A TAXONOMIC REVISION OF THE GENUS ONOSMIDIUM

by

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INTRODUCTION

This thesis presents a taxonomic revision of the species of the genus *Onosmodium* (Boraginaceae). The genus as presently defined is exclusively confined to North America. It is evident from the published works and the available herbarium specimens that the recognition of the taxonomic entities is not uniform.

The main problems involved in this genus are two. First there is no agreement with regard to the limits of the genus (Macbride, 1917). No attempt is made in the present work to settle this issue; the concept of Mackenzie (1905) is adopted in this regard. The second is with regard to the attribution of rank to the infrageneric taxa. The concept adopted in this work is presented later.

HISTORICAL ACCOUNT

Mackenzie (1905) revised *Onosmodium* as it occurred north of Mexico, and recognized seven species and three varieties. He transferred *O. thurberi* Gray to the genus *Macromeria*, stating that "It differs from *Onosmodium* in the greatly elongated corolla, exerted stamens, long filaments and versatile anthers, in usually ripening more nutlets, and in the persistence of the enlarged base of the style." Macbride (1917) disagreed with his viewpoint stating that *Macromeria* is distinguished principally by the keeled nutlets; accordingly he transferred a few species from *Macromeria* to *Onosmodium*. Small (1903) described six species as occurring in South Eastern U.S.A. Johnston (1924) treated *O. occidentale* Mack. as a variety
of *O. molle* Michx. on the basis of "material from Illinois which shows repeated tendencies to intergrade with *O. molle*." Cronquist (1959) regards *O. beiariense* D.C., *O. hispidissimum* Mack., and *O. subsetosum* Mack. and Bush ex Small as "intergradient geographic varieties" and treats them as varieties under *O. molle* Michx.

No cytological studies seem to have been done in the genus *Onosmodium*. However, Britton (1951) suggests that the basic chromosome number of the family Boraginaceae is 8, although species with haploid numbers of 7 were recorded in the tribe Lithospermeae which includes the genus *Onosmodium*.

In the present revision, five species are recognized; two of them are restricted to Mexico, the other three to U.S.A. and Canada. One species, *O. molle*, has five varieties. This is essentially in accord with the treatment of Cronquist mentioned above.

**SOURCES OF DATA**

This revision is based primarily on herbarium specimens and the pertinent literature. Field collections and observations were confined to Kansas. Approximately 2000 herbarium specimens, representing the entire geographical range of the genus have been examined.

The following institutions have kindly loaned specimens. The abbreviations for these institutions as indicated in parentheses are in accord with Lanjouw and Stafleu, Index Herbariorum, Part I (1964). These same symbols are used in the citations of specimens.

University of California, Berkeley  
UC

University of Colorado  
COLO
The distribution maps were made by plotting the collection localities as noted on the herbarium specimens examined. In general, one dot represents one collection. Even though an entity may have been collected at or near the same locality at different times, only one spot was plotted for the locality.

The main intent of the maps is to graphically depict the geographic distribution of the different entities. Inasmuch as the maps merely indicate collection localities, they may give an erroneous impression for the entities that occur in poorly collected regions.
CONCEPT OF THE TAXA

Genus Concept

In the present revision, the genus *Onosmodium* is delimited as defined by Mackenzie (1905). This concept is mainly based on the characters of flower (corolla lobes, erect or converging, acute or acuminate; stamens, included; style exerted cf. plate 1, figs. 1 and 2) and nutlet (attached by a broad base to a flat receptacle). When circumscribed on this basis, the genus may be regarded as a natural group.

Species Concept

The taxonomic (or the morphological-geographical) species concept is employed in the present treatment. The lines of separation between species are based on discontinuity in natural variation as judged through morphological characters. The contiguity in geographical distribution is also used as an additional criterion. When separated on these criteria, the species fall into more or less distinct natural entities.

