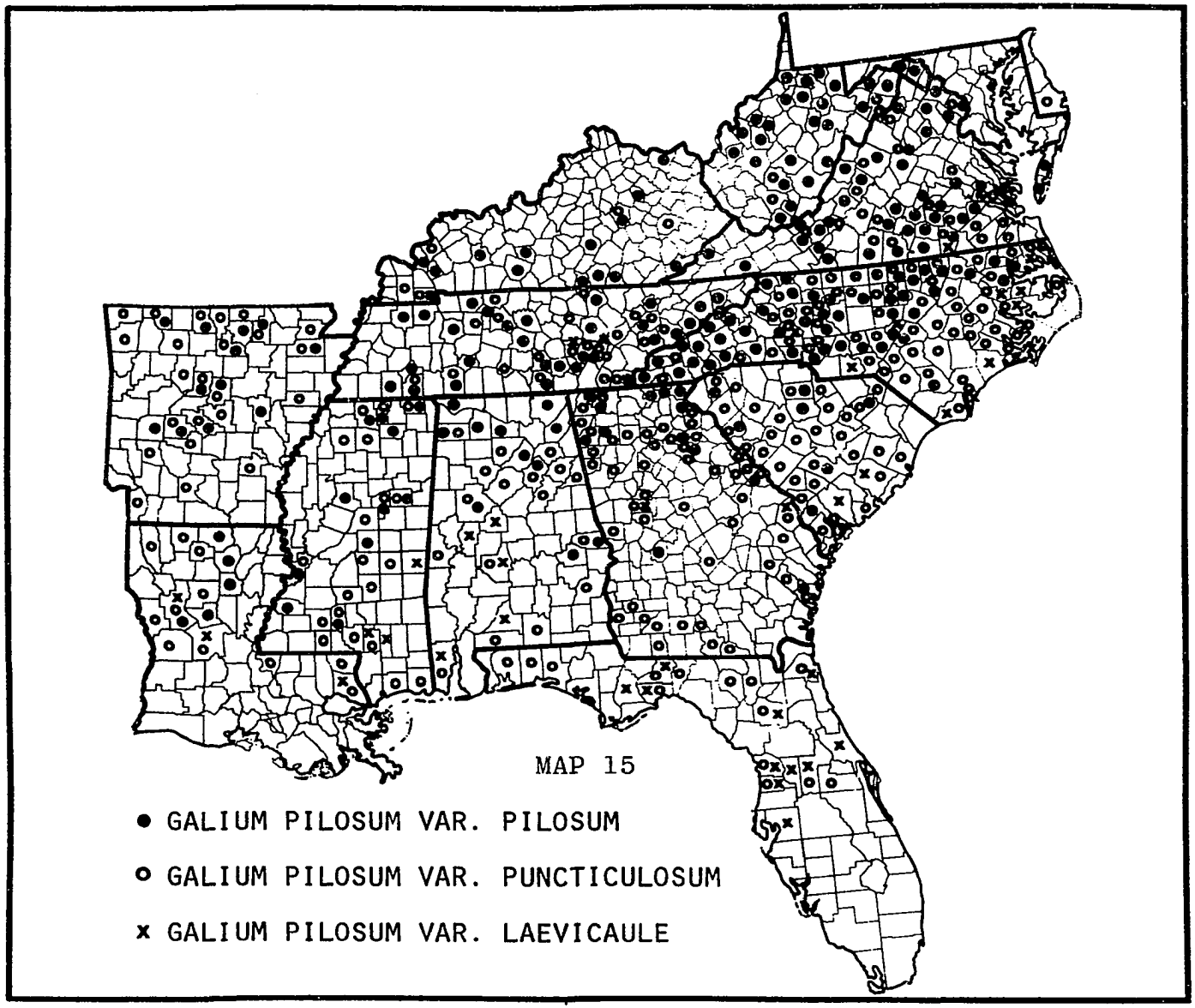
G. walteri J. F. Gmel., Syst. ed. 13. 2: 237. 1791.

G. punctatum Pers., Syn. 1: 128. 1805.

Angles of upper stem nearly glabrous or with mostly retrorsely or antrorsely uncinate hairs.

Type locality: "In Carolina inferiore."

Range: Mostly southeastern United States (Map 15), west to Missouri, Oklahoma, and Texas.


MAP 15
● GALIUM PILOSUM VAR. PILOSUM
o GALIUM PILOSUM VAR. PUNCTICULOSUM
x GALIUM PILOSUM VAR. LAEVICAULE

Flowering - Fruiting time: Rarely May in the southern-most states; mostly June through August with mature fruiting material through October.

Habitat: Similar to that of variety pilosum and also occasionally along sandy beaches.

S.E. United States specimens examined: Six hundred and twenty-four sheets.

15c. G. PILOSUM VAR. LAEVICAULE Weath. & Blake, Rhodora 18: 194. 1916.

Angles of stem glabrous or nearly so throughout.

Type: A. H. Curtiss 6420, low fertile ground near Jacksonville, Florida, June 18, 1898 (GH).

Range: Mostly the southern portion of the southeastern United States (Map 15), west to Texas.

Flowering - Fruiting time: May through August.

Habitat: Frequent in pine and hardwood forests; also along roadsides and swamp margins.

S.E. United States specimens examined: One hundred and twenty-four sheets.

16. GALIUM TEXENSE Gray, Proc. Am. Acad. 19: 80. 1883.

G. californicum var. texanum Torr. & Gray, Fl. N. Am. 2: 20. 1841.

G. texanum (T. & G.) Wieg., in Small Fl. S. E. U. S. ed. 1. 1338. 1903, not Scheele, 1848.

Erect or prostrate annual, up to 5.3 dm tall; stems simple or branching at the base, angles of the stem glabrous in the upper portion of the plant or pubescent throughout with straight, spreading hairs frequently 0.4 - 0.6 mm long and occasionally up to 0.9 mm long; leaves in whorls of four, two of these slightly larger than the other two, elliptical to broadly elliptical or sometimes ovate, acute and often tipped with a stiff, straight hair, largest leaves on the main stem mostly 4 - 6 mm long and 1.7 - 2.5 mm wide, nerve one, leaf surfaces with scattered, stiff, straight hairs and with secretory glands present only near the apex on the lower surface, margins with straight, spreading or slightly ascending hairs (surface and marginal hairs similar in length to those on the stem angles); inflorescence of axillary, compound dichasia, each simple dichasium subtended by four unequal leaves with the central flower on a naked, glabrous pedicel, the lateral branches pubescent, forming peduncles for the next dichasium; corollas four-lobed, light green to yellow, minute, lobes acute, 0.4 mm or less long and 0.3 mm or less wide, margins and submargins of the lobes beset with long, straight hairs up to 0.4 mm long; fruits with uncinate hairs up to 0.4 mm long, each mature carpel mostly 1.3 - 1.6 mm long and 1.1 - 1.4 mm wide.—Fig. 22.

Type: Drummond 115 , "Hills and riverbanks, Texas...." (GH). v.s. (For phototype, see Lawson, 1973).

Range: Texas, Oklahoma, and Arkansas (Southeastern United States, Map 16).

FIGURE 22

GALIUM TEXENSE: A, habit x 1; B, fruit x 13; C, flower x 25; D, lower leaf surface, margin, and apex x 25; E, leaf whorl and stem x 6. A - E from C. A. Lawson 714 (OKL).


A
B
C
D
E

Flowering - Fruiting time: The one known collection from the southeastern United States was made in June with the specimens in late fruit. This species can generally be found from April through early June in Oklahoma (Lawson, 1973) and March through May in Texas (Correll and Johnston, 1970).

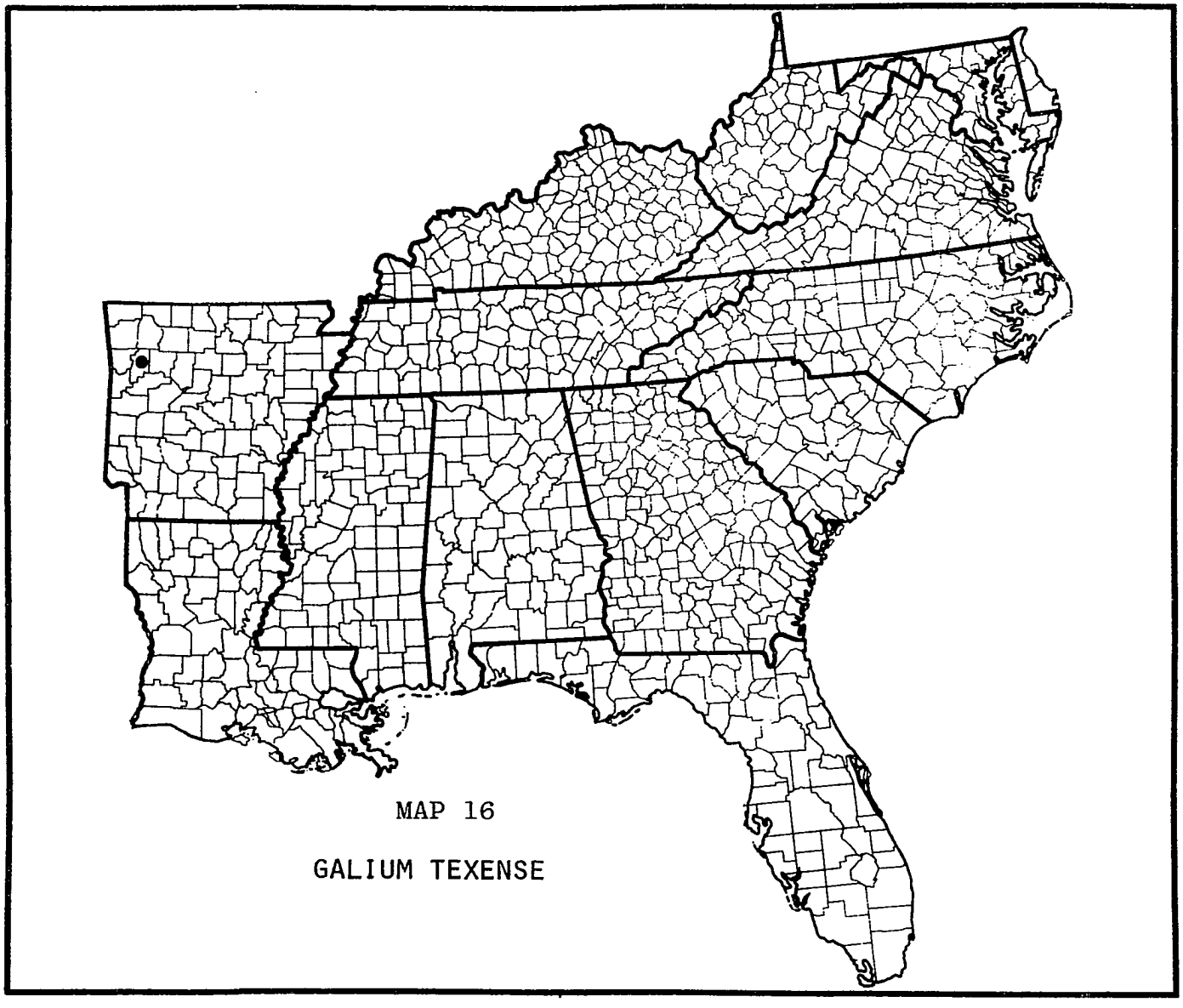
Habitat: These Arkansas specimens were found in a steep, rocky glade. Other possible habitats would include granitic slopes and sandy, open woodlands.

