

THE *DESMODIUM PANICULATUM* (L.) DC. (FABACEAE) COMPLEX REVISITED¹

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ABSTRACT

This paper presents new information, derived from herbarium data, about the nature of variation in the *Desmodium paniculatum* complex. Three confluent species, *Desmodium paniculatum*, *D. perplexum*, and *D. glabellum*, are recognized, their discrimination, however, being subjective. Determination of the level of interbreeding in nature and of the effect of environment on the expression of phenotypes might lead to a clarification of interpretations.

The *Desmodium paniculatum* complex [*D. paniculatum* (L.) DC., *D. glabellum* (Michx.) DC., and *D. perplexum* Schubert], is widely distributed and common through most of the eastern and central United States. That it has frustrated several generations of botanists is evidenced by differences in published interpretations. It has seemed desirable, therefore, to reexamine the group preliminary to an account in the Vascular Flora of the Southeastern United States (University of North Carolina). This report presents documentation for treatment of the *Desmodium paniculatum* group in the Flora.

Nomenclature follows Schubert (1950a) who has examined types.

Because this paper refers repetitively to leaflet proportions, I use the abbreviation *r* (*ratio* of leaflet length to width) to designate leaflet proportions; i.e., leaflets 3–5 *r* means leaflets are 3–5 times as long as wide.

THE *Desmodium paniculatum* (L.) DC. COMPLEX

The members of this group, reasonably consistent in flower and fruit characters but highly variable in leaflet proportions and amount and nature of pubescence, are usually distinct from others of the series *Stipitata* Schubert (1950a). Collectively the *Desmodium paniculatum* complex may be described as follows:

Perennial herbs from a woody crown and tap root with usually clustered, erect, ascending or spreading stems 0.3–1.5 m long. Medial stems and leaf-stalks glabrous, or scantily or conspicuously uncinately or pilose-pubescent, less frequently with a mixture of both kinds of hairs. Stipules subulate, caducous. Leaves usually well-petioled (exception *D. paniculatum* var. *epetiolatum* Schubert). Leaflets diverse in proportions, broadly ovate or

¹ Journal Paper No. 10960 of the Iowa Agriculture and Home Economics Experiment Station, Ames. Project No. 1983.

rhombic to narrowly oblong, ranging from ca 1.5–10 r , variable also in the amount and quality of pubescence: glabrous, scantily strigose with short, appressed hairs, or sparsely or (especially of lower surface) abundantly spreading-villous with longer hairs; uncinulate hairs present along veins of upper surface in some forms, infrequently so beneath. Inflorescence usually much branched. Bracts narrow, caducous. Pedicels usually 5–12 (-20) mm long. Flowers on dried materials ca 6–8 (-9) mm long. Loment stipe 1–3 (-4) mm, exserted beyond the calyx tube or not. Loments sinuate above, incised beneath, with (2-) 3–5 segments each (4-) 5–7 (-8) mm long, convex above, obtusely angled below.

INTERPRETATIONS OF THE *Desmodium paniculatum* COMPLEX

The following summarizes presentations of authors who have studied this group in some detail or (and) whose treatments are (or have been) widely used. Author's views are presented in key form, the differential characters being derived from their keys and descriptions or/and discussion. Direct quotations from the keys are so marked.

SMALL (1933). Four species as *Meibomia*.

1. Loment segments straight on the back, much longer than wide; standard 5–6 mm long; stems glabrous or sparingly pubescent..... *M. dillenii* (Darl.) Kuntze
1. Loment segments rounded or angled on the dorsal suture, various in length as follows; standard 4.5–7 mm long; stems variously pubescent.
 2. Blades of the leaflets broad, of an elliptic, ovate, or lanceolate type; standard 4.5–7 mm long; loment segments 3–5 mm wide; stem pubescence follows.
 3. Stem glabrous or nearly so; segments of the loment rounded on the ventral side; standard 4.5–5.5 mm long; loment segments 4–5 mm wide. *M. paniculata* (L.) Kuntze
 3. Stem puberulent or finely pubescent; segments of the loment prominently angled on the ventral side; standard 6–7 mm long; loment segments 3–4 mm wide..... *M. pubens* (T. & G.) Young
2. Blades of the leaflets narrow, of a linear or linear-lanceolate type; standard 4–6 mm long; loment segments 4–5 mm wide; stems puberulent or nearly glabrous. *M. chapmanii* (Britt.) Small

Meibomia glabella (Michx.) Kuntze, another species listed by Small, is neither the *Desmodium glabellum* (Michx.) DC. of Schubert (1950b) or Wilbur (1963, 1964) nor a member of this group.

Although some herbaria yet contain specimens named according to Small's criteria, his views have been followed by no other author.

SCHUBERT (1950a). Three species.

This author, providing the first critical evaluation of the group, reduced *Desmodium paniculatum* var. *angustifolium* T. & G. and *Meibomia paniculata* var. *chapmanii* Britton (and their nomenclatural synonyms) to synonymy under her var. *typicum* and described *D. paniculatum* var. *epetiolum*, a form with obsolescent petioles.

The traditional *Desmodium dillenii* Darl., which was not compared with *D. paniculatum*, was felt to be composed of two elements as follows (abstracted from text).

1. Petioles long; leaflets acute, thinner with little or only obscure reticulation, more abundantly pilose. *D. perplexum* Schubert
1. Petioles shorter; leaflets obtuse, usually retuse [presumably thick], with prominent venation, less conspicuously pilose. *D. glabellum* (Michx.) DC.