Variety Concept

Varieties are the only infraspecific taxa recognized in the present revision. The term variety is used in this treatment for nomenclatural reasons. When two or more taxa having distinct geographical distributions are connected with one another through the occurrence of intermediates in
the regions of overlapping ranges, such entities are treated as varieties. Two difficulties are involved in this concept. One is in deciding whether a specimen is intermediate or whether it represents a segment of the extreme variation of the taxon; the other one is how frequent the intermediates must be for treating two entities as varieties. Both are subjective. In addition, the latter depends on the extent of collections made from such 'critical' areas. In spite of this, the concept is useful in bringing out the nature of variation exhibited in a taxon.

**DIAGNOSTIC CHARACTERS**

In addition to gross morphological similarity, useful characters are found in variation in plant height, indument, shape of corolla lobes, anthers and nutlets. They are discussed individually. All measurements were made from herbarium specimens. Measurements of plant height, leaves and bracts were made from dried specimens; measurements of the flower and its parts were made after soaking them in Pohl's wetting agent. In one species, *O. molle* var. *occidentale*, such measurements were compared with those of pickled flowers; they were seen to agree well. Length of inflorescence was measured when flowers were present at or near its tip. The range of measurements for each item represents measurements taken from the corresponding parts all over the plant; for example, the range in length of hairs on the stem represents sample measurements made both on young and old stems. For short hairs, the average measurement only was often given wherever the variation was negligible.

**PLANT HEIGHT:** The height of the plants ranges from 1.5 to 10 dm.
O. dodrantale is the only species which is shorter than 3 dm. in all specimens seen.

INDUMENT: This word is used to include all the hairs on the external parts of the plant. The term pubescence is avoided as it is used in a narrower sense in the literature.

The pattern of indument is in general distinctive of a taxon or groups of taxa. The characteristic appearance of the hairiness is due to relative differences in length, frequency and orientation of the hairs; their coarseness and color are additional features that contribute to the range of variation. All hairs are non-septate and arise from a basal disc which is less conspicuous in short hairs. The hairs are nonglandular except in O. unicum where both glandular and nonglandular hairs occur.

With regard to length, the hairs are of two types—short hairs and long hairs; this distinction is purely arbitrary and relative. If the hairs on an organ are of one type (i.e., either short or long), the pattern of indument is referred to as simple; if they are of two types (i.e., both long and short), it is termed duplex. In the description of the individual taxa, terms like hispid, hirsute or retuse are used to refer to the long hairs to bring in the characters coarseness and/or orientation; the respective diminutives are used in connection with the short hairs.

Frequency of hairs: The descriptive terms used are glabrous, occasional, sparse, moderate, abundant, very abundant (Eiten, 1963). The hair abundance classes are illustrated in plate I, figs. 3-8.

Orientation of hairs: The descriptive terms used are appressed, ascending, patent, descending, spreading, and retrorse (Eiten, 1963). Hairs whose orientation is 0-30° from the surface on which they are borne and are
pointing toward the apex of the organ (stem, leaf, corolla lobes, etc.) are considered as "appressed upwards," and are described in this work as simply "appressed"; hairs from 30-60° as "ascending," etc. The classes "ascending," "patent," and "descending" together form the class "spreading"; the classes "descending" and "appressed downwards," collectively form the class "retrorse." The different classes are illustrated in plate I, figs. 9-11.

The patterns of indument vary from organ to organ in a plant; as such they are described separately for stem, leaves, and corolla lobes.

STEMS:

The portion of the stem that is just below the inflorescence is chosen for the purpose of description. The stems are hairy down to the base in all the taxa except in O. molle var. subsetosum in which the lower (basal) part of the stem is glabrous or nearly so. The short hairs measure about 1 mm. long or less. Indument on stems in all taxa is of duplex type, except in O. virginianum in which the hairs measure 0.4-1 mm. long and the distinction between short and long is not clear. In general, the short hairs are appressed; the long ones may be ascending (often in var. occidentale) or spreading (var. bejariense, and often in var. hispidissimum).