S.E. United States specimens examined: Four sheets representing one collection.

The one collection of G. texense made in Arkansas represents the known range of this species in the southeastern United States. The measurements cited in the description were taken from four duplicates of this collection. This species is known to produce slightly longer and wider leaves and corolla lobes than are indicated in the description. When additional specimens of G. texense are collected in the southeastern United States (probably in Arkansas or Louisiana), alteration of measurements will likely be necessary.

The flower color given in the description was observed from specimens I collected in Oklahoma. Shinners (1958) listed "whitish" in addition to "light green to yellowish" for the flower color of this species.

In the ultimate branches two of the four leaves subtending each simple dichasium are extremely minute or even absent. This reduction in size or number of leaves is



MAP 16

GALIUM TEXENSE

probably due to the immaturity of the simple dichasia in the ultimate branches.

Lauramay Dempster has pointed out to me that the fruit bristles in this species turn downward.

17. GALIUM TINCTORIUM L., Sp. Pl. 1: 106. 1753.

G. claytoni Michx., Fl. Bor. Am. 1: 78. 1803.

G. trifidum β. tinctorium (L.) Torr. & Gray, Fl. N. Am. 2: 22. 1841.

G. tinctorium var. floridanum Wieg., Bull. Torr. Bot. Cl. 24: 397. 1897. Type: Nash 152, Florida, 1894 (CU).

G. trifidum subsp. tinctorium (L.) Hara, Rhodora 41: 388. 1939.

G. tinctorium subsp. floridanum (Wieg.) Puff, Beitr. Biol. Pfl. 51:

Erect or reclining perennial, up to 15 dm tall (mostly 2.9 - 7 dm); stems usually branching once at each of the occasionally hairy nodes, retrorsely scabrous on the angles with hairs up to 0.1 mm long or nearly glabrous; leaves in whorls of four, five, or six, narrowly elliptical to oblanceolate, mostly obtuse, largest leaves (6.2) 9.6 - 15.5 (22.9) mm long and (1) 1.8 - 3.1 (4.9) mm wide, nerve one, leaf surfaces mostly scabrous along the margins and usually on the midnerve beneath (these hairs up to 0.14 mm long, often flattened-hispid, and generally descending) or rarely completely glabrous, secretory glands absent on the lower surface, margins often revolute; inflorescence cymose;

flowers on glabrous pedicels, usually borne 2 - 3 at the end of lateral and terminal peduncles, the pedicels often subtended by one or more reduced leaves; corollas minute, three- or four-lobed, white, lobes obtuse or acute, usually (0.4) 0.6 - 0.9 (1.1) mm long and (0.4) 0.5 - 0.7 (0.8) mm wide, glabrous; fruits glabrous, each mature carpel (1.1) 1.3 - 1.8 (2.4) mm long and (1.1) 1.3 - 1.7 (2.4) mm wide.—Fig. 23.

Type: "Habitat in America septentrionali. Kalm." "... probably Crown Point, New York, at the foot of Lake Champlain" (Fernald, 1935).

Range: Eastern United States and adjacent Canada, west to Nebraska, Kansas, Oklahoma, and Texas (Southeastern United States, Map 17).

Flowering - Fruiting time: May through September, occasionally October.

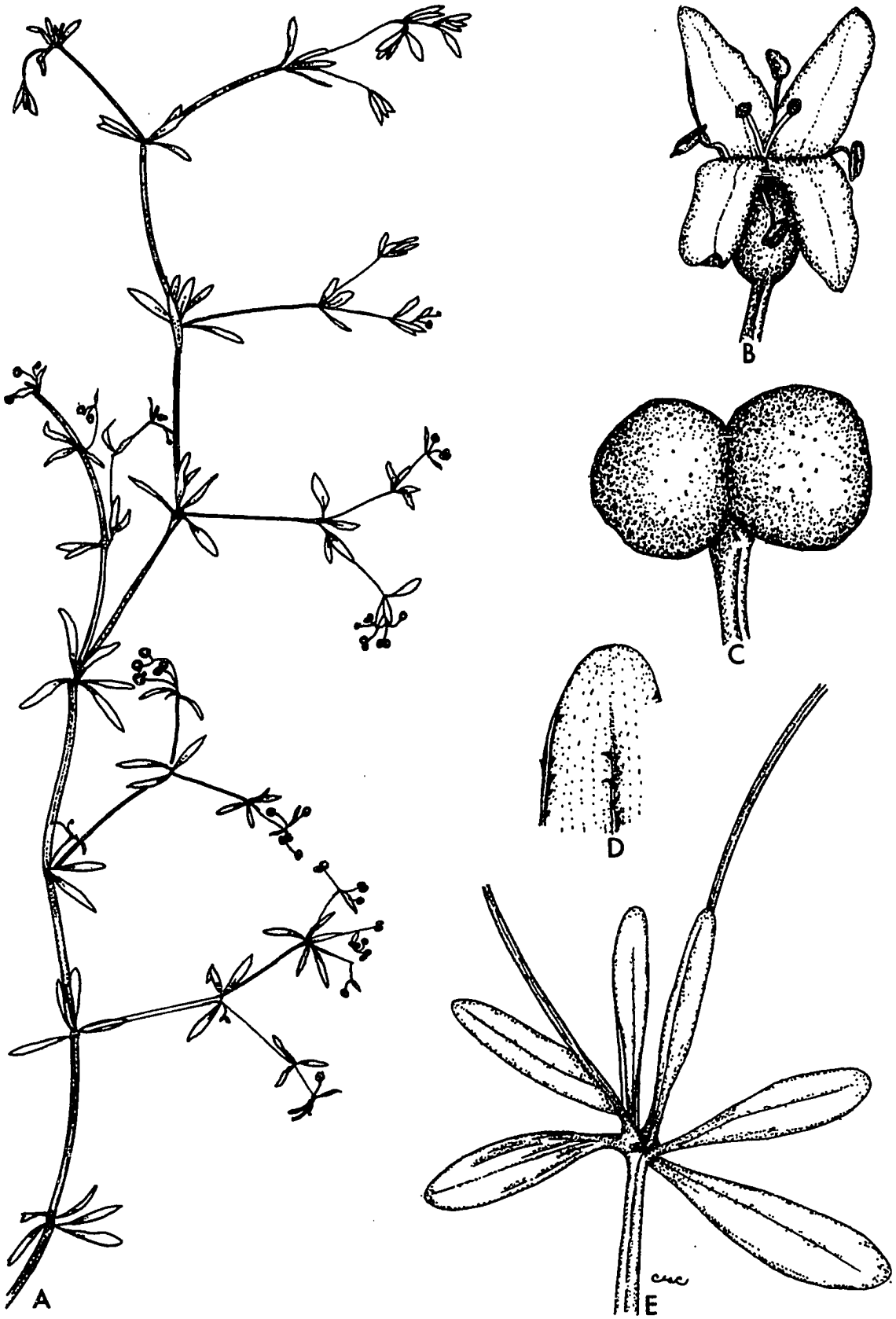
Habitat: Mountainous areas along roadsides, wooded slopes, ridges, and hillsides; in deciduous woods; and on shale and limestone embankments.

S.E. United States specimens examined: Nine hundred and eighteen sheets.

Galium tinctorium, like G. obtusum, is very polymorphic. There exists within the species a wide range of variation in leaf shape and size and in overall habit, the latter affected greatly by the variation in internode length. It is possible that these variations are expressions of

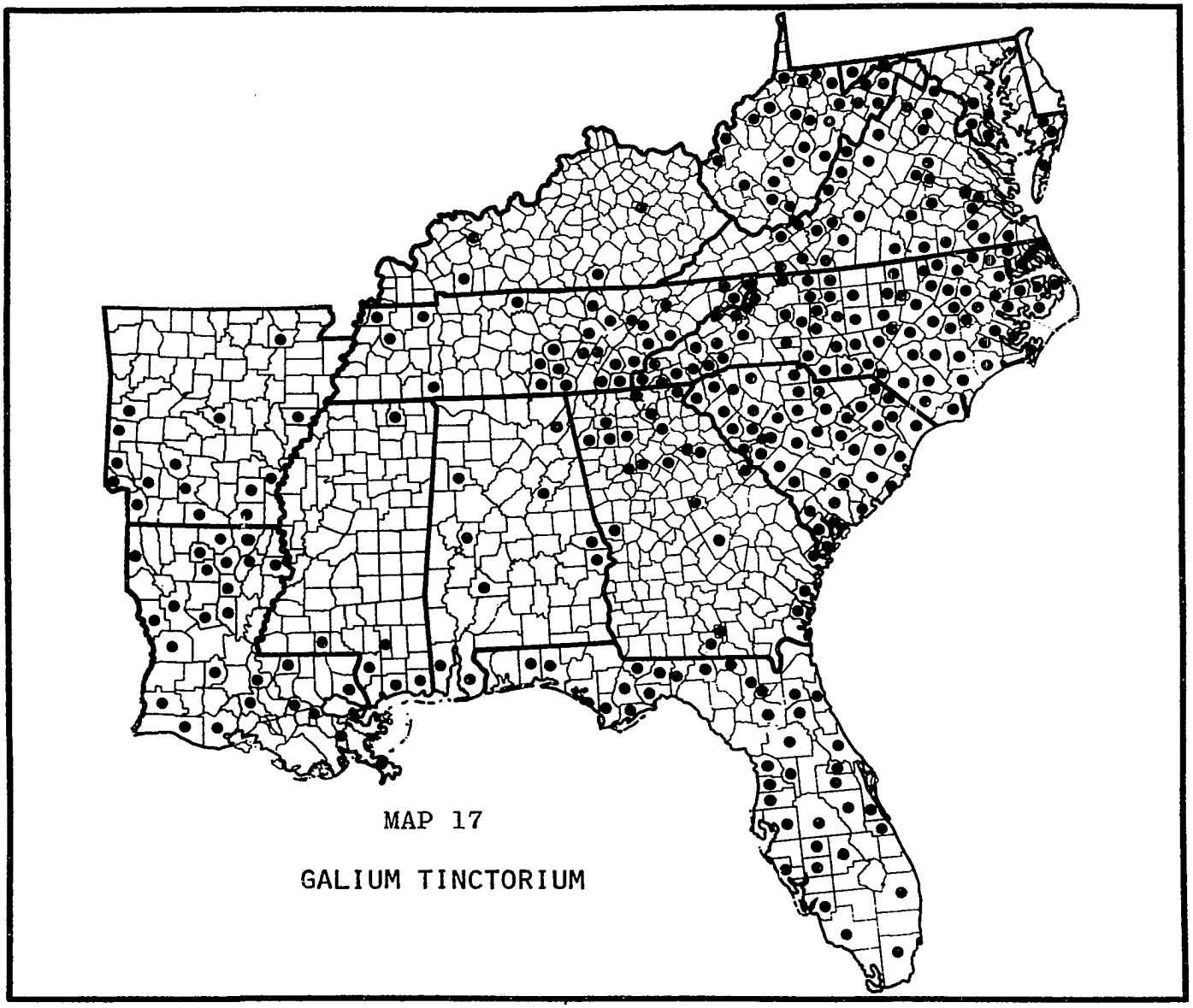
FIGURE 23

GALIUM TINCTORIUM: A, habit x 1; B, flower x 24; C, fruit x 17; D, lower leaf surface, margin, and apex x 8; E, leaf whorl and stem (pubescence detail not showing at this magnification) x 3. A, C from C. A. Lawson & D. Dotts 797 (OKL), B from J. R. Massey & H. F. Massey 3964 (OKL), and D, E from C. A. Lawson & D. Dotts 827 (OKL).