In this listing, *D. perplexum* partially replaces the traditional *D. dillenii* that was discarded as a *nomen confusum*.

SCHUBERT (1950b). Three species.

Schubert's (1950a) views were expanded and modified in her treatment of *Desmodium* in the eighth edition of the Gray's Manual.

1. Plants with coriaceous and conspicuously reticulate leaflets that are usually appressed-pilose on both surfaces, usually uncinulate pubescent above; stems uncinulate-puberulent and usually at least sparsely spreading-pilose; terminal leaflet broadly obtuse and slightly emarginate. *D. glabellum* (Michx.) DC.
1. Plants with thinner leaflets that are less conspicuously reticulate, are inconspicuously to evidently pilose, and usually lack uncinulate pubescence; stems glabrous, puberulent or uncinulate-puberulent; terminal leaflet usually acute, not emarginate.
 2. "Leaflets thin with appressed, sparse to moderate pubescence; terminal leaflets mostly lanceolate and twice to many times as long as broad; stems sparsely if at all pilose, usually uncinulate-puberulent." *D. paniculatum* (L.) DC.
 3. Petioles ca 1.5–5 cm long; loment segments angled; distribution of species. var. *typicum* Schubert
 3. Petioles lacking or short; loment segments rounded; mostly Coastal Plain. var. *epetiolum* Schubert
 2. "Leaflets mostly thicker, abundantly to densely appressed-pilose on both surfaces; terminal leaflet usually elliptic or rhombic to ovate and about twice as long (sometimes longer) as broad; stems, petioles and usually rachis of inflorescence moderately to very densely spreading-pilose as well as uncinulate-puberulent." *D. perplexum* Schubert

GLEASON (1952). Two species.

1. Leaflets linear to oblong-lanceolate, commonly 3–5 (-10) times as long as wide, usually with some hairs scattered on lower surface of leaflets; flowers usually 6–8 mm long; loment joints 3–6, 5–7.5 mm long. *D. paniculatum* (L.) DC.
1. Leaflets oblong-ovate, commonly 1.5–3 times as long as wide, sparsely pubescent above, densely to sparsely pubescent beneath; flowers 7–10 mm long; loment joints 2–4, 5–9 mm long. *D. dillenii* Darl.

Under *Desmodium paniculatum*, Gleason noted the variation in leaflet shape; from plants with leaflets "a third to even two-fifths as wide as long . . . there is every gradation in leaflet width to plants with linear leaflets only a fifth to a tenth as wide as long." Of pubescence, he says "there is every gradation from glabrous plants to others softly pubescent on the leaves and more or less villous in the inflorescence." He considered that "those with broader leaves cannot be distinguished from *D. dillenii*."

GLEASON AND CRONQUIST (1963). Two species.

This treatment, derivative from Gleason (1962), includes the brief statement that "the broader-leaved forms [of *D. paniculatum*] seem to grade into No. 19" [*D. dillenii*]. Both of these Gleason treatments also include a *D. glabellum* (Michx.) DC., but that name is used for a species [*D. humifusum* (Muhl.) Beck] that is not a member of this complex.

ISELY (1953). One species.

Isely tabulated leaflet proportions and amount of leaflet pubescence for 200 specimens from throughout the range of the complex. His data, presented in graphs and scatter diagrams, confirmed Gleason's empirical statements ("every gradation") and suggested that variation represents a quantitative continuum. There was, however, reasonable correlation between leaflet portions and abundance of leaflet pubescence; i.e., plants with broad leaflets were usually more pubescent than those with narrow leaflets. Thus an idealized *Desmodium paniculatum* and *D. dillenii* might be recognized on the basis of an arbitrary definition of the pubescence/leaflet proportions relationship. Isely believed, however, that the complex probably represented a single polymorphic entity in which there was partial genetic linkage between leaflet form and amount of pubescence. His view was strengthened by previous field experience in which he had observed nearly all types through the total range of the complex. He had noted also that single populations might include several phenotypes. Consequently he designated the groups as one species, *D. paniculatum*, containing several intergrading forms of which these two were most clearly distinguishable:

1. Terminal leaflets usually 3–8 times longer than wide; leaflet pubescence moderate to scant, commonly appressed; stems glabrate or, if sparsely pubescent, most of hairs uncinatae. var. *paniculatum*
1. Terminal leaflets usually 1.5–3 times as long as wide; lower surface of leaflets pubescent, predominantly with spreading trichomes; stems pubescent, usually with a mixture of uncinatae and spreading hairs. var. *dillenii* (Darl.) Isely

ISELY (1955). One species.

A brief reiteration of the 1953 views.

STEYERMARK (1963). One species.

Working in Missouri, Steyermark followed Isely almost exactly. As with Gleason and Isely, he was unable to recognize Schubert's *Desmodium glabellum*. "It has not been found possible to arrange the Missouri material formerly identified as *D. dillenii* into the categories *D. perplexum* and *D. glabellum* as distinguished by Dr. Schubert."

WILBUR (1963). One species.

