

Desmodium glabellum and *D. perplexum* (Fabaceae): a morphological reevaluation

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ABSTRACT. — Traditional morphological distinctions between *Desmodium glabellum* and *D. perplexum* are investigated. The ambiguity of traditional concepts is verified. Alternative distinctions based on less variable character states are proposed and tested as a new prescription for taxonomic concepts and as a model for accommodating ambiguities in organismal biology.

INTRODUCTION

Conceptualizing morphological, genetic, and ecological distinctions among species within diverse genera of organisms is notoriously difficult. The process lends itself to error largely from overlapping or cryptic character states, biased weighting of characters states, and the degree to which the interpreter has experienced the organisms in situ as expressions of the natural world. In short, cryptic taxa are not only difficult to physically discern, they are also conceptually difficult to grasp. It is challenging to mentally untangle the technical complexity of such entities, where doing so requires an intuitive familiarity beyond simple observation. This familiarity, dedication to practice, and openness to detail endows one with an optimistic intuition regarding the myriad ways nature can express itself that otherwise cannot be fully explained to the uninitiated. Polanyi's Paradox states that it is possible to understand real truths and phenomena that can only be explained through heuristics. Such is nearly the case here.

Desmodium Desv. are trifoliate herbaceous perennials that produce articulated loments (specialized legumes that separate between their single-seeded segments). The segments of loments are called articles. The articles are a notorious nuisance to late summer explorers who fall victim to their ingenious dispersal mechanism (via their uncinat puberulence) and who then spend hours picking and scraping them off their clothes.

While contemporary interpretations of the taxa within North America's *Desmodium* are mostly stable, there are problematic complexes. To field-focused practitioners, the "*Desmodium paniculatum* complex" has remained one of the more persistently confounding. This complex includes such familiar names as *D. paniculatum*, *D. glabellum*, *D. perplexum*, *D. dillenii*, and *D. fernaldii*. All of these names except *D. dillenii* are currently in use. Contemporary practitioners consider *D. paniculatum* and its closely allied *D. fernaldii* to be distinct from *D. glabellum* and *D. perplexum*, if not from each other. The real confusion in the complex has largely emanated from

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the relationship of *D. glabellum* and *D. perplexum*, even when they were collectively called *D. dillenii*. Schubert (1950) invalidated the name *D. dillenii* as a *nomen confusum* and split its interpretation into *D. glabellum* and *D. perplexum*. There is a history of gradual resolution from only *D. paniculatum*, to the recognition of both *D. paniculatum* and *D. dillenii*, to the revelation of *D. paniculatum* and *D. fernaldii* differing from *D. glabellum* and *D. perplexum* (the latter two comprising the former *D. dillenii*). This process involved intermediate designation of varietal statuses along the way, just as there are currently accepted varieties within our continually evolving concepts of *D. paniculatum*.

Isely (1983) thoroughly and concisely summarized the history of concepts around this complex. His account is well worth reading, not only for the content but also as an example of a structure and philosophy that is scarcely seen in contemporary published material. Since Isely's work, little has changed at the species scale. As outlined by Isely, the works of Schubert (1950) and Wilbur (1963) hypothesized that *D. glabellum* has densely uncinatate-puberulent internodes which can also be sparsely pilose, and *D. perplexum* has moderately to densely pilose internodes that either lack uncinatate-puberulent vestiture (Wilbur 1963) or also have uncinatate-puberulent hairs (Schubert 1950). Isely tested these hypotheses by reviewing each author's annotated material and applying their concepts to 650 specimens.

Finding little satisfaction in the complex, especially between *D. glabellum* and *D. perplexum*, Isely remarked:

"I think it is fairly clear that all of us who have studied this complex are somewhat groping in the dark."

Based on a graph provided in his analysis, roughly half of the non-*D. paniculatum* specimens he examined were categorized as "ambiguous." He provided a synoptic key that included a code to what he interpreted as "groups" of morphologies within the complex, and suggested that in lieu of satisfaction, of which he found little, all three taxa could be defaulted to *D. paniculatum sensu lato*. Finding no differences in other morphological characters or habitat preferences, his key, like those of Schubert and Wilbur, is largely based on stem pubescence type and density, with the expressed caveat that it does not work well except in segregating most specimens of *D. paniculatum sensu stricto*.