LEAVES:

The leaves that are just beneath the inflorescence are chosen for describing the indument. It is often possible to identify a taxon with the use of hairiness of leaves alone. The short hairs usually measure about 0.5 mm. or less in length. The pattern of indument on the upper and lower surfaces differs.

Upper surface: The indument is simple in O. helleri and O. virginianum; the hairs in the former measure 0.90-2.25 (3.4) mm. long and in the latter,
they measure (0.2) 0.5-1 mm. long, and the distinction between long and short is not clear. In other taxa, the indument is of duplex type. The long hairs are hispid (often in var. occidentale and var. bejariense) or hirsute (var. hispidissimum) or weak (var. molle); straight (var. occidentale) or arched or falcate (var. hispidissimum); appressed (O. virginianum), ascending (var. hispidissimum) or erect (O. helleri). The short hairs are appressed (var. molle) or ascending (often in var. occidentale) or erect (often in var. bejariense); sparse (var. occidentale) or abundant (often in var. bejariense) or very abundant (var. molle, O. unicum).

Lower surface: The indument is simple in O. helleri (hairs 0.8-1 mm. long), O. virginianum ((0.2) 0.5-1 mm. long) and var. subsetosum (0.7 mm. long or shorter). In other taxa, the indument is of duplex type. The long hairs are usually sparse or very sparse. The short hairs are sparse (var. hispidissimum) or abundant to very abundant (var. bejariense and var. molle); appressed (var. molle) or ascending (sometimes in var. bejariense).

COROLLA LOBES:

Indument: In general, the indument on corolla lobes is variable and hence they serve as mere guides. Only in O. dodrantale is the inner surface of the lobes hairy. The outer surface of the lobes is hairy in all the taxa. The hairs in O. dodrantale measure (0.3-1.6 mm. long) and are not readily separable into short and long; in the other taxa, the indument is of duplex type. The long hairs are more or less straight (O. helleri) or undulate to flexuous (var. subsetosum) or flexuous (var. molle). The short hairs are appressed or ascending and extend down the corolla tube to about one half of its length in many taxa.

Shape: There are essentially two types: 1. acuminata or broadly-
acuminate (var. bejariense, O. dodrantale), to linear-acuminate (O. virginianum); and 2. acute (var. molle, var. hispidissimum). In var. occidentale, the lobes are often acute, sometimes broadly acuminate.

Length: The length of lobes shows almost continuous variation. However, based on average length, the lobes which measure about 2.5 mm. in length may be described as short (var. molle, and var. hispidissimum), and those that measure about 3.5 mm. in length as long (var. occidentale and var. bejariense).

Color: The yellowish or orange-tinged lobes are distinctive of O. virginianum. The greenish lobes are characteristic of some taxa (var. occidentale, and var. bejariense).

ANTHERS: The shape of the sterile apices of the anthers may be a good guide. This character is not used in the present work, because it seemed desirable to check for its consistancy in the fresh specimens. The length of the anthers varies from 2 mm. to 4 mm. and shows great variation even within a taxon. However, on the average, the anthers of var. occidentale are long (3.5 mm. long) and those of var. hispidissimum and var. molle are short (about 2.2 mm. long). The apex of the anther is usually a little below the sinuses of the corolla lobes in O. virginianum; whereas in the other taxa, the apex of the anther is often at or a little above the sinuses.

NUTLET: Usually only one nutlet matures in each flower.

Length: This is a variable character, and ranges from 2.5 mm. to 4.4 mm. On the average, the nutlets in var. occidentale, O. dodrantale, and O. unicum are large (about 4 mm. long); those in var. molle and O. virginianum are short (about 3 mm. long).

Pitting: Nutlets may be smooth (i.e., without pitting) as in var.
occidentale, or pitted to a varying extent as in the other taxa. Even in the same taxon, pitting shows great variation in its density.

Constriction: The base of the nutlet may be strongly constricted (var. hispidissimum and O. unicum) or shallowly constricted (var. molle, sometimes in var. bejariense and var. subsetosum) or not at all constricted (var. occidentale). The collar-like strong constriction appears to be very consistent in the respective taxa.