A
B
C
D
E

differing environmental pressures; however, a comparison of the ecological data available from specimens in the southeastern United States showed no positive correlation with these extremes of habit. In addition, this polymorphic species does not separate well into distinct morphological - geographical groups even within individual states. The extremes in variation are quite distinct from one another, but the wide range of intermediates present, along with the lack of morphological - geographical separation, make the subdivision of this group difficult. Galium tinctorium seems best considered only at the species level within the southeastern United States as a whole.

For example, one extreme frequently has rather large, oblanceolate leaves and elongated internodes. Here the flowers are frequently four-lobed, and the leaf number, too, is frequently four. This extreme variation appeared to fit, for the most part, Wiegand's (1897) G. tinctorium var. floridanum with the exception that the stems were at least somewhat retrorse scabrous. Wiegand described var. floridanum with glabrous or nearly glabrous stems. Also, he reported var. floridanum to occur only in Florida. Later this variety was reported (Fernald, 1950) from "Fla. to La., n. on or near Coastal Plain to se. Va.," but in this study specimens fitting this description have been examined from inland areas as far west as Oklahoma and as far north as West Virgina. This extreme, therefore, either did not appear to have the definite



MAP 17

GALIUM TINCTORIUM

geographical or ecological limits as originally believed or it was not the plant Wiegand described. The resolution of the problem was made even more difficult by the confusion in the literature. The following summarizes the problem:

G. tinctorium var. floridanum Wiegand has been treated by some as G. obtusum var. floridanum (Wieg.) Fern., a combination never made by Fernald. A literature search and a check of the Gray Card Index at the Gray Herbarium by Mr. Michael Canoso revealed no reference for such a combination. It seemed desirable to examine Wiegand's type to determine its proper placement as to species. Fernald (1935) clearly pointed out that Wiegand's G. tinctorium var. filifolium belonged to the species G. obtusum, but in that particular article he made no comment as to the disposition of G. tinctorium var. floridanum. He continued (Fernald, 1950) to retain var. floridanum as a variety of G. tinctorium. After examining a phototype (Fig. 24) from Cornell University and reviewing information concerning stem pubescence sent to me by Dr. Robert Clausen, who reported retrorse hairs on the stems of the type specimen, I have concluded that the extreme variant discussed above corresponds to Wiegand's type, and, whether serendipitous or not, the type and corresponding plants of this study belong to G. tinctorium.

Chemotaxonomic studies of Puff (1975) further supports my conclusions that var. floridanum belongs to the species G. tinctorium. Having examined specimens annotated

FIGURE 24

PHOTOTYPE OF

GALIUM TINCTORIUM VAR. FLORIDANUM



Galium tinctorium
Floridanum, Wiegand
Type specimen
Bull. Torr. Cl. 24, 389 (1894)

PLANTS OF CENTRAL PENINSULAR FLORIDA,
COLLECTED IN VICINITY OF EUSTIS, LAKE COUNTY
By Geo. V. Nash.

158. Galium tinctorium, L.

by Puff as G. tinctorium subsp. floridanum (Wieg.) Puff, I find our concept, though not our treatment, of this extreme to be the same and to correspond to Wiegand's type. In Puff's study of leaf flavonoids, he showed that his subspecies of G. tinctorium lacked flavones, whereas his subspecies of G. obtusum had both flavones and flavonoles. This chemical evidence strengthens my previous interpretation that var. floridanum belongs to G. tinctorium rather than G. obtusum.

Galium tinctorium and G. palustre show close similarities. These similarities are discussed under G. palustre. G. tinctorium is also easily confused with G. obtusum, the major difference being the retrorsely scabrous and glabrous stems, respectively. As discussed under G. concinnum, there has been, on occasion, some confusion between this species and G. tinctorium.

Galled flowers are seen infrequently in this species.

18. GALIUM TRICORNUTUM Dandy, Watsonia 4: 47. 1957.

G. tricorne Stokes, in With. Bot. Arrang. Brit. Pl., ed. 2. 1: 153. 1787 (name frequently applied, but illegitimate).

Erect annual, up to 4.3 dm tall; stems branching near the base, retrorsely scabrous on the angles with hairs 0.1 - 0.3 mm long; leaves in whorls of six to ten, linear to narrowly oblanceolate, cuspidate, largest leaves 12 - 20 mm long and 1.4 - 2.4 mm wide, nerve one, prominent, upper leaf surface glabrous, lower leaf surface glabrous or retrorsely

scabrous on the midrib and lacking secretory glands, margins retrorsely scabrous throughout and also usually antrorsely scabrous distally (hairs on the margins and midrib 1.4 - 2.4 mm long); inflorescence of axillary, usually compound, dichasia mostly subtended by one or two reduced leaves, the lateral branches of one dichasium frequently forming peduncles for the next dichasium, the retrorsely scabrous peduncles usually shorter than the leaves on the main stem; flowers on retrorsely scabrous pedicels which recurve in fruit (the hairs on both the pedicels and peduncles 0.1 - 1.6 mm long); corollas four-lobed, white, lobes acute, 0.5 - 0.7 mm long and 0.3 - 0.4 mm wide, glabrous; fruits tuberculate, each mature carpel 3.7 - 4.4 mm long and 2.8 - 4 mm wide.—Fig. 25.

Type: Dawson Turner and William Borrer, "in field near Carisbrook, Isle of Wight, gathered in June, 1806: (BM).

Range: Eurasian; introduced sporadically in the northeastern United States, established in California, and reported from western Oregon (Southeastern United States, Map 18).

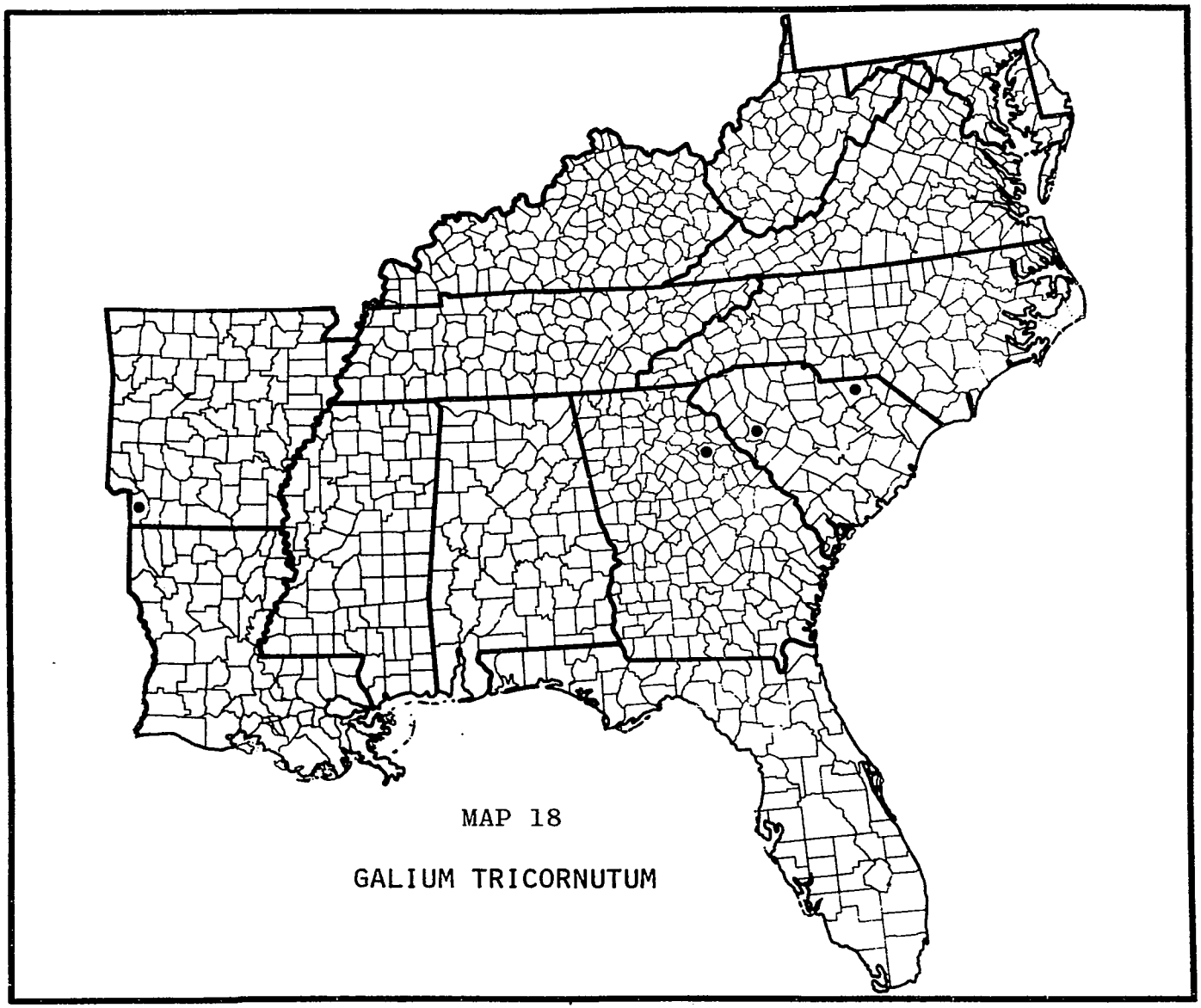
Flowering - Fruiting time: The four specimens seen from the southeastern United States were collected in March through May and are in both flower and fruit.

Habitat: The four specimens were collected, respectively, on the banks of an artificial pond, in a roadside ditch, along a river, and in a field. This Eurasian introduction is known to occur sporadically along

FIGURE 25

GALIUM TRICORNUTUM: A, habit x 1; B, fruits on recurved pedicels x 14; C, flower x 23; D, leaf whorl and stem x 5; E, lower leaf surface, margin, and apex x 12. A - E from W. H. Duncan 13541 (GA).