Isely hypothesized about the sources of confusion and reiterated that, despite not finding consistent distinguishing characters for *D. glabellum* and *D. perplexum*, he, Schubert, and Wilbur agreed that they seem to be real entities. Isely provided what he called "the conventional apologia" that more detailed work is needed, including greater field familiarity with the taxa. One could summarize Isely's findings as: while *D. glabellum* and *D. perplexum* seem to be valid species distinct from *D. paniculatum*, investigations have failed to elucidate a consistent set of characters to effectively differentiate them. Variations of Isely's key and, if only by association, the keys of Schubert and Wilbur, are still used in contemporary regional floras.

UNTANGLING THE PROBLEM

For years, botanists in the field have struggled with Isely's stem pubescence characters, and its derivations in subsequent floristic treatments. It has been frustrating for me working primarily throughout the Midwest and midsouth where there appear to be two morphological entities that differ in leaf shape, leaf abundance, leaf distribution, and stem branching. These frustrations peak when attempting to rigidly apply Isely's stem pubescence characters, which ultimately leads to an ungratifying hodge-podge of unconsolidated character states. In order to better test and perhaps elucidate meaning from the combinations of these characters, I compiled the entire collection of 179 Missouri specimens at the Missouri Botanical Garden herbarium (MO), and sorted them by Isely's stem pubescence characters. Serendipitously, Isely's stem pubescence characters had already been applied to the Missouri material and annotated by Dr. Jay Raveill in preparation for the treatment of *Desmodium* in Yatskievych (2013). My interpretation of Isely's stem pubescence characters in the Missouri material were congruent with those of Raveill, with the only exceptions being specimens that I felt were too ambiguous to make a clear determination.

During this sorting, I noted that much of the *D. glabellum* material indeed lacked long hairs except at the nodes, and much of the *D. perplexum* material had long hairs. But, as I'd observed previously in the field, specimens with similar characters (leaf shape, leaf distribution, and leaf texture) were conceptually divided by the stem hair characters. Hoping to dispel some confusion, I independently sorted the traditional *D. glabellum* and *D. perplexum* stacks into two piles each: one with narrower terminal leaflets and a gradual reduction in leaf size along the stems (phyllotomy), and one with wide leaflets that are not gradually reduced in size along the stem.

While this was moderately satisfying, I worried that the narrowness and gradually reduced leaflet character could be induced by the sunniness of the habitat. So, I re-sorted based on label data and found that these characters did not correlate with openness of the habitats from which they were collected, although a few more narrow-leaved specimens were associated with more open habitats. In examining the loment, I noticed in looking directly down on the broad faces of the triangular articles, that the ventral margins that meet at the bottom of each article were of two forms: concave in some specimens, and straight to slightly convex in others (Fig. 1). I then re-sorted the specimens with mature fruit and found that the leaf differences by which I had sorted earlier matched exceedingly well. However, this meant that many of the specimens that were referable to *D. glabellum* by Isely's stem pubescence characters better fit with *D. perplexum* and vice versa.

Next, I consulted images of the type specimens. Luckily, each is a fruiting specimen. The type specimen of *D. perplexum* (Fig. 2) has mostly concave article margins (Fig. 1 A) and stem leaves of approximately the same size, except for a few in the inflorescence. The type specimen of *D. glabellum* (Fig. 3) has straight to convex article margins (Fig. 1 B) and although it lacks many leaves and is likely a branch of a plant rather than a whole plant, it exhibits some degree of a gradual reduction below the inflorescence or at least a suggestion of that tendency. I then did a

final sort of the Missouri specimens, compiling a hierarchical list of characters that seemed to well differentiate them. I then tested these characters using all the available material from across the geographical range of the species and found that the characters held. From this emerged a key bridging the disparities between field and herbarium observations, but one that differs markedly from conventional concepts

While this treatment varies from conventional concepts of this species pair, the conventional view, according to experts in the group (Isely 1983, Schubert 1950, and Wilbur 1963), was not particularly defensible. When the new interpretation provided here was applied to the 179 Missouri specimens housed at MO, it changed the identification of 59% of them (65% of “new” *D. glabellum* had previously been annotated as *D. perplexum* and 53% of “new” *D. perplexum* had been annotated as *D. glabellum*). Similar ratios occurred in evaluation of the non-Missouri material. All specimens were annotated according to these new concepts (Tropicos 2020).