Wilbur, treating the legumes of North Carolina, however, came to a different conclusion. Although (p. 169) he qualified his treatment of "the

puzzling range of variation exhibited within the complex" as "tentative," he asserted "there appears to be but little difficulty in separating" the glabrous or moderately appressed-pubescent plants with narrow leaflets (i.e., *D. paniculatum*), from the others. Concerning the others, he said, "Those specimens with broader leaflets and almost always much more pubescent are quite satisfactorily separated into two piles but not by using most of the characters indicated by Schubert . . ." He then used quality of stem pubescence to achieve a segregation of *D. perplexum* and *D. glabellum* and posited three species as follows.

1. "Leaflets narrow, usually 3–8 times longer than broad; plants glabrous to sparsely appressed short-pubescent..... *D. paniculatum* (L.) DC.
1. "Leaflets wide, usually less than 3-times longer than broad;" plants pubescent, often conspicuously so.
 2. "Pubescence of medial portion of stem densely uncinulate-puberulent and very sparingly if at all supplied with pilose trichomes." *D. glabellum* (Michx.) DC.
 2. "Pubescence of medial portion of stem moderately to densely pilose.".....
.....*D. perplexum* Schubert

WILBUR (1968). Three species.

Wilbur's treatment in the *Manual of the vascular flora of the Carolinas* reiterated the preceding stated interpretation.

PROCEDURE

Working with 650 specimens (holdings of FLAS, ISU and NCU, number reduced to 607 for tabulation because of excessive within-county redundancy) and using features conveniently discernible to conventional binocular magnification, as Wilbur, I attempted to put material into "piles." After discarding several arrangements, specimens were arranged in a scheme whose irregularity stems from the fact that it seemed "to work" better than any other. It may be summarized as follows:

GROUP 1. The *paniculatum* types. Leaflets 3–8 (-10) *r*. Plants of glabrate aspect. Pubescence on leaflets usually scant, of short, appressed hairs. Medial stems glabrate or with a trace of appressed or uncinuate hairs. In some plants the leaflets are graduated upwards on stem; i.e., they are broader below than above. If upper ones exceeded 4 *r*, the specimens were placed in this category.

To separate group 1 from groups 2–5 when leaflet proportions were in the overlap zone (+ 3 *r*), specimens were placed in the pubescence group they best fitted.

- 1a. The typical *paniculatum* type. Leaflet pubescence scant, of short, appressed hairs. Stems glabrate, Leaflets 3–8 (-10) *r*.
- 1b. Leaflet pubescence more abundant, that on lower surfaces of longer, somewhat spreading hairs. Stems with or without scant pubescence. Leaflets mostly 3–5 *r*.

Because of variation in stem pubescence, this subgroup was subsequently

subdivided on the basis of stem pubescence. 1b(a), 1b(c), 1b(d), 1b(e), the stem pubescence characters being those of 1a, and of 1c, 1d, and 1e, following.

1c, 1d, 1e, 1f. All of these with the typical scant (i.e., 1a) leaflet pubescence but medial portion of stem slightly or evidently pubescent as listed following. Leaf portions various.

1c. Some *perplexum*-type pilose pubescence (see Group 2).

1d. Some *glabellum*-type uncinata pubescence (see Group 3).

1e. Mixture of *perplexum* and *glabellum* pubescence types or pubescence of intermediate form.

1f. The *epetiolum*-type; petioles 2–10 mm; upper leaves subsessile.

GROUPS 2-5. The *perplexum*-*glabellum*, etc. types. Leaflets 1.5–3 (-4) *r*. Plants usually (not so in group 5) of pubescent aspect. Pubescence of both medial stems and/or leaflets usually evident, of longer and/or uncinata hairs, and not appressed.

GROUP 2. The *perplexum* type. Medial stems and leafstalks with pilose pubescence.

2a. Pubescence evident and conspicuous.

2b. Pubescence scant, sometimes almost entirely restricted to leafstalks.

GROUP 3. The *glabellum* type. Medial stems and leafstalks with uncinata pubescence, sometimes a few pilose hairs also on leafstalks and pulvini.

3a. Pubescence dense and conspicuous.

3b. Pubescence scant.

GROUP 4. The *perplexum*-*glabellum* type. Medial stems with both pilose and uncinata hairs; or pubescence of intermediate form, i.e. the hairs intermediate in length and vaguely hooked at the tip.

4a. Lower surface of leaflets with evident or conspicuous pubescence.

4b. Lower surface of leaflets with reduced or negligible pubescence.

The abundance of stem pubescence among plants in group 4 is usually scant. Note that the secondary classification in this group and the following one (no. 5) is on the abundance of leaf pubescence rather than stem pubescence as in groups 2 and 3.

GROUP 5. Types with obsolescent stem pubescence but broad (1.5/3 *r*) leaflets.

5a. Lower surface of leaflets with evident pubescence.

5b. Lower surface of leaflets with reduced pubescence.

After specimens were assigned to these categories, the number in each category and their distribution by states were recorded.

OBSERVATIONS

Ranges given in regional and state floras indicated that the members of the *Desmodium paniculatum* complex, however classified, are approximately

sympatric, and this is confirmed in this sampling except that *D. perplexum* does not extend into Florida. The range is southern Maine (slightly into Ontario), west to Iowa, south to eastern Texas, and eastward to Florida. The sampling is neither sufficiently complete nor representative to justify a statement that the ranges are precisely the same, to analyze the extent to which the proportions of the different types may differ in various parts of the range, or to assert that all the smaller segregate categories may be found throughout this large area. It does indicate, however, that none except *Desmodium paniculatum* var. *epetiolum* have a specific geographic orientation; the others are distributed throughout most of the range.