A
B
C
D
E



MAP 18

GALIUM TRICORNUTUM

ballasts near seaports in the eastern United States, on waste land, and on cultivated ground.

S.E. United States specimens examined: Four sheets representing four collections.

The measurements given in the description above represent those taken from the four known collections in the southeastern United States. Other sources indicate specimens with longer leaves. Additional collections in the Southeast may warrant the amendment of the measurements given here.

Galium tricornutum resembles G. aparine. Of the four known collections, three were misidentified as G. aparine, and one was unidentified. Glabrous upper leaf surfaces, tuberculate fruits, and dichasial inflorescences most readily distinguish this species from G. aparine. The absence of villous hairs at the stem nodes and retrorsely scabrous pedicels in G. tricornutum are additional differentiating characters.

No fresh flowers have been examined, but the color is reported to be dull white (Fernald, 1950) or white (Munz, 1968).

19. GALIUM TRIFLORUM Michx., Fl. Bor. Am. 1: 80. 1803.

G. brachiatum Pursh, Fl. Am. Sept. 1: 103. 1814, not Muhl.

G. pennsylvanicum Barton, Comp. Fl. Philad. 1: 83. 1818, not Muhl.

G. triflorum β. viridiflorum DC., Prod. 4: 602. 1830.

G. triflorum var. asprelliforme Fern., Rhodora 37: 445. 1935. Type: Fernald & Long 4205, border of wet woods near Great Bridge, Norfolk Co., Virginia, Aug. 4 & 5, 1934 (GH).

G. triflorum forma hispidum Leyendecker, Iowa St. Coll. J. Sci. 15: 180. 1941. Type: L. H. Pammel, R. E. Buchanan, and C. M. King 3934, Ledges State Park, Boone Co., Iowa, July 25, 1903 (ISC).

G. triflorum forma glabrum Leyendecker, Iowa St. Coll. J. Sci. 15: 180. 1941. Type: Bush 6029, Webb City, Jasper Co., Missouri, July 23, 1910 (MO). v.s.

Erect or prostrate, rhizomatous perennial, up to 14.5 dm tall (mostly 3.4 - 8.4 dm); stems branching at the base and commonly once or twice at the upper nodes, glabrous to long, straight hairy or retrorsely short hispid on the angles or both (the former hairs up to 0.5 mm long; the latter up to 0.2 mm long); leaves mostly in whorls of six, narrowly elliptical to oblanceolate, mucronate or cuspidate, largest leaves (14) 18 - 34.6 (68) mm long and (2.8) 5.4 - 8.7 (13.6) mm wide, the upper most whorls of leaves sometimes reduced, nerve one and glabrous to retrorsely scabrous beneath or antrorsely scabrous above, leaf surfaces glabrous, margins mostly antrorsely scabrous (hairs on the midrib and margins seldom over 0.2 mm long), secretory glands lacking on the lower surface; inflorescence a compound cyme primarily on the upper two-thirds of the plant, thus appearing both lateral and terminal; flowers on mostly glabrous pedicels;

corollas four-lobed, greenish-white to greenish-yellow, lobes caudate (the appendage usually 0.2 - 0.4 mm long, often folded inside or broken off), usually (0.5) 0.7 - 1 (1.3) mm long excluding the appendage and (0.4) 0.6 - 0.8 (0.9) mm wide, glabrous; fruits with uncinate hairs seldom over 0.6 mm long, each mature carpel (1.1) 1.3 - 1.8 (2.6) mm long and (0.7) 0.9 - 1.3 (1.8) mm wide.—Fig. 26.

Type locality: "Hab. in umbrosis Canadae sylvis."

Range: Circumboreal; south in the United States from Florida to California (Southeastern United States, Map 19).

Flowering - Fruiting time: May through September, rarely October.

Habitat: Mostly in woodlands and open thickets; occasionally on rocky slopes, borders of swamps, and banks of rivers and streams; rarely along roadsides, marshes, and pond margins. Associated frequently with sandstone, shale, or limestone.

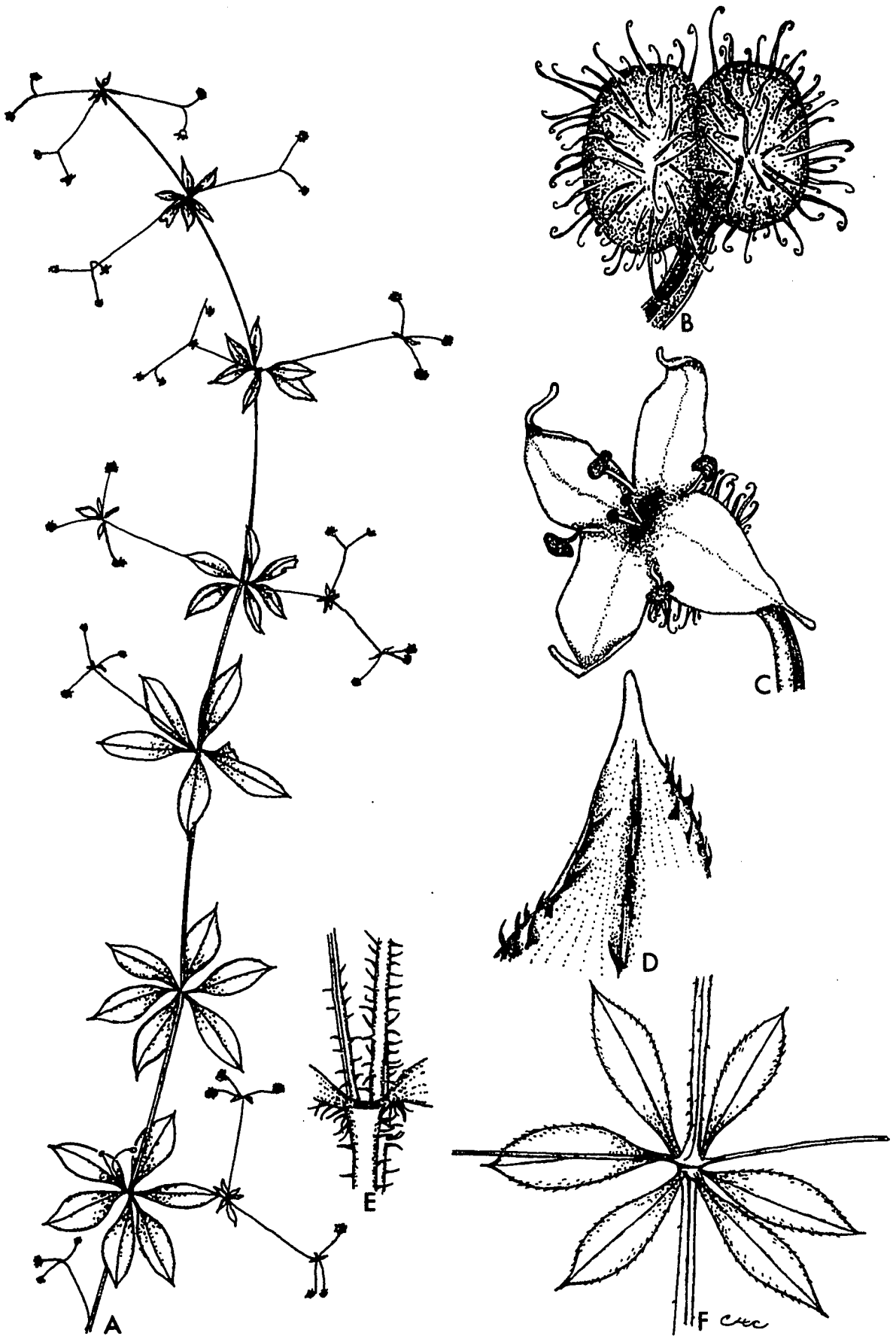
S.E. United States specimens examined: Seven hundred and twenty sheets.

The southeastern United States material includes plants with three major stem types: glabrous, retrorsely short-hispid, and long, straight-hairy.

Leyendecker (1941) described the glabrous-stemmed plants of this species as G. triflorum forma glabrum. He applied the name G. triflorum forma hispidum to those plants which had long, straight hairs on the stem angles. Many

FIGURE 26

GALIUM TRIFLORUM: A, habit x 1; B, fruit x 22; C, flower x 25; D, upper leaf surface, margin, and apex x 18; E, node with long, straight stem hairs x 4; F, leaf whorl with retrorse hispid stem x 3. A from L. E. Franklin & J. D. Freeman 288 (VDB), B from D. Martin 622 (OKL), C from A. M. Harvill 22178 (LONG), D, E from C. A. Lawson & D. Dotts 898 (OKL), and F from C. A. Lawson & D. Dotts 763 (OKL).