These characters were subsequently tested in the field for several seasons across a large geographical range, since characters that apply in the herbarium don’t always work in the field and vice versa. These new concepts were also tested by other experienced field botanists (Andrew Braun, Brett Budach, Jacob Hadle, and Scott Namestnik) over three field seasons (2018-2020). We all found that the new characters held, often contradicted the old characters, and ultimately provided more consistent and predictable results than previous interpretations.



Figure 1. The subtle differences in general outline of the articles. The articles of the type specimen of *Desmodium perplexum* (A) are slightly concave on the lower (ventral) margin. The articles of the type specimen of *Desmodium glabellum* (B) are straight. Another way to see this is in the negative space the articles create, in that of *D. perplexum* (A) is more rounded and *D. glabellum* (B) is more angular.



Figure 2. Type specimen of *D. perplexum* showing overall habit.



Figure 3. Type specimen of *D. glabellum* showing overall habit.

KEY TO THE SPECIES

Ventral margins of most articles straight to slightly convex (Fig. 1 B); leaves gradually but noticeably reduced in size and petiole length distally along the stem, often with small leaves extending well onto the flowering branches; terminal leaflets lanceolate to broadly ovate (most specimens, especially of full sun habitats, are on the narrow end of this range; see field notes below), broadest nearer the base than the middle..... 1. *Desmodium glabellum*

Ventral margins of most articles concave (Fig. 1 A); leaves mostly all the same size and not or little extending onto the flowering branches (the few leaves that do extend into the inflorescence branches will also be reduced in size but more abruptly so); terminal leaflets narrowly ovate to broadly elliptic-ovate (most specimens are on the wider end of this range), broadest nearer the middle than the base..... 2. *Desmodium perplexum*

DISCUSSION

1. *Desmodium glabellum* (Michx.) DC.

Vegetative characters: The most straightforward specimens of *D. glabellum* have lanceolate to narrowly ovate terminal leaflets, leafy stems with the leaflets and petioles becoming notably reduced distally, and leaves progressing well onto the stems beyond the bases of the lowermost flowering branches. The more expressive plants in this regard tend to be found in more open habitats. Fig. 4 demonstrates this condition. The average condition for *D. glabellum* has wider terminal leaflets that taper to a more defined point than is expressed in *D. perplexum*. Fig. 5 demonstrates this average condition. A smaller percentage of plants produce more ovate terminal leaflets with blunt tips. These plants also tend to be less leafy and have less reduction in the size of leaflets and length of petioles along the stem. These plants tend to be found in deeper shade and have thinner leaves than plants in sunnier habitats. Fig. 6 demonstrates this more broad-leaved condition. While these plants do cross into the vegetative expressions of *D. perplexum*, the similarities are superficial, as is most evident when fruiting characters are available.

Fruiting characters: As the key describes, the fruits of *D. glabellum* have straight to convex margins on the lower (ventral) side of articles. Fig. 7 shows an example of the most convex expression of *D. glabellum*. The fruits of some specimens are not this dramatically convex. Fig. 8 shows example of the average condition, which has more of a straight edge. A minority of specimens have slightly concave article margins, especially if the loment is immature and dry with a curve, in which case experience with the degree of concavity/convexity both taxa can express must be weighed against the characters of the vegetative condition. Fig. 9 is an example of nearly *D. perplexum*-like articles found in occasional specimens of *D. glabellum*.

Field notes: As shown in Figure 10, based on specimens at MO, *Desmodium glabellum* appears to be distributed throughout most of Missouri, while *D. perplexum* appears to be mostly absent in the

prairie regions north and west of the Ozarks. This pattern has been corroborated by extensive field work throughout Missouri and west into the Flint Hills of Kansas. Jacob Hadle (pers. comm.) has tested these characters throughout eastern Kansas and agrees that everything in the region is *D. glabellum*, with the exception of the Cross Timbers region of southern Kansas where some *D. perplexum*-like specimens have been found in woodland communities. In the Ozarks *D. glabellum* and *D. perplexum* occur in the same habitats, which are varied, though *D. glabellum* tends to be more common in acidic upland woodlands and *D. perplexum* tends to be more common in mesic woodlands and forests.