Color: Nutlets are white in var. occidentale, but white or brownish in the other taxa.

SYSTEMATIC TREATMENT

Onosmodium Michx.

Purshia Spreng. Anleit. ed. 2. ii. 450. 1817. (non Purshia DC.)

Erect or ascending, hairy, leafy perennials with a stout rootstock. Stems terete, hairy down to the base (except in var. subsetosum). Flowers in summer. Leaves alternate, sessile or shortly-petioled (O. helleri), mostly lanceolate or oblanceolate to ovate, hairy on both sides, ciliate on margins, strongly-veined, 3-9 nerved; nerves convergent, often sulcate on the upper surface and ridged on the lower. Basal leaves in a rosette, oblanceolate or spatulate, drying or deciduous at flowering. Lower or middle cauline leaves bigger; upper ones smaller and gradually grade into
bracts. Inflorescence a terminal bracteate scorioid cyme, often branched and many flowered, usually coiled when young but straightening during anthesis and fruiting. Flowers secund, regular, shortly-pedicelled; pedicel usually elongates in fruit. Calyx shorter than the corolla, deeply 5-parted, persistent. Sepals lanceolate or oblanceolate-spathulate, hairy on both sides with distinct midvein; margins ciliate. Corolla 15 mm. long or less, tubular slightly enlarged at the throat; sinuses thick and somewhat inflexed, usually glabrous within, hairy outside especially on the lobes; lobes yellowish, orangish or greenish, triangular, acute or acuminate, erect, barely spreading or tending to be connivent, not longer than the limb; tube usually whitish. Corolla turns brown on drying in some taxa. Stamens 5, included, inserted on the limb; filaments minute, dorsally attached one third above the base of anther. Anthers introrse, glabrous, lanceolate, often sagittate at base, apiculate or mucronate with sterile tip; apex usually about the level of the corolla sinuses. Ovary superior, deeply 4-lobed, each lobe with one ovule. Style gynobasic, filiform, glabrous, exerted, 21 mm. long or less, long persistent; stigma faintly bifid. Fruit short stalked, usually one nutlet maturing, sometimes two. Nutlet 5 mm. long or less, bony, erect, ovoid to subglobose, white to brownish, smooth or shallowly pitted, constricted or not at base, attached by a broad base (about 2 mm. wide) to the nearly flat receptacle.

The genus can be distinguished from related genera by the following combination of characters: corolla short, tubular; corolla lobes erect, triangular, acute or acuminate; stamens included with filaments minute; style exerted; nutlet attached by a broad base to a flat receptacle.
Key

A. Plants glanduliferous. Central Mexico.

5. *O. unicum*.

A. Plants not glanduliferous.

B. Corolla lobes hairy within, tube yellowish; plants 1.5-2.5 dm. tall; cauline leaves 1.6-4.5 cm. long; inflorescence about 5 cm. long, unbranched, few-flowered; Central Mexico.

4. *O. dodrantale*

B. Corolla lobes not hairy within tube not yellowish; plants 3 dm. tall or more; inflorescence often 5 cm. long or more, usually branched, many flowered; U.S.A., Canada.

C. Leaves shortly petioled, glaucous, cross nerves nearly perpendicular to longitudinal ones; indument simple on upper surface of leaf, (hairs hispid or stiff); sepal spatulate-oblong; corolla 9-11 mm. long, lobes 3.2-5 mm. long, broadly acuminate; Fruit stalks 5-13 mm. long; Texas.

3. *O. helleri*

C. Leaves sessile, not glaucous, indument on upper surface of leaf of duplex type (except *O. virginianum*); Fruit stalk not so long.

D. Stems glabrous or nearly so below, strigose above; upper surface of leaf strigose and strigulose, abundantly hispidulous on the lower surface; corolla 7-12 mm. long, lobes 2-2.25 (3.25) mm. long, triangular, acute; Missouri, Arkansas, Oklahoma in U.S.A.