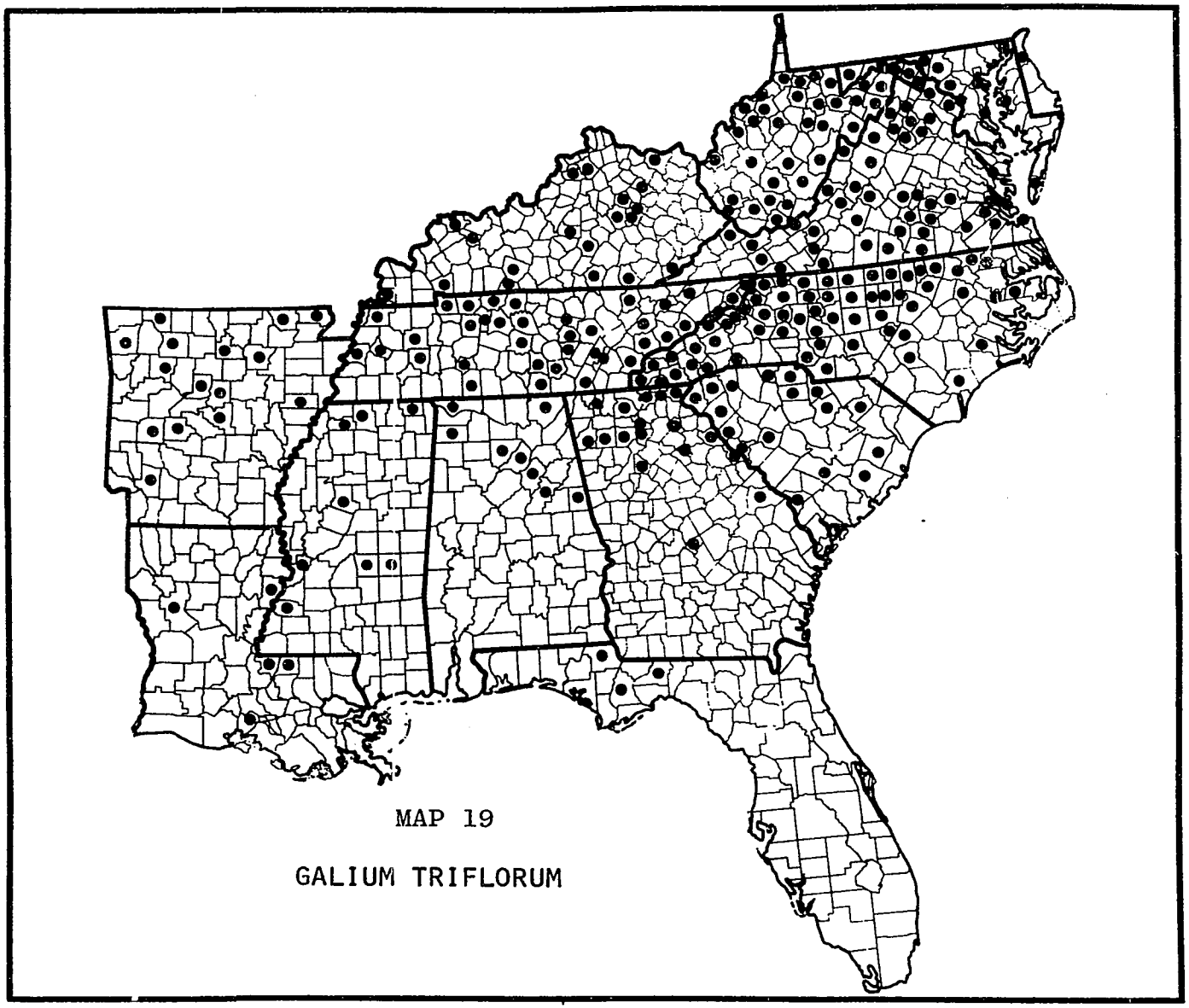

A
B
C
D
E
F

plants fitting the descriptions of these types are found in the southeastern United States; however, many gradations in stem pubescence are noticeable. There is a gradation from glabrous to retrorsely short-hispid stem angles. Other plants range from long, straight-hairy on the stem angles to long, straight-hairy only at the nodes. Plants having both retrorse-hispid hairs and long, straight hairs on the stem angles have been found also. Mixed collections containing plants with the variations in stem pubescence described above are present also. These mixed collections may or may not represent mixed populations.

Plants with retrorsely short-hispid stem angles are the most common in the southeastern United States. Plants with long, straight hairs present on the stem angles in any position or combination mentioned above occur only sporadically in this region.

Since geographical separation based on stem pubescence is lacking, and gradations are abundant, the recognition of taxa below the species level does not seem warranted.

Fernald (1935) segregated many of the southeastern plants of G. triflorum as variety asprelliforme based on reduced upper leaves and diffuse inflorescences. These plants do not always separate well from those plants of G. triflorum with only slightly reduced leaves and three-flowered peduncles. For this reason, variety asprelliforme is not being recognized



MAP 19

GALIUM TRIFLORUM

in this study. Based on an isotype of variety asprelliforme, Fernald and Long 4205 is retrorsely hispid on the stem angles.

This species is frequently misidentified as G. aparine or G. asprellum. The upper leaf surface of G. aparine is pubescent, and the leaf margins are retrorsely scabrous. Glabrous upper leaf surfaces and usually antrorsely hispid leaf margins are found in G. triflorum. The lower leaf surface is retrorsely scabrous on the midnerve in G. asprellum, while it is glabrous or retrorsely hispid in G. triflorum. The same differences found between G. aparine and G. triflorum in the direction of hairs on the leaf margins are found here. Also, the fruits of G. asprellum are glabrous.

Enlarged, galled flowers are found also in this species.

20. GALIUM UNIFLORUM Michx., Fl. Bor. Am. 1: 79. 1803.

Bataprine uniflora (Michx.) Niewl., Am. Midl. Nat. 1: 264. 1910 (basionym corrected l.c. page 293).

Erect, stoloniferous perennial, up to 3.5 dm tall (mostly 1.8 - 2.9 dm); stems simple or occasionally branching at or near the base, glabrous; leaves in whorls of four, mostly linear or narrowly elliptical to sometimes linear oblong, acute to slightly acuminate, largest leaves (14) 19.5 - 26.6 (33.2) mm long and (1.8) 2.3 - 3.4 (4.8) mm wide, nerve one, prominent, upper leaf surface muriculate,

glabrate or with short, scabrous, ascending hairs 0.08 - 0.16 mm long along the margins and midrib (these hairs sometimes scattered over the upper surface), lower leaf surface glabrous and with scattered secretory glands, margins sometimes revolute; inflorescence a simple dichasium subtended by two pairs of unequal bracts with lateral branches most frequently reduced or obsolete, thus appearing as a monochasium; flowers pedicellate, borne singly, sometimes 2, or rarely 3 at the ends of axillary, naked peduncles, lateral flowers when present frequently subtended by 2 - 4 small bracts, pedicels and peduncles usually glabrous or with a few short, scabrous hairs 0.04 mm long; corollas four-lobed, white to light green, lobes caudate (the appendage up to 0.3 mm long, often folded inside or broken off), mostly 0.8 - 1 mm long excluding the appendage and 0.6 - 0.9 mm wide, glabrous; fruit a glabrous, purplish-black berry, each mature carpel (1.7) 2.2 - 2.7 (3) mm long and (1.3) 1.6 - 2 (2.6) mm wide.—Fig. 27.

Type locality: "Hab. in Carolina."

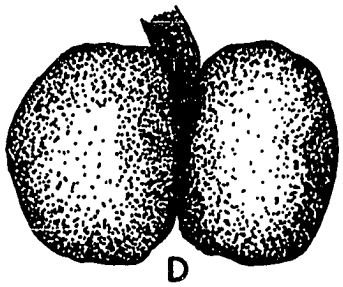
Range: Virginia south to Florida and west to Texas (Southeastern United States, Map 20).

Flowering - Fruiting time: May through September. A few plants may be found in late fruit in October.

Habitat: Rich, shaded, often damp or rocky, woods (frequently magnolia - beech or oak - hickory - pine associations), damp creek banks often associated with granitic outcrops, low hammocks, and savannahs.

FIGURE 27

GALIUM UNIFLORUM: A, habit x 1; B, upper leaf surface, margin, and apex x 6; C, leaf whorl x 2; D, fruit x 13; E, flower x 25. A, B, C, D from M. L. Fernald & B. Long 8857 (OKL), and E from L. Hubricht B2922 (MO).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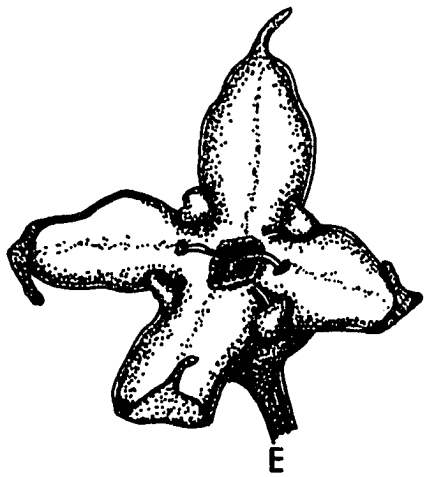
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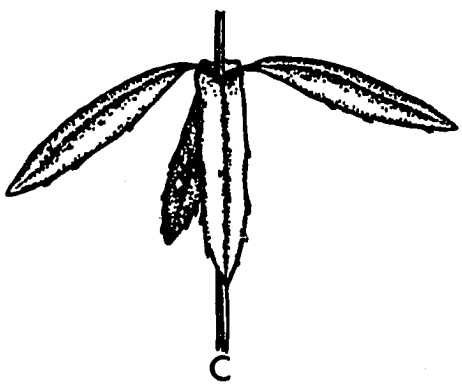
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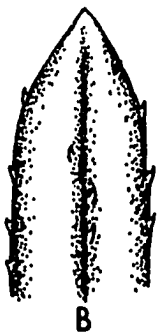
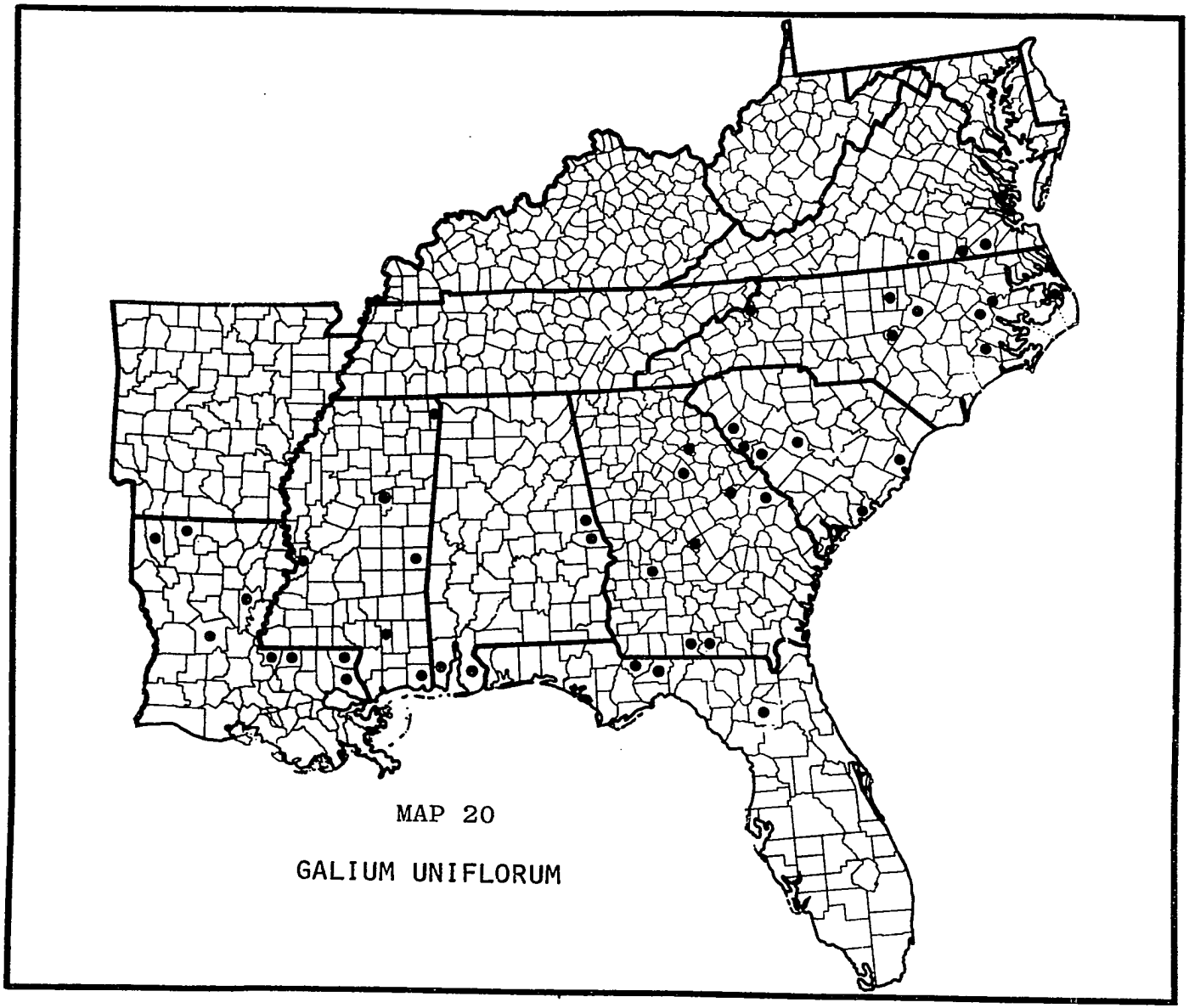

B


A



MAP 20

GALIUM UNIFLORUM

S.E. United States specimens examined: One hundred and fifty-five sheets.