Although no specimens in this study closely resembled *D. paniculatum*, the morphological characters of *D. glabellum* do seem somewhat intermediate between *D. paniculatum* and *D. perplexum*, potentially supporting Isely's (1983) notion that *D. glabellum* could have derived from introgression of these two. That said, given the findings of this study, *D. glabellum* has sufficiently consistent morphological, ecological, and biogeographic cohesiveness across a large geographical area to warrant continued recognition as a species. Stipules aside, narrow-bladed specimens of *D. glabellum* also resemble *D. canadense*.

2. *Desmodium perplexum* B.G. Schub.

Vegetative characters: *Desmodium perplexum* expresses much less morphological variability than *D. glabellum*. Most specimens of *D. perplexum* have fewer leaves, ovate to broadly ovate terminal leaflets, leaves below the inflorescence branches of nearly equal size, and few to no leaves along the stems of the flowering branches. Figs. 11-13 demonstrate the typical morphological range of the vegetative condition.

Fruiting characters: As the key describes, the fruits of *D. perplexum* have concave to essentially straight margins on the lower (ventral) side of articles. Fig. 14 shows an example of the most concave expressions and Fig. 15 shows an example of straighter margins. Most fruits of *D. perplexum* are this easily interpreted, but occasionally one must rely on a combination of fruiting and vegetative characters, at least until the combination of signatures is experienced and understood. Additionally, the articles of *D. perplexum* tend to be longer, more angular, and thinner-walled than those of *D. glabellum*. In order to understand the range of variation in *Desmodium* article shapes, I also examined, in the field and herbarium, the range of expressions of numerous other species. All were very uniform, though many closely related species had similarly shaped articles. While this is certainly not proof of anything, it does suggest that the subtle but consistent morphology observed between *D. glabellum* and *D. perplexum* articles is typical of many members of the genus.

Field Notes (also see notes under *D. glabellum*): *Desmodium perplexum* appears to attain its northwesternmost extent along the Ozarks/Plains border region of Missouri (Fig. 10). Despite over a century of botanical collecting, including from such prolific collectors as B.F. Bush, there are no specimens of *D. perplexum* from the Kansas City area. Although I have looked for it at several

potentially suitable locations, I have never seen it north or west of the Ozarks. As discussed previously (Jacob Hadle, pers. com.) all of the material in this complex from the Flint Hills of Kansas is referable to *D. glabellum*. This geographical relationship emerged independently during testing of morphological characters, providing additional support for this conceptual approach. This is a common geographical range limit for many species more associated with eastern woodlands and/or Coastal Plain where they meet the Great Plains. This also corresponds to the tendency for *D. perplexum* to be more common in mesic and dry mesic woodland and forest communities than *D. glabellum*, which, though the two often co-occur, is more common in upland woodland and even grassland habitats. These community affinities break down in old-field, clear-cut, and slash-burn habitats where either species can be equally common. While they are not extreme generalists, neither species is particularly sensitive to ecosystem disturbance (in the sense that disturbance is anything that reduces the ecological integrity/complexity of a site).



Figure 4. *Desmodium glabellum*, showing narrow leaf dimensions, distribution of leaves well beyond and within the flowering branches, and general phyllotomy seen in many specimens.