A tabulation of the groups 1–5 described in the *Procedures* section follows, and the data are summarized in Figure 1. Notation of range observed among these specimens follows the sequence: northeast, northwest, southwest, southeast. The number of specimens for each group and subordinate group provides an estimate of their abundance. The accompanying text summarizes the major features of this classification.

THE *D. PANICULATUM* TYPES. GROUP 1.

Vermont, Iowa, Louisiana, Florida. 375 specimens: 1a, 305; 1b(a), 25; 1b(c), 1; 1b(d), 12; 1b(e), 1; 1c, 2; 1d, 19; 1e, 3; 1f, 7 (Figure 1, Group

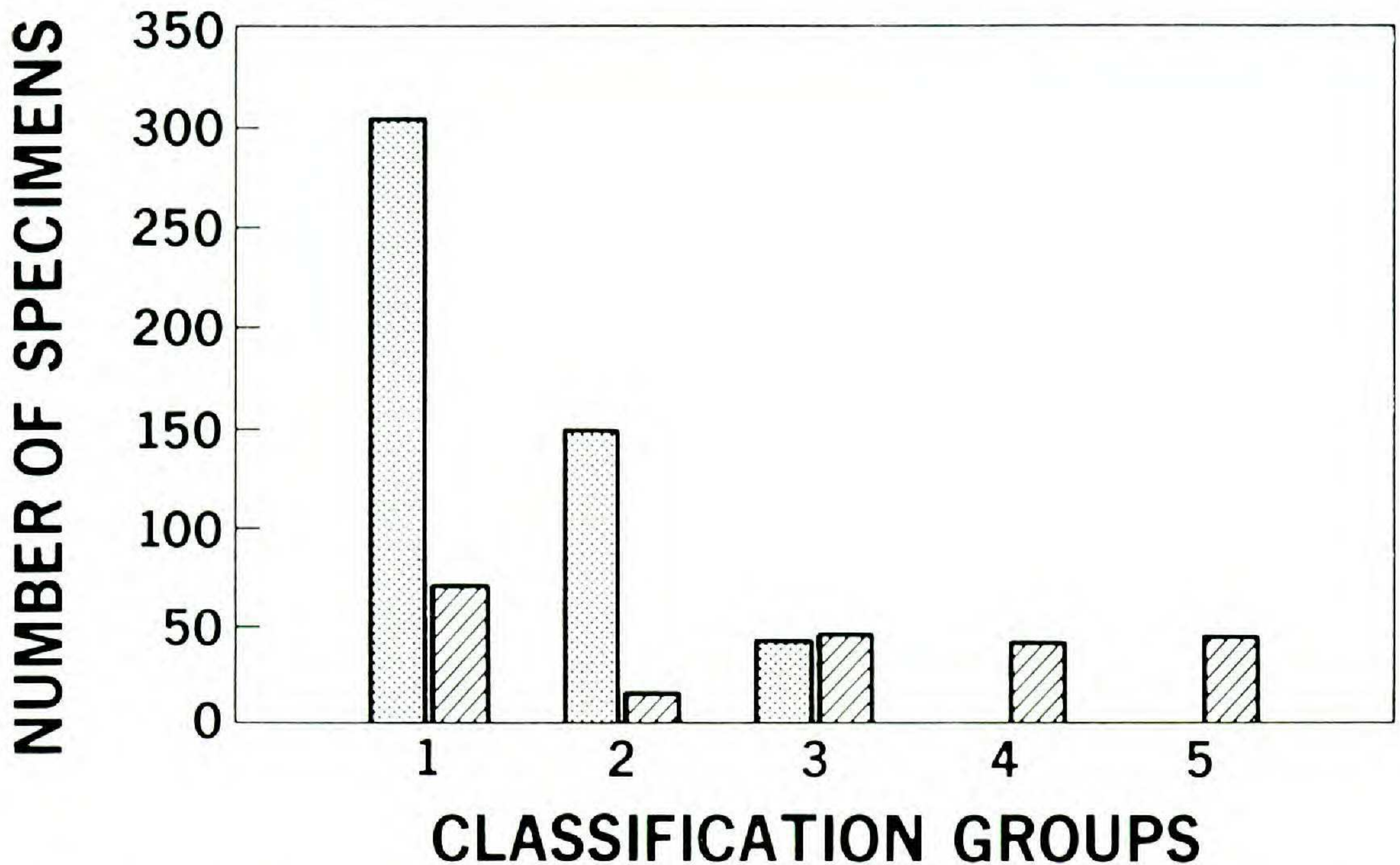


Figure 1. Comparison of number of specimens of three taxa of the *Desmodium paniculatum* complex. Data listed under Observations. Stippled bars: Specimens "typical" and identity definitive. Oblique-line bars: Specimens "atypical," identity ambiguous or equivocal. 1. *Desmodium paniculatum*. 2. *D. perplexum*. 3. *D. glabellum*. 4. Intermediate types, *D. perplexum-glabellum*. 5. Recondite types with broad leaflet and glabrous or glabrate stems.

1). (In Figure 1, the "atypical" group represents the total of the several categories, 1b-1f, listed here).

What this tabulation tells us is that most of the abundant material fits the ideal *Desmodium paniculatum* formula (narrow leaflets, scant pubescence; hairs short and appressed), but that an appreciable number of plants have longer, spreading leaflet pubescence or/and *glabellum* type uncinuate stem pubescence (but almost none with *perplexum* stem pubescence). The aberrant pubescence forms are distributed through the leaf-proportion range.