The fruits wrinkle in drying and shrink in size. They have been described as glabrate (Radford, Ahles, and Bell, 1968), but I see them as glabrous.

The infolding and fragile nature of the caudate appendage of the corolla lobes very possibly caused Fernald (1950) to describe them as "blunt."

This species is seldom misidentified. It is on occasion confused with G. hispidulum, the other fleshy-fruited species in the southeastern United States.

21. GALIUM VERUM L., Sp. Pl. 1: 107. 1753.

Erect, rhizomatous, perennial, up to 14 dm tall (mostly 6.3 - 9.8 dm); stems mostly simple, occasionally branching at the base or lower nodes, villosulous throughout on the angles and sides or only in the inflorescence (these hairs frequently 0.1 - 0.3 mm long); leaves in whorls of six to twelve, narrowly oblanceolate to linear, cuspidate, largest leaves (12) 16.2 - 27.2 (36.8) mm long and 1.8 - 2.4 mm wide (only 0.5 - 1.4 mm wide if margins revolute), nerve one, prominent on the lower leaf surface, upper leaf surface strigillose with hairs up to 0.2 mm long, lower leaf surface densely and minutely pubescent to glabrous (the midnerve most often glabrous), secretory glands absent on the lower surface, margins usually revolute; inflorescences primarily on the upper half of the plant, thus appearing terminal, the

axillary inflorescences forming cymose panicles; flowers on glabrous pedicels, showy, fragrant; corollas four-lobed, yellow, lobes mostly obtuse, acute, or broadly caudate (the appendage rarely over 0.1 - 0.2 mm long), usually (0.7) 0.9 - 1.2 (1.3) mm long excluding the appendage if present and (0.5) 0.6 - 0.7 (0.9) mm wide, glabrous; fruits glabrous each mature carpel 1.1 - 1.7 (2.0) mm long and (0.6) 0.7 - 1.2 (1.4) mm wide.—Fig. 28.

Type locality: "Habitat in Europa frequens."

Range: Eurasian; introduced in the United States from New England, south to North Carolina, west from Ohio to Missouri, Kansas, and the Dakotas (Southeastern United States, Map 21).

Flowering - Fruiting time: May through August.

Habitat: Disturbed areas along roadsides, railroad right-of-ways, and fence rows; in fields, pastures, and meadows; occasionally on creek banks.

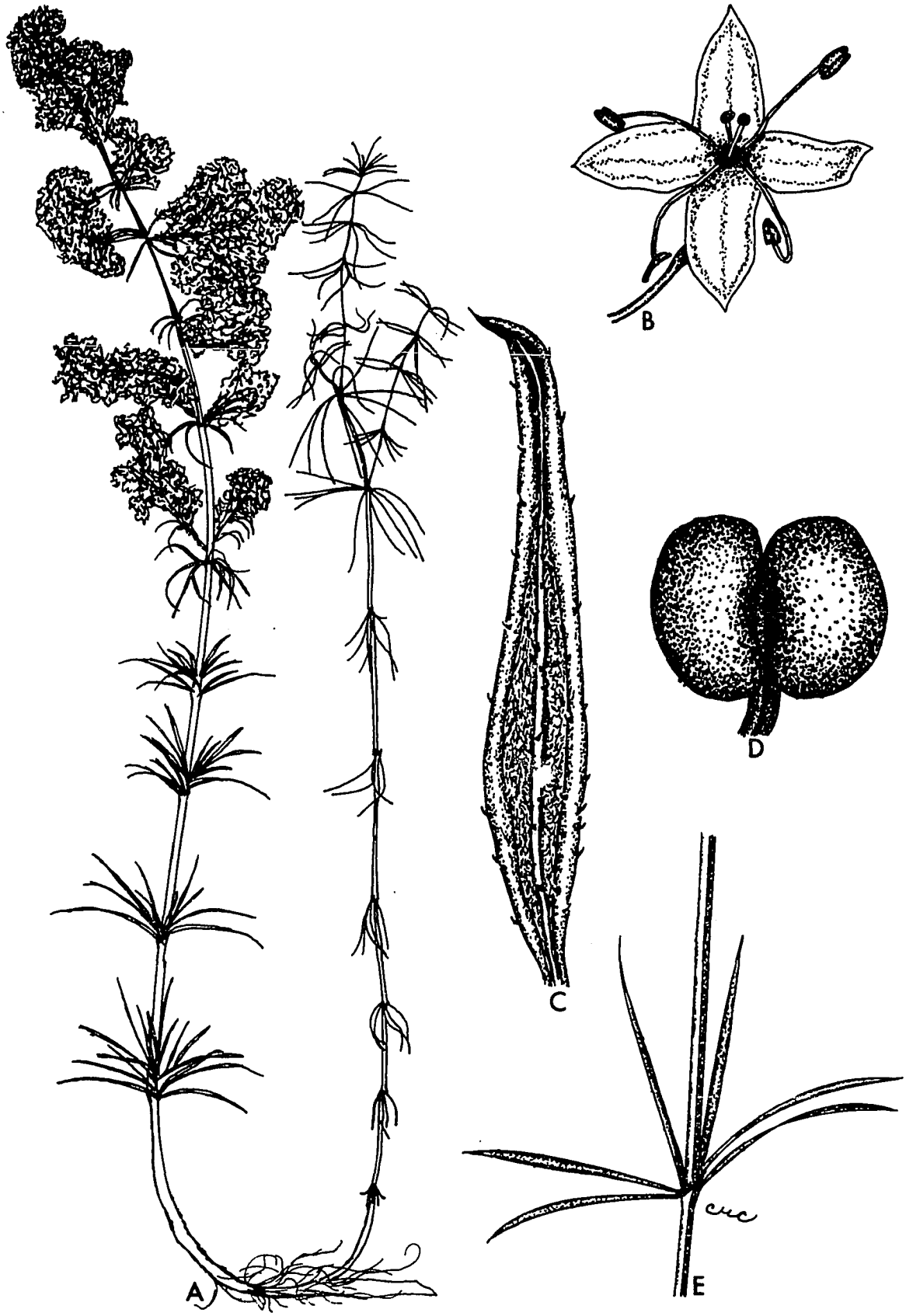
S.E. United States specimens examined: Sixty-two sheets.

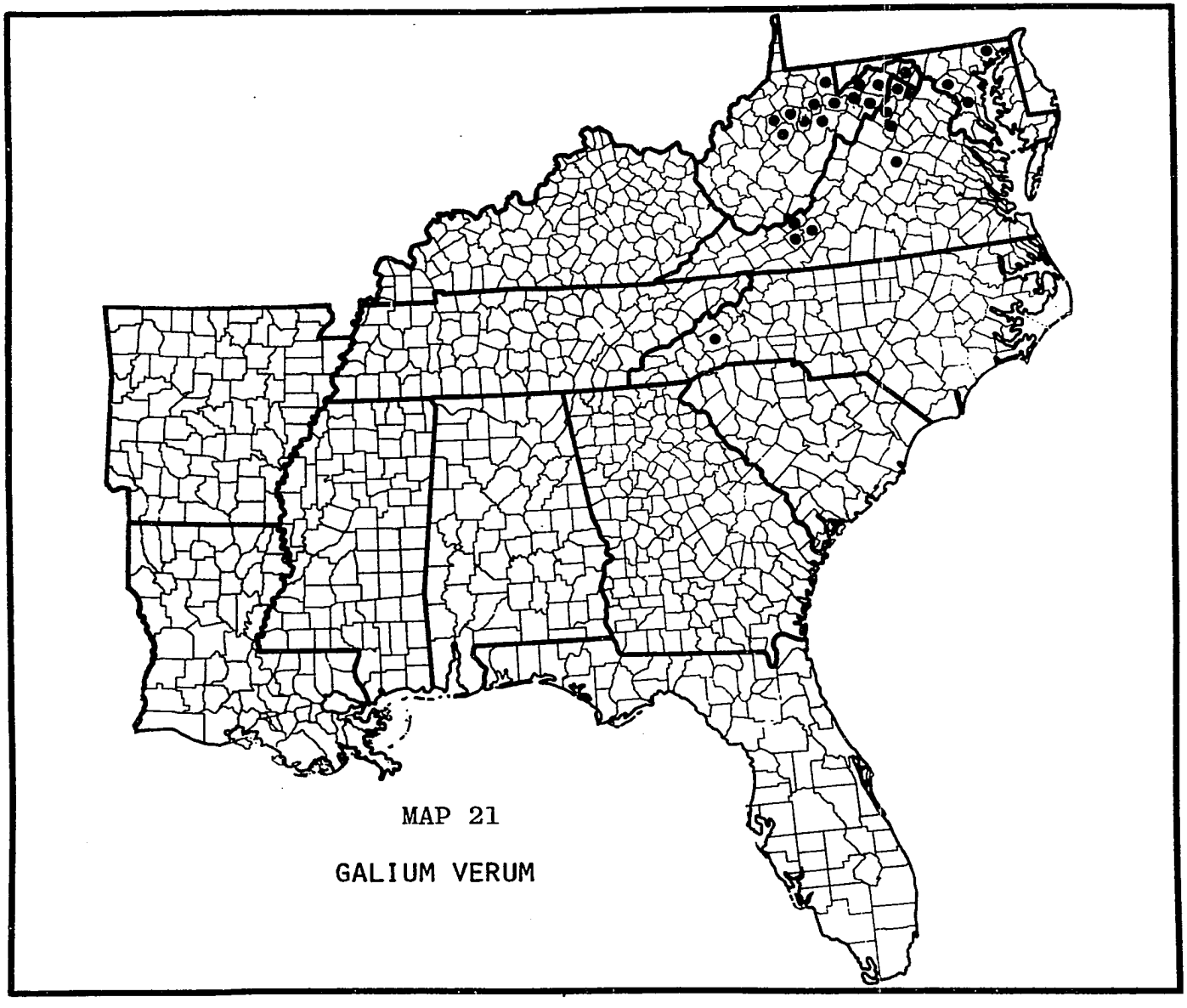
In dried specimens, the leaf shape of G. verum most often appears linear rather than oblanceolate. The leaf margins are strongly revolute, and this, in part, accounts for the dominantly narrow leaf shape.