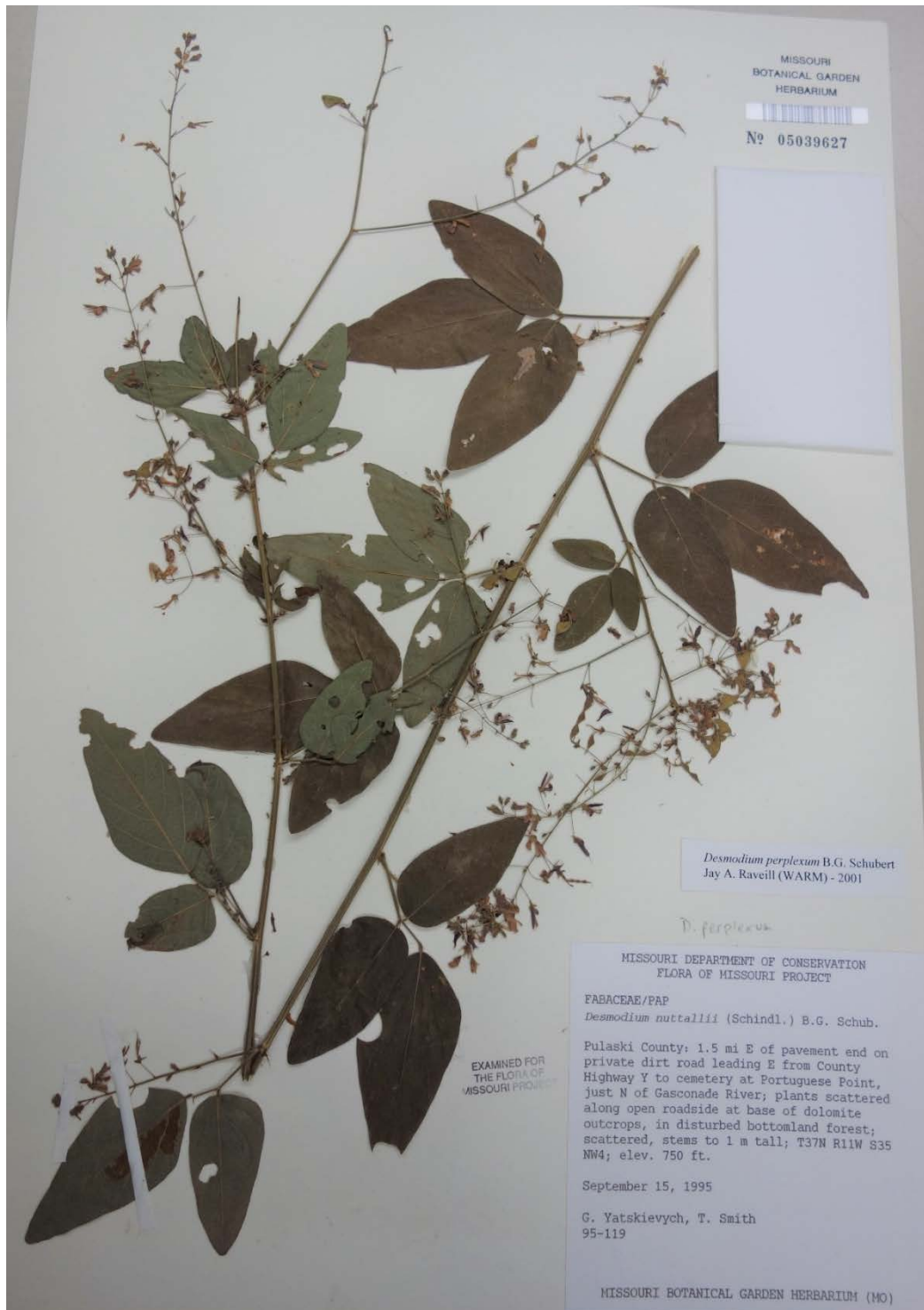


Figure 5. *Desmodium glabellum*, showing average leaf dimensions, distribution of leaves beyond the flowering branches, and general phyllotomy seen in many specimens.