Botanists have been unanimous in determining plants with narrower leaflets as *D. paniculatum* regardless of pubescence. Among those with broader leaflets (3-5 r), determinations as *D. paniculatum* or *D. glabellum/perplexum* become inconsistent depending on the relative weight that the worker places upon leaflet proportions and nature of pubescence. If leaflet proportions are entirely disregarded, group 5 (broad leaflets, reduced or nil pubescence) would mostly be referred to typical glabrate *paniculatum*, 1a. Indeed from 1a one wavers at the border line, not only of group 5 and of 2b and 3b (these are the *perplexum* and *glabellum* types with scant pubescence) but also of groups 1b and 1d. Subjective judgment is such that passes that I have made through this material brought some repositioning each time.

The nature of Group 1f (Schubert's *D. paniculatum* var. *epetiolum*) is different from any of the preceding. Not only does it stand out on a morphological basis (much shortened petioles and some rounding of loment segments) but it has a specific eastern Coastal Plain range from southeastern Virginia to northern South Carolina. This statement is based on specimens I have seen plus those cited by Schubert (1950a, excluding her anomalous Texas reference). A hybrid combination between *D. paniculatum* and *D. ciliare* might be visualized, but these species are sympatric over a much more extensive range.

THE *D. PERPLEXUM* TYPES. GROUP 2.

Maine, Iowa, Louisiana, Georgia. 166 specimens. 2a, 149; 2b, 17. (Figure 1, Group 2).

These have broad leaflets and characteristic pilose pubescence on the stems and petioles that, however, is variable in amount. Most of this variation is included in group 2a in which the pubescence is conspicuous or at least evident. Most of the 2b group, on the other hand, has almost no stem pubescence but it is evident on the petioles where it is possibly more persistent than on the stems.

Leaflet blade pubescence is most abundant on the under-surface and, though diverse in amount (almost velvety to scant), is of much longer hairs than of the *D. paniculatum* group, and these hairs are characteristically spreading, incumbent or slightly ascending. The upper leaf surface usually ranges from scantily pubescent with similar (though usually shorter) hairs to glabrate.

Some specimens have tiny uncinulate hairs along the major veins of the upper surface.

Between the *D. paniculatum* and *D. perplexum* types there is an obvious correlation of three characters—leaflet proportions, presence or absence of stem pubescence and the nature of leaflet pubescence. But there are a sufficient number of failures of such correlation and of intermediates to render sharp discrimination impossible.

THE *D. GLABELLUM* TYPES. GROUP 3.

Connecticut, Missouri, Texas, Florida. 89 specimens. 3a, 43; 3b, 46. (Figure 1, Group 3).

My annotation essentially agrees with that of Wilbur (NCU specimens) except that I have divided *D. glabellum* into two groups and have relegated some of his *D. glabellum* to groups 4 and 5.

D. glabellum, as *D. perplexum*, has broad leaflets (usually 2–3 *r* but sometimes to 4 *r*; or to 5 *r*, if one regards pubescence as more important than leaflet proportions). Typical *D. glabellum* (3a) with a dense, close covering of uncinulate hairs on the stem is unmistakable. But it fades into the equally abundant scantily or barely pubescent plants (3b) that merge with *paniculatum* 1d forms that have broad leaflets and with the glabrate types of group 5. It includes both plants with some pilose pubescence on the pulvini and those with negligible pubescence on the stems but distinct uncinulate pubescence on the petioles.

Leaflet pubescence of *D. glabellum* is similar to that of *D. perplexum* and, though likewise variable in abundance, perhaps averages less in amount. This tends, on the average, to give the leaflets a more reticulate aspect. Uncinulate hairs along the veins on the upper surface are common, though not invariable, and such pubescence is sometimes present also along veins on lower leaflet surfaces.

THE *D. PERPLEXUM-GLABELLUM* TYPES. GROUP 4.

Pennsylvania, Iowa, Louisiana, Florida. 42 specimens. 4a, 32; 4b, 10. (Figure 1, Group 4).

Here is a heterogeneous catchall for seeming intermediates, usually with relatively inconspicuous stem and leafstalk pubescence, in which the *Desmodium glabellum* influence perhaps predominates. It may include a mixture of a few hairs of the two contrasting kinds, or the hairs themselves may be intermediate in form, as described in the foregoing description of classification.

Wilbur, as to annotations, placed these plants with the species (*Desmodium perplexum* or *D. glabellum*) that he believed they most closely resembled. They indeed merge not only with the scantily pubescent forms of the named species but also with those of group 5 following. The subclassification (4a and 4b) indicates that the kinds with reasonably evident leaflet pubescence are most abundant.

THE *D. PANICULATUM* COMPLEX. Ambiguous specimens with glabrous (glabrate?) stems and broad leaflets. Group 5.

Maine, Iowa, Louisiana, Florida. 45 specimens. 5a, 20; 5b, 25. (Figure 1, Group 5).

Leaflet pubescence may be spreading or (5b, reduced leaflet pubescence) short and appressed as in the *paniculatum* type, but tends to be uncinulate along the veins. A correlation between pubescence abundance on stems and leaves is indicated by the fact that 5b constitutes proportionately a larger subsegment than does 4b of group 4 among which there was at least some pubescence on the stems.