No living material of G. verum was examined in this study. The information concerning flower color and fragrance was taken from specimen labels or from Fernald (1950).

FIGURE 28

GALIUM VERUM: A, habit with mature and immature branches x 1; B, flower x 17; C, lower leaf surface, apex, and revolute margins x 6; D, fruit x 20; E, leaf whorl x 3. A, B, E from F. R. Fosberg 41087 (GH), C from O. H. Weiss 262 (VPI), and D from E. A. Bartholomew & D. Wilson s.n., July 31, 1965 (WVA).


A
B
C
D
E



MAP 21

GALIUM VERUM

As pointed out by Fernald (1950), the flowers often turn blackish in drying.

Galium verum and G. mollugo are reported to hybridize where the parent races meet in Central Europe (Hegi, 1918). The ranges of these two species overlap somewhat in the southeastern United States in Maryland, Virginia, and West Virginia; however, no mixed populations of G. verum and G. mollugo were found, and no apparent hybrids were found in the field studies in Virginia and West Virginia in 1974.

Several European varieties of G. verum have been proposed. Specimens as they occur in the southeastern United States, although variable, are not clearly separable into these entities. The variation which does occur seems to be within the range of species variability.

22. GALIUM VIRGATUM Nutt., in Torr. & Gray Fl. N. Am. 2: 20. 1841.

G. texanum Scheele, Linnaea 21: 597. 1848.

Type: Roemer, New Braunfels, Texas.

Erect annual, up to 4.3 dm tall (mostly 1.2 - 2.6 dm); stems simple or branching mostly near the base, glabrate to moderately pubescent on the angles with stiff, straight, spreading or descending hairs up to 0.4 mm long; leaves in whorls of four, oblong to narrowly elliptical, acute, sometimes obtuse, and often tipped with a stiff, straight hair, largest leaves mostly (3) 4.7 - 7.1 (9.6) mm long and

1.4 - 2.1 (3.2) mm wide, nerve one, prominent, leaf surfaces glabrous to densely pubescent with somewhat appressed, apically directed hairs, lower leaf surface often with scattered, secretory glands, margins with straight, spreading, apically directed, or slightly descending hairs (surface and margin hairs frequently flattened and broadened at the base and mostly 0.2 - 0.4 mm long); flowers sessile, supported by very short, axillary peduncles and subtended by two leaf-like bracts, usually two flowers at a node (sometimes only one and a branch), developing racemosely on the virgate stem, the peduncles not proliferous, reflexed in fruit; corollas four-lobed, yellowish white to white, lobes acute, mostly 0.4 - 0.6 mm long and 0.3 - 0.5 mm wide, glabrous; fruits with uncinate hairs up to 1 mm long, each mature carpel mostly 1.5 - 1.9 (2.2) mm long and 1 - 1.3 (1.5) mm wide.—Fig. 29.

Lectotype: Nuttall s.n. (PH, accession No. 910263), Red River (doubtless Choctaw or McCurtain County, Oklahoma, 1819).—Fig. 30.

Range: Tennessee west to Missouri and Kansas, south to Oklahoma and Texas, and east to Alabama (Southeastern United States, Map 22).

Flowering - Fruiting time: April through June.

Habitat: Cedar glades, limestone outcrops, prairies, dry ridges, rocky ledges, roadsides, and along railroads.

S.E. United States specimens examined: Fifty-seven sheets.

FIGURE 29

GALIUM VIRGATUM: A, habit x 1; B, fruit x 12; C, flower x 25; D, upper leaf surface, margin, and apex x 12; E, leaf whorl with reflexed fruit at node x 8. A from R. Kral 30604 (VDB), B, D, E from G. E. Tucker 4824 (NCU), and C from E. J. Palmer 39296 (MO).

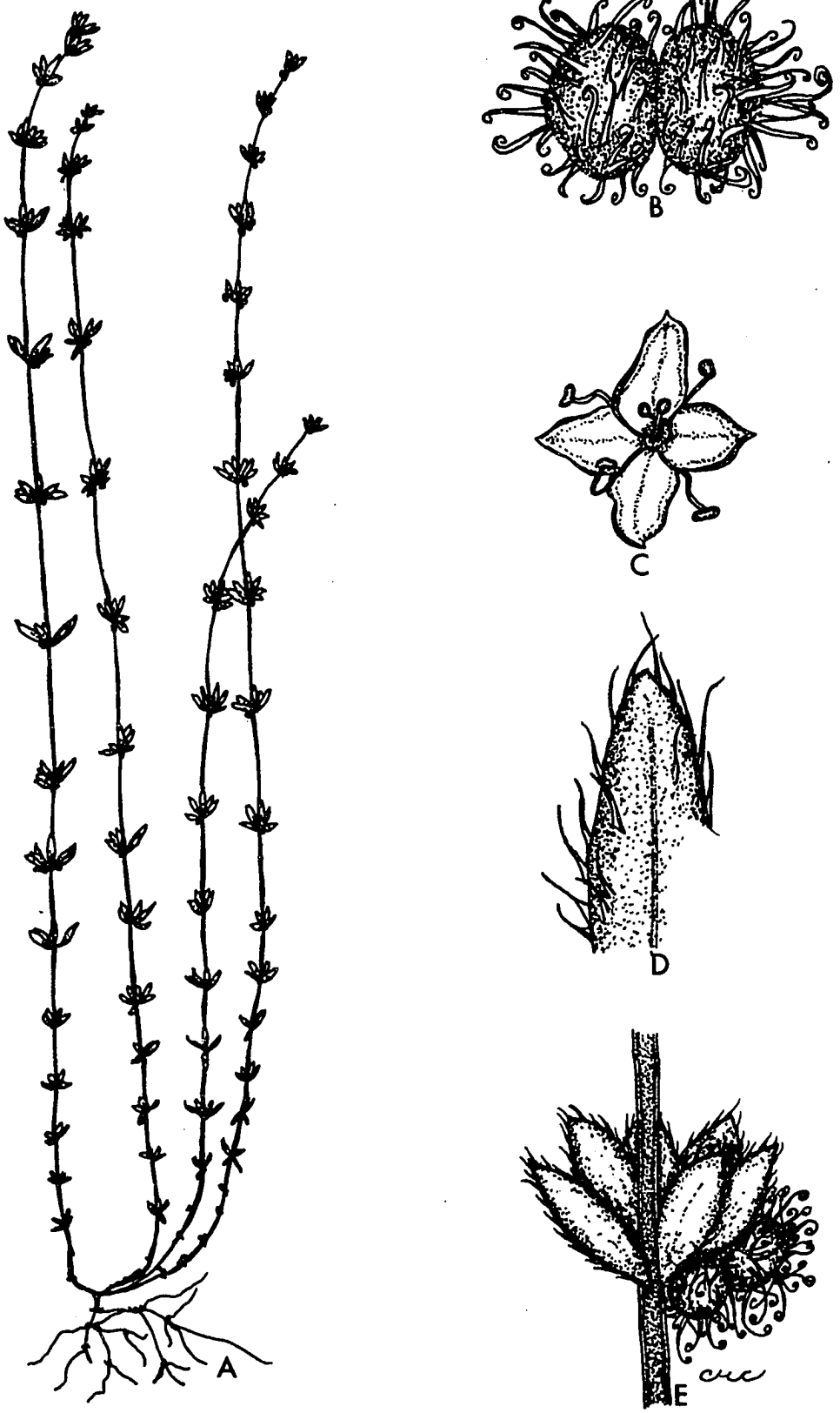
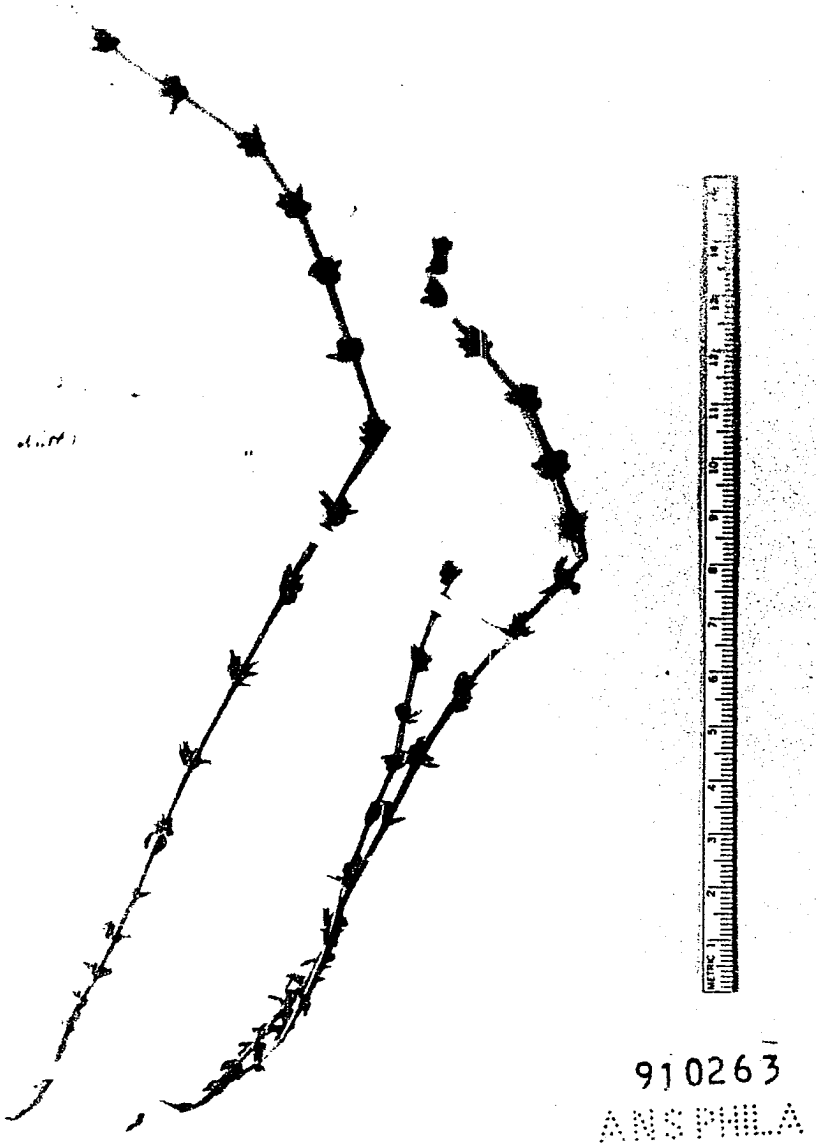