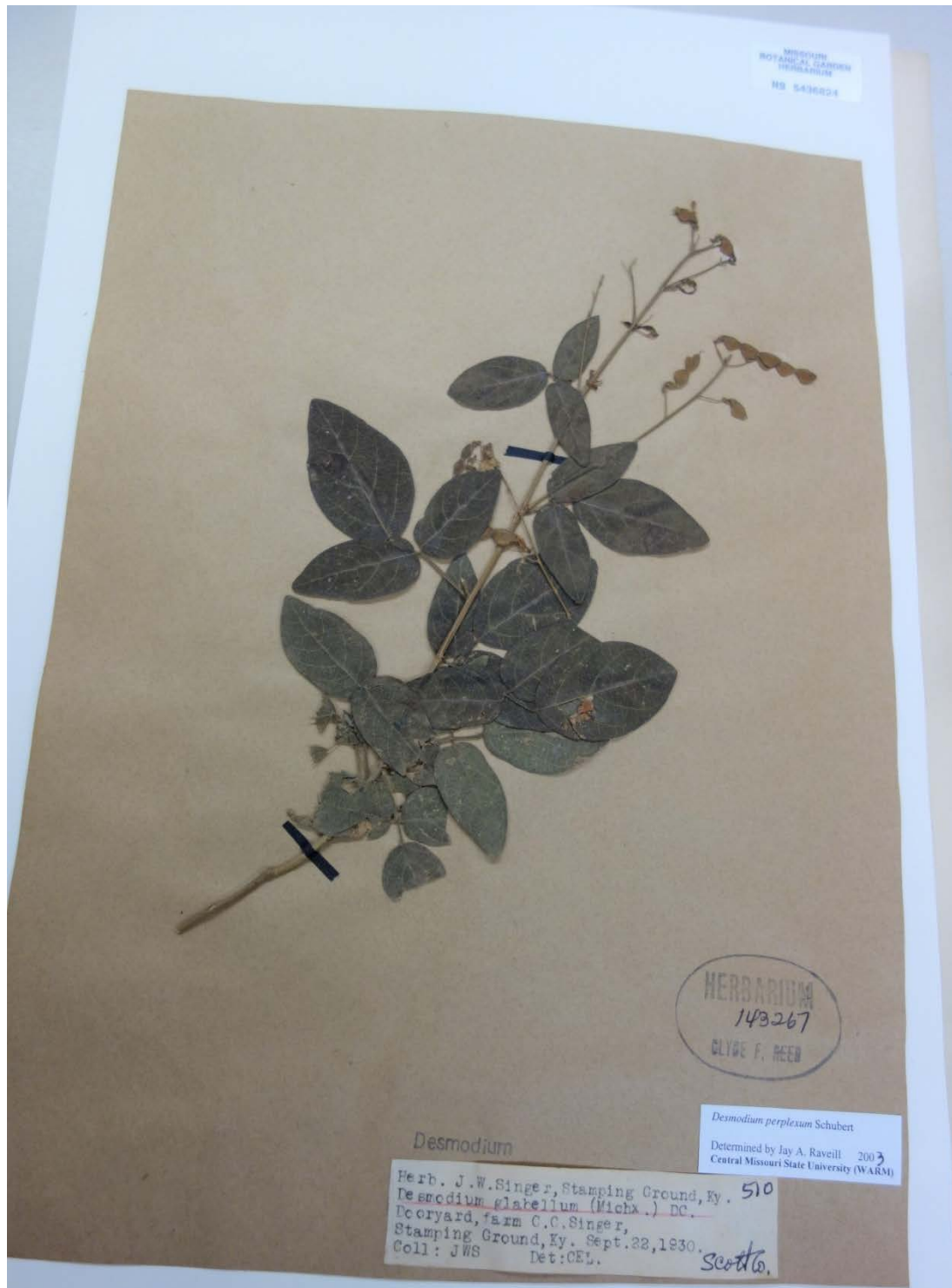


Figure 6. *Desmodium glabellum*, showing wider leaf dimensions, more restricted distribution of leaves towards the flowering branches, and reduced phyllotomy seen in rare specimens.



Figure 7. *Desmodium glabellum*, showing more pronounced expression of convexity to the lower margins of the articles seen in many specimens; scale in centimeters.



Figure 8. *Desmodium glabellum*, showing the straight lower margins of the articles seen in most specimens.



Figure 9. *Desmodium glabellum*, showing some concavity to the lower margins of the articles seen in rare specimens; scale in centimeters.