The group 5 plants seemingly represent a mixture of reduced-pubescence forms related to group categories 2, 3, 4, but some may be essentially *paniculatum* (group 1) with broader leaflets than conventionally attributed to that type. Plants with conspicuous pubescence on the leaves (5a) or/and those with a few pilose hairs on leafstalks or pulvini perhaps can be associated with group 2 (*perplexum*); those with uncinulate hairs along the leaflet veins suggest group 3 (*glabellum*), and those with but short, strigose hairs on the leaflets, resemble broad-leaved forms of *paniculatum* and are but subjectively separated from the several categories of that group. Perhaps some of these latter kinds might represent hybrids with *Desmodium laevigatum* (Nutt.) DC.

OTHER "MIXTURE" DATA.

Field observations easily reveal different phenotypes of the *Desmodium paniculatum* complex growing in association. Contrasting plants may occur in adjacent colonies that within themselves are relatively uniform, or a single colony may include several kinds of plants. Unfortunately, I have never attempted to document these observations except that I once gathered six leaves from representative plants in a single colony (Powell Co, KY: *Isely* 7422, ISC). Three are of the *paniculatum* type, 1a, with leaflet proportions 5.3, 5.5 and 3.5 *r*; one is *perplexum*, 2a, 2.3 *r*; two are *perplexum*, 2b, both 1.7 *r*. Also, from Marion Co, TN, *Isely* and *Wemple* 9409, 9411 and 9412 (ISC) represent three phenotypes from three contiguous colonies. These are *D. paniculatum* (1a) and *D. glabellum* (3a and 3b).

I have scanned ISC for specimens containing two stems not organically connected and hence possibly from different plants in a colony. Among about 15, I found sheets with different phenotypes from Kentucky, Arkansas, Georgia, Alabama and Florida.

Leaflet proportions on a single plant are usually reasonably consistent but in some the leaflets are graduated narrower upwards on the stem. Among a stem cluster from a single crown, one can sometimes discern slightly different leaflet proportions between stems.

EXOMORPHIC VARIATION NOT TABULATED.

The flowers seem to be identical except for some variation in color and size, those of *Desmodium perplexum* perhaps averaging somewhat the largest. But they have not been studied in detail.

Pedicle length is variable, (3-) 5-12 (-20) mm. Those of ideal *Desmodium paniculatum* not uncommonly exceed 10 mm and appear filamentous. Those of *D. perplexum*, on the other hand, are usually less than 10 mm in length and appear stouter. Those of *D. glabellum* are diverse.

Loment stipe ranges in length from 1 mm, and hidden by the calyx remnants, to 3.5 (-5) mm and strongly exerted. The proximal 1-2 mm of the first segment is sometimes abruptly narrowed, making the stipe appear longer. Most commonly, *Desmodium paniculatum* and especially *D. glabellum* have plainly exerted stipes while those of *D. perplexum* are usually little evident above the calyx. But the difference is not diagnostic.

Length of the loment segments falls within the range (3.5-) 5-7 (-8.5) mm. *Desmodium perplexum* on the average has the larger segment but there is no diagnostic distinction. There seems to be no differential trend in the number of segments nor in the variation in their shape among the species.

As a means of checking these generalized statements, I measured pedicle, stipe and loment segment length on 15 specimens each of "typical" *D. paniculatum*, *perplexum*, and *glabellum*, (groups 1a, 2a, and 3a) randomly chosen from throughout their range. Summarized data follows:

		PEDICLE LENGTH	STIPE LENGTH	LOMENT SEGMENT LENGTH
<i>Paniculatum</i>	Range	4.5-13 mm	1.2-3 mm	3.5-7 mm
	Mean	7.9 mm	2 mm	5.5 mm
<i>Perplexum</i>	Range	3-7 mm	1-3.1 mm	4-8.5 mm
	Mean	5.7 mm	1.6 mm	6.1 mm
<i>Glabellum</i>	Range	5.2-13 mm	1.5-5 mm	4-7.6 mm
	Mean	7.7 mm	3 mm	5.7 mm

These limited data of course have no statistical significance. But they roughly confirm the ad hoc observations of the preceding paragraph. The differences are not diagnostic and disappear among the various intermediate forms.

HABITAT

Neither my field observations over a period of some years nor herbarium data reveal significant differences in habitat.

HYBRIDIZATION (INTERMEDIACY) WITH OTHER SPECIES?

Nearly all phenotype combinations encountered can be referred to variation from within the gene pool(s) of this group. Thus, ostensibly, hybridization between members of this complex and other species is infrequent. This

statement must be qualified by the fact that putative hybrids are more difficult to detect than in *Lespedeza* where strongly contrasting characters of different species are easily evident. A few 3b and 5a plants with quite long loment stipes and pedicels might represent hybrids with *Desmodium laevigatum* (Nutt.) DC. From another direction, certain specimens in these same groups possibly suggest *D. fernaldii* Schubert. I have seen one plant that is seemingly intermediate between *D. paniculatum* and *D. ciliare* (Muhl.) DC. *D. paniculatum* var. *epetiolum* Schubert is conceivably of hybrid origin.

DISCUSSION

Although prior authors, as reviewed, have presented differing taxonomic treatments, most have referred to intermediacy between taxa and have recognized inadequacies in present understanding of the complex. These observations then primarily detail what is believed, and provide no new shining light.