A
B
C
D
E

FIGURE 30

PHOTOLECTOTYPE OF

GALIUM VIRGATUM



910263
ANSPHILA

30

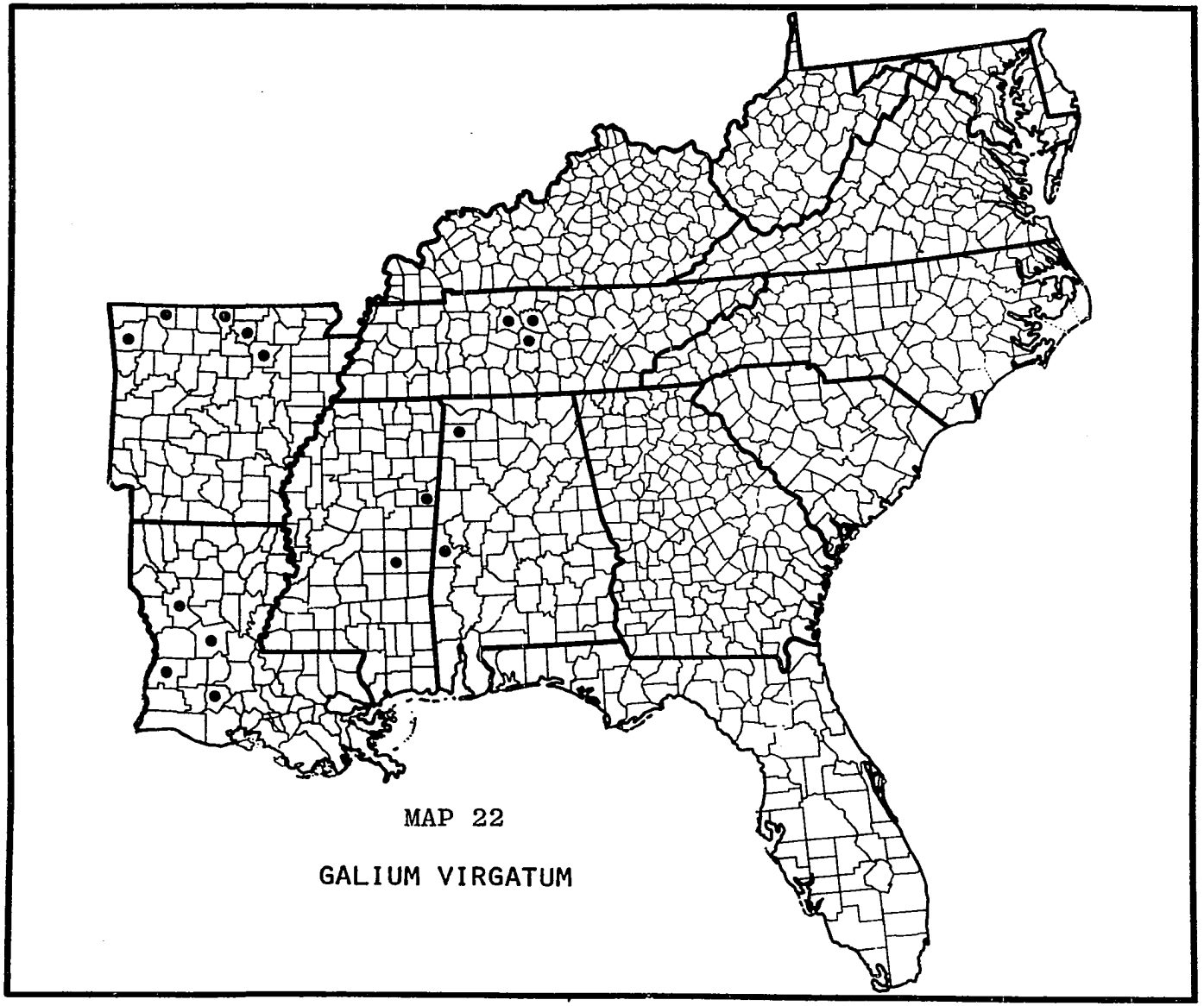
LECTOTYPE

Galium virgatum Nutt., in T. & G.,
Fl. N. Am. 2:20. 1841

Cheryl A. Lawson, 1976

ACADEMY OF NATURAL SCIENCES, PHILADELPHIA.

Galium virgatum Nutt.



MAP 22

GALIUM VIRGATUM

Two collections of G. virgatum from South Carolina were examined. Both were collected a year apart on waste ground at the Santee Wool Combing Mill. Here this species is a waif or locally adventive and does not represent the natural range of the species.

The bristles on the fruits of this species turn upward as pointed out to me by Lauramay Dempster.

Galium virgatum var. leiocarpum, a glabrous fruited variety, was described by Torrey and Gray (1841). As they indicated, Nuttall had called this variety G. nutans in his manuscript. The collections of this glabrous-fruited variety which have been made available to me include Nuttall's collection from the "Red River" (doubtless collected in 1819 in Choctaw or McCurtain County, Oklahoma); Drummond 113, Texas, 1835; E. Hall 273, Texas, 1872; and two collections of Charles Wright s.n., Texas. All these collections are on two sheets (GH), the second sheet containing only one Wright collection. Shinners (1958) also reported this variety from Dallas County, Texas.

Since it was Nuttall who first collected this glabrous-fruited material, I am designating the lectotype of G. virgatum var. leiocarpum T. & G. as follows:

Nuttall s.n. (GH) "Red River" (doubtless Choctaw or McCurtain County, Oklahoma, 1819).—Fig. 31.

FIGURE 31

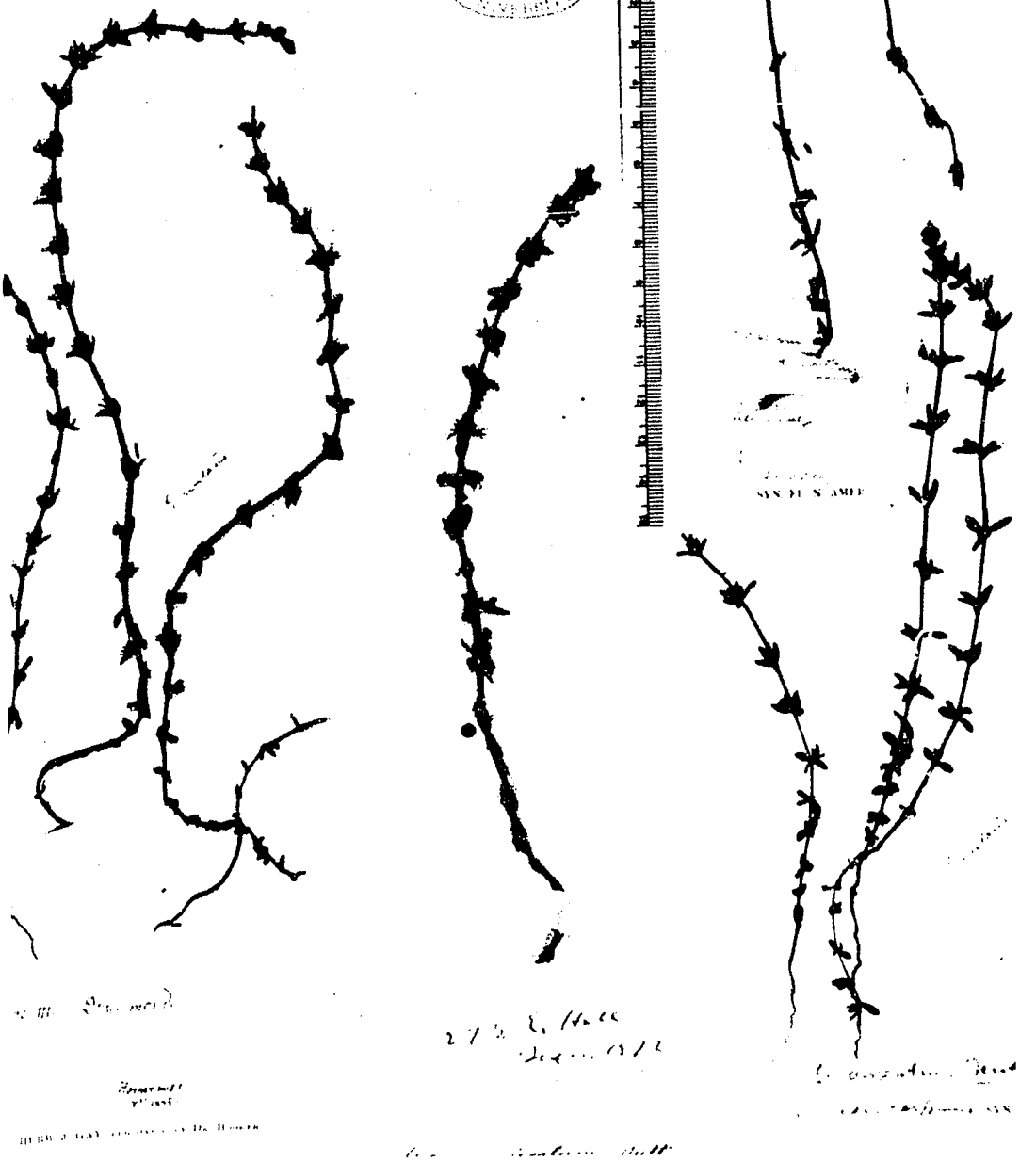
PHOTOLECTOTYPE OF

GALIUM VIRGATUM VAR. LEIOCARPUM

LECTOTYPE

Galium virgatum Nutt.
var. loiocarpum T. & G.
Fl. N. Am. 2:20. 1841

Cheryl A. Lawson, 1976



Variety leiocarpum is found "with the ordinary form" (Gray, 1884), but no plants with glabrous fruits have been examined from the southeastern United States; therefore, this variety is not included in synonymy although its rank as a variety seems dubious based on its lack of geographical separation from the typical variety.

CHAPTER V

DOUBTFUL AND EXCLUDED NAMES

GALIUM CUSPIDATUM Muhl. ex. Ell., Sk. S. Carol. & Ga. 1: 197. 1816.

Name based on G. cuspidatum Muhl., Cat. ed. 1. 16. 1813, a nomen subnudum. Elliott's description fits G. triflorum except the leaves are said to be "sprinkled with hairs." Torrey and Gray (1841) remarked under G. asprellum that "There is a specimen in Elliott's herbarium, mixed with his G. cuspidatum; but no locality is given." This specimen may account for Elliott's statement that the leaves are "sprinkled with hairs," a character of G. asprellum.

GALIUM LONGICAULE Raf., Fl. Ludov. 75. 1817.

This species has been considered a synonym of G. triflorum, but the description fits rather better, both as to morphology and flowering time, G. aparine.

GALIUM OBTUSUM VAR. FLORIDANUM (Wieg.) Fern.

This name appears in the literature, but it has never been validly published.

GALIUM PENNSYLVANICUM Muhl., Cat. ed. 1. 15. 1813, not Barton.

This species has been placed in synonymy under G. asprellum by Torrey and Gray (1841).

GALIUM MICRANTHUM Pursh, Fl. Am. Sept. 1: 103. 1814.

A questionable synonym of G. asprellum fide Torrey and Gray (1841).

GALIUM SPINULOSUM Raf., Prec. Decouv. 40. 1814.

A questionable synonym of G. asprellum fide Torrey and Gray (1841).

RUBIA TECHENSIS Raf., Fl. Lud. 76. 1817.

Probably a specimen of G. hispidulum, but possibly G. tinctorium and G. obtusum.

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