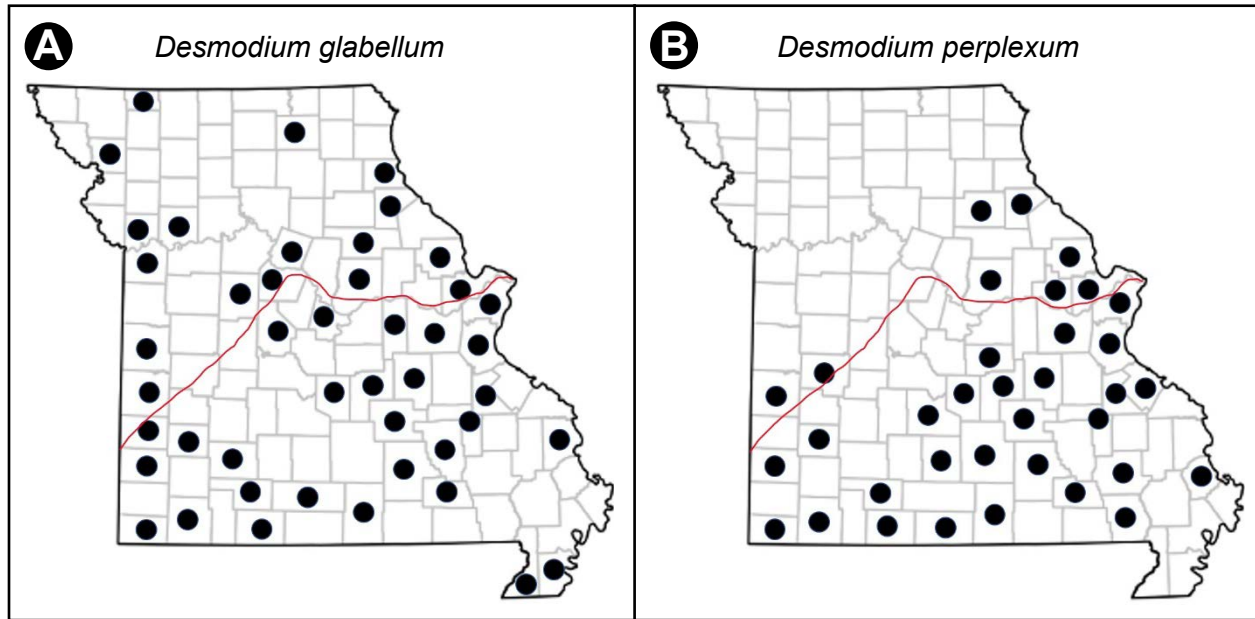
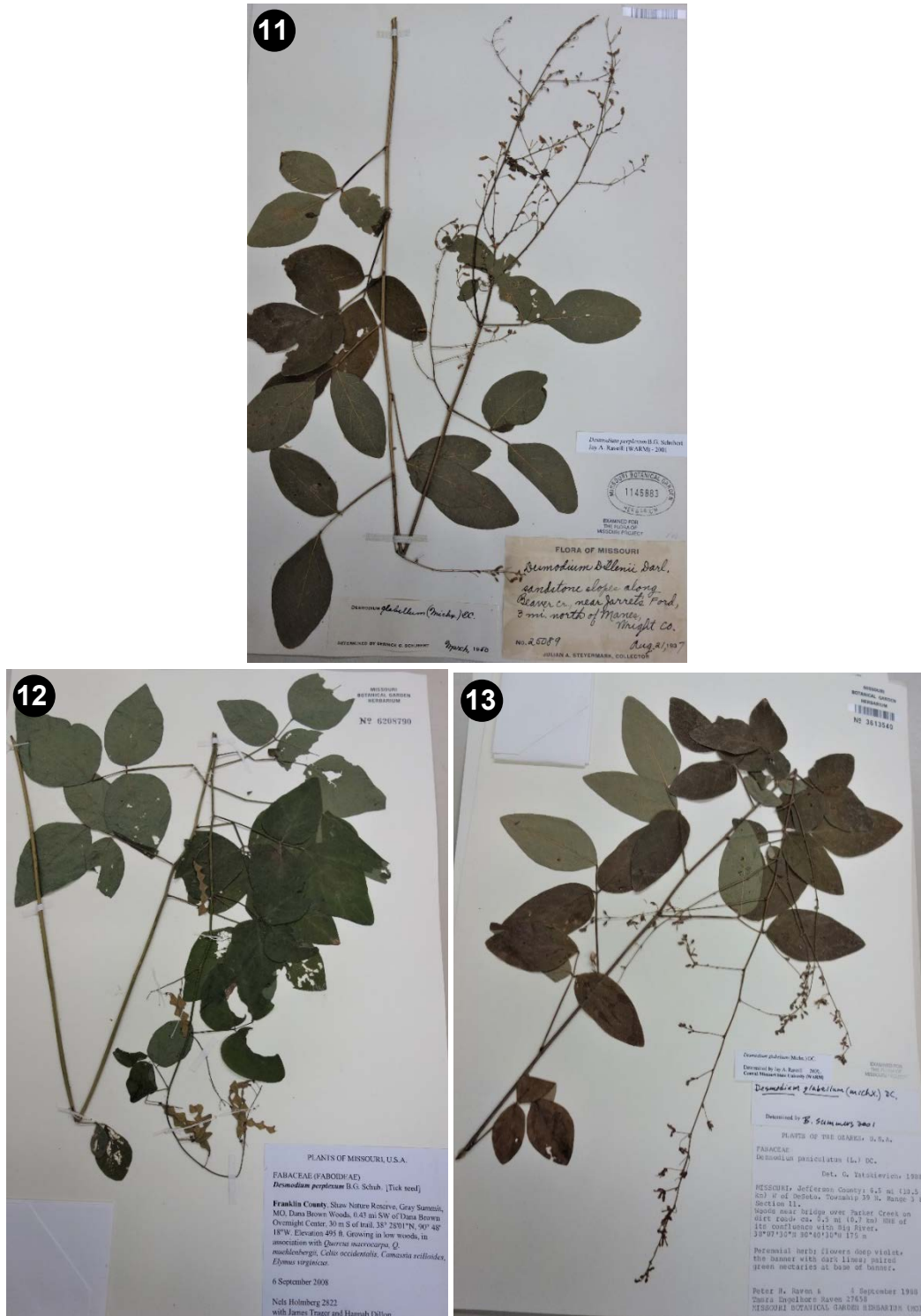