Among available treatments, I view Wilbur's (1963, 1968) as most satisfactory. The germ for discernment, however, perhaps derives from Schubert (1950a, 1950b) even though several of us (Isely, 1953; Wilbur, 1963; Steyermark, 1963) have stated inability to use Schubert's differential characters for *Desmodium glabellum*. Evidently she had a "feel" for that taxon because those of her annotations I have seen closely match both Wilbur's and mine. The idealized concepts of Wilbur and Schubert are, indeed, validated by the majority of specimens, which fall into discernible categories. The problem then is that the identification of too many others is ambiguous.

Wilbur's annotations reveal that he placed ambivalent material with the species it most closely resembles following subjective but rather consistent criteria. For example, in the differentiation of *Desmodium paniculatum* from the two kinds with usually broader leaflets, he, as others preceding him, identified those with narrow leaflets, ca 4–8 *r*, as *D. paniculatum* regardless of the nature of the pubescence. However, at about 4 *r*, he abandoned leaf proportions as a diagnostic character and made determinations on the basis of pubescence. The distinction between *D. glabellum* and *D. perplexum*, as indicated in his key, is based on stem pubescence, but only a minority of his *D. glabellum* have stems that are "densely uncinulate puberulent." Instead, it includes the entire range of variation in the amount of such pubescence, those with scant pubescence being excluded only if the pilose pubescence of *D. perplexum* is also present and more conspicuous. The key statement for *D. perplexum* allows for variation in pubescence ("stem moderately to densely pilose") but actual separation not only allows a wider range of stem pilosity but includes some plants in which the stems are essentially glabrate, the pubescence being limited almost entirely to the leafstalks. His assignment of plants with intermediate or both kinds of pubescence is based on

judgment as to which kind is predominant. Wilbur then has followed a fairly consistent course in identification, but it does not entirely accord with the statements in his key, nor with a concept that the species are as clearly defined as he (1963) states.

The preceding paragraphs imply that observed variation is genetic, but this may not be entirely true. The weight of environmental factors, however, is unknown. It is possible (or probable) that some plants with especially thin, large and broad leaflets that also have reduced pubescence are shade forms in which the conventional distinctions between the species are enfeebled or obliterated. If, however, three species can be distinguished only by features whose diagnostic value is vitiated by environmental influences, this in itself possibly questions the validity of the taxa.

Another factor leading to ambiguity of classification may be the condition of the specimens. Pubescence in *Desmodium perplexum* and *D. glabellum*, particularly the former, is probably partially lost as stems age. I tried to nullify this consideration by also checking leafstalks where pubescence seems to be more persistent, but this may result in confusion with forms in which the pubescence clearly is mostly limited to the leafstalk. One can also examine the upper (i.e., younger) foliose portions of the stem, but care has to be used to avoid proximation with the inflorescence pubescence that is uncinata in all species.

I think it is fairly clear that all of us who have studied this complex are somewhat groping in the dark. We have been limited to subjective interpretations based primarily on herbaria holdings. None of us know what is going on biologically. Perhaps the present state of knowledge allows three overlapping hypotheses as follows:

(1) There are three closely related but genetically reasonably discrete taxa whose range of exomorphic variation overlaps with respect to the characters treated as diagnostic. We do not yet know how to best interpret their differentiation and relationship among patterns of variation in the "diagnostic" features. If other discriminating characters exist they have yet to be discerned.

(2) There were originally three taxa, differing in leaflet shape and pubescence, that owed their identity to some kind of isolation, presumably ecological. *Desmodium*, except for those of the *D. glutinosum* group, are sun-loving plants. With destruction of the forests and the increased prevalence of open habitats, this isolation was eliminated, and no doubt the plants are much more common than they were 300 years ago. The consequent invasion of abundant hybrid habitats has spawned a maze of intermediates perhaps in somewhat the same way as is believed to have happened in *Crataegus*.

(3) The entire complex is a single polymorphic species containing within its gene pool conspicuous variation in the amount and nature of the pubescence and in leaflet proportions. The variation observed is that of a com-

monly cross-pollinated heterozygous species in which there is sufficient linkage between leaflet proportions and pubescence that some genotypes are much more prevalent than others.

None of these hypotheses are entirely satisfactory on the basis of present information. Among them, hesitantly, I favor two or three because the plants grow in association in similar habitats and have similar if not identical ranges, and because I find the unifying characters more significant than the several patterns of variation. For example, most species of *Desmodium* exhibit differences in their fruits. Those in this group, however, are fundamentally consistent in aspect and usually easily recognized. True, there are some differences in the range of variation of stipe length and loment-segment size, between the putative taxa, but these are not of diagnostic nature. Thus, whether differences among populations, or of individuals, are of leaflet proportions, of nature of pubescence, or of loment characters, the species are separated only by features that are highly variable. Possibly the very conspicuous variation in leaflet proportions has maintained the traditional view that there must be several species.

Among these alternatives, one might favor number three (that the taxa were originally more discrete) were there some basis for postulating the nature of their original isolation.

A conventional apologia to a report of this kind is a statement that detailed biosystematic (and perhaps chemical and taximetric) studies of these species are needed and must be conducted before the group can be understood. No doubt, such investigations would be welcome, but vast accumulation of data does not necessarily lead to congruence in classification. Relatively elementary information that could respond to the following questions might, however, lead to some clarification.

(1) Are these species capable of crossing? If so, how frequent is this in nature? (This information could be obtained by using routine methodology of plant breeding or biosystematics).

(2) To what extent does environment, particularly incidence of light, affect expression of genotypes?