Figure 10. Distribution of *Desmodium glabellum* and *D. perplexum* in Missouri based on MO material. **A:** *D. glabellum*, showing statewide pattern; **B:** *D. perplexum*, suggesting a distribution within the Ozarks and Ozark border regions. The red line approximates the border between the Ozarks and the Great Plains.



Figures 11-13. *Desmodium perplexum*, showing typical examples of the wider leaf dimensions, fewer stem leaves, infrequency of leaves beyond or within the inflorescence branches, and lack of phyllotomy.



Figure 14. *Desmodium perplexum*, showing typical example of the concave margins of the articles.



Figure 15. *Desmodium perplexum*, showing an example of more straight-edged article margins that can occur; scale in centimeters.

CONCLUSIONS

As is often the case with morphologically similar taxa, when presented with an individual specimen, it can be difficult to derive an accurate identification. Even when placed side by side, the differences can be obscure. Such is the case here (Fig. 17) where archetypical examples of *D. perplexum* and *D. glabellum* are juxtaposed. There are similarities for sure, but there are also differences. Those differences cannot be expressed in simple character states, which are too subtle. Strict adherence to the key should lead to a conclusion, but the consistency and accuracy of that conclusion depends on experience with the ranges of variation in the character states. While users of taxonomic treatments abhor the frustration that comes from such antinomy, the nature of living systems demands that one experience phenomena before one understands them. After all, understanding is an emergent property of experience. The entities embroiled in species complexes, such as presented here, require more patience and experience than more approachable and easily interpreted taxa. The goal here is to set the stage for that experience rather than provide an absolute shortcut to an absolute solution.



Figure 16. Side-by-side comparison of archetypical average specimens of *D. perplexum* (left) and *D. glabellum* (right).

This situation illustrates the inherent difficulty of field biology in general. Even with character states clearly enumerated, one must often experience deeply and intimately the nature of things to understand them. Interpretation is always performative and a function of the interpreter. Many taxa that require experience and intuition for accurate identification are sunk into synonymy and buried under phrases like “needs more study” and “further research is needed.” Yet, that which cannot be expressed clearly in a key, that which ultimately is experiential, is often discouraged from publication. Not because they are not accurate, but because they are not easily explainable – they are tacit and proto-hypothetical. In a society that cares less and less about the interdependence of real organisms and the real systems they create, it has become too easy to lose the pieces in the puzzle and therein lose the puzzle. The true test of our intention – the ability to devise a functional philosophy – is hidden by our inability to accept complexity for the sake of complexity and to look not only harder, but deeper, and with more than our eyes. In short, studying and discerning taxa is as much about the phenomena of experience and interpretation as it is about the biota itself. Understanding the biota means understanding living processes, including the variations in the motives and awarenesses of we the living interpreters.

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