(3) How does the expression of pubescence and its senescence change as the plants grow and mature?

CLASSIFICATION

Presently for floristic purposes, I propose a procedure similar to that employed in *Flora Europaea* (Tutin et al., 1964, 1968). "In certain cases where it is difficult to distinguish between a number of closely similar species, an ad hoc 'group' has been made, and these groups, not the individual species, are keyed out in the main species-key." Thus this assembly could be called the *Desmodium paniculatum* (L.) DC. (complex) under which the component members are keyed as follows:

1. Leaflets (2.5-) 3-8 (-10) *r*; leaflet pubescence usually scant, of short, appressed hairs (infrequently more conspicuous and of somewhat longer spreading hairs), uncommonly including some uncinulate pubescence; medial stem glabrous or glabrate, or if with a few hairs, these usually minute and uncinulate (rarely a few pilose hairs present on leafstalks and pulvini). *D. paniculatum* (L.) DC.
1. Leaflets 1.2-3 (-4) *r*; leaflet pubescence usually evident and of longer spreading or somewhat incumbent hairs, commonly including some uncinulate pubescence, primarily along nerves on upper surfaces of leaflets; medial stems usually with evident pubescence of either pilose or uncinulate hairs or both.
 2. Stem and leafstalk pubescence of pilose hairs, these abundant and conspicuous or scanty and limited primarily to leafstalks; some uncinulate pubescence occasionally also present on stems and along veins on upper surface of leaflets.
..... *D. perplexum* Schubert
 2. Stem and leafstalk pubescence of uncinulate hairs that form a dense or scant covering; a few pilose hairs sometimes also present on pulvini, rarely also on leafstalk; uncinulate pubescence commonly present along veins on upper surface of leaflets.
..... *D. glabellum* (Michx.) DC.

The above key, though arbitrary, more completely partitions variation than do those of Wilbur (1963, 1968). If the member within the group is evident, identification can be extended to it. On the other hand, if identity is ambiguous, the worker can determine a plant as a member of the *Desmodium paniculatum* (L.) DC. complex and leave the matter at that. If more precision is desired, the code identification supplied in this classification could be added (specimens I have seen are so marked). By so proceeding, some consistency of determination, though at varying levels of diagnosis, might be obtained.

The species names, synonymy as to authors cited in previous discussion, and the Isely code listings follow.

DESMODIUM PANICULATUM (L.) DC.

Meibomia paniculata (L.) Kuntze; *M. paniculata* var. *chapmanii* Britton and nomenclatural synonyms; *D. paniculatum* var. *pubens* T. & G. and nomenclatural synonyms; *D. paniculatum* var. *angustifolium* T. & G. and nomenclatural synonyms; *D. paniculatum* var. *epetiolum* Schubert; *Desmodium paniculatum* var. *typicum* Schubert. 1a, 1b, 1f; 1c, 1d, 1e in part; some approaching 2b, 3b, 4b, and 5b.

Schubert (1950a, p. 153) examined the syntypic cited specimens of *Desmodium paniculatum* var. *pubens* T. & G. and felt they represented "the more pubescent extreme of *D. paniculatum* var. *typicum*," and I have listed that name accordingly. Small (1933), however, treated plants of this type as a separate species, *Meibomia pubens* (T. & G.) Young. By description ("stem puberulent; leaves oblong-lanceolate, rather rigid, pubescent, especially beneath") they would probably fall in one of the several intermediate groups listed herein.

Varieties *chapmanii* and *angustifolium* both represent phases of *D. paniculatum* with narrow leaflets. Var. *typicum* includes the whole scope of idealized *D. paniculatum*. Var. *epetiolum* is a regional form that probably deserves nomenclatural listing.

DESMODIUM GLABELLUM (Michx.) DC. but not of Gleason (1952) nor Gleason and Cronquist (1963); nor *Meibomia glabella* (Michx.) Kuntze of Small (1933).

Meibomia paniculata var. *obtusa* (Desv.) Schindl. *D. dillenii* Darl. and nomenclatural synonyms of authors in part. 3a, 3b; 4a and 4b in part; some approaching 1a, 1b, 1d, 1e.

Reference of *Meibomia paniculata* var. *obtusa* to *Desmodium glabellum* is based on Schubert's (1950a, p. 154) statement about it. As previously noted, the *Desmodium* (or *Meibomia*) *glabellum* of literature refers to two different species.

DESMODIUM PERPLEXUM Schubert

Desmodium dillenii Darl. and nomenclatural synonyms of authors in large part; *Desmodium paniculatum* var. *pubens* T. & G. and nomenclatural synonyms of authors in part. 2a, 2b; 4a and 4b in part; some approaching 1a, 1c, 1e, 5a.

Prior to 1950, most *Desmodium perplexum* and *D. glabellum* passed under the classic *D. dillenii* Darl. Schubert (1950a) found four specimens in the Darlington herbarium to be non-congruent, and a Dillenian plate cited unidentifiable. Consequently she abandoned this name as a *nomen confusum*.

ACKNOWLEDGEMENTS

I extend thanks to Drs. Bernice Schubert and Robert L. Wilbur who reviewed this manuscript, but this does not imply that they agree with the conclusions. Rebecca R. Johnson provided technical and clerical help. The loan of specimens from the herbaria of the University of North Carolina (NCU) and the University of Florida (FLAS) is appreciated. Research supported in part by NSF Grant DEB-8103505.

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