1e. *O. molle* var. *subsetosum*
D. Stems hairy from the base upwards.

E. Corolla lobes distinctly acuminate.

F. Lobes linear-acuminate, yellowish-orange, indument simple; strigose on both sides of leaf; corolla 7.5-12.5 (14.4) mm. long, lobes 1.8-2.7 (4.9) mm. long, 1-1.3 mm. wide; nutlet 2.5-3 mm. long, 1.6-2.1 mm. wide, often pitted; New York southwards along the coast to Georgia, Florida, and westward to Alabama, Mississippi, and Louisiana.

2. O. virginianum

F. Lobes broadly-acuminate, greenish; indument duplex on upper surface of leaf, hispid, (hairs sparse, appressed) also hirtellous (hairs abundant, often ascending); corolla (10) 12-15 (18) mm. long, lobes 3.5-4.5 mm. long, 2-2.75 mm. wide; nutlet 2.9-3.8 mm. long, 2.5-3.15 mm. wide; Texas.

1d. O. molle var. bejariense

E. Corolla lobes acute (sometimes acuminate in var. occidentale).

G. Nutlets strongly constricted at base, often pitted, 3-3.4 (4) mm. long, 2.2-2.5 (2.9) mm. wide; indument duplex on upper surface of leaf, hirsute (hairs ascending, falcate) also hirtellous (hairs straight, appressed); corolla 7-9 mm. long; New York westwards to Minnesota through Ohio, Illinois, Missouri and
Iowa in U.S.A.; lower part of Ontario between Toronto and Detroit.

lc. O. molle var. hispidissimum

G. Nutlets not strongly constricted.

H. Corolla 11-15 mm. long, lobes 3-4 mm. long, nutlet 3.8-5 mm. long, 3.1-3.6 mm. wide; smooth, not at all constricted, at base; leaves not grayish; upper surface of leaf hispid (hairs moderate-abundant, often ascending, and 'combed'), also hirtellous (hairs ascending, sparse-moderate); widely distributed from Manitoba, to Texas through the central prairies.

lb. O. molle var. occidentale

H. Corolla 7.75-10 mm. long, lobes 2.25-2.75 mm. long; nutlet 2.7-3.6 mm. long, 2.5-2.7 mm. wide, shallowly constricted at base, pitted; leaves grayish; upper surface of leaf hirsute (hairs ascending, moderate, falcate) also abundantly hirtellous (hairs appressed); mostly Tennessee, southern Illinois, and Kentucky.

1a. O. molle var. molle
Onosmodium molle Michx.

Plants 5-12 dm. tall, suffructicose, often branching, branches ascending or erect. Stems 5-10 mm. thick, hairy from the base upwards except in var. *subsetosum* in which the lower part of the stem is glabrous. Leaves 4-12 cm. long, 1.4-3.4 cm. wide, 5-7 nerved, ob lanceolate, lanceolate, ovate or elliptic; indument of duplex type. Inflorescence 8-20 (29) cm. long, branched. Flowers secund. Sepals 3.5-9 mm. long, 0.8-1.4 mm. wide, lanceolate, ob lanceolate or oblong. Corolla 7-15 mm. long, tube whitish; lobes 2.3-4.5 mm. long, 1.5-2.8 (3) mm. wide at base, acuminate (var. *bejariense*, sometimes var. *occidentale*) or acute, greenish, glabrous within, hairy without. Anthers 1.75-4 mm. long. Style 10.5-20.6 mm. long. Nutlet 2.8-5 mm. long, 2.2-3.6 mm. wide, ovoid, strongly constricted at base (var. *hispidissimum*), or not constricted (var. *occidentale*) or shallowly constricted, whitish or brownish.

From Manitoba and Ontario in Canada to New Mexico and Texas in U.S.A. and between Appalachian mountains and foothills of Rockies. Prairies, woods, limestone glades.

*Onosmodium molle* encompasses five varieties which are discussed individually below.

1a. *Onosmodium molle* Michx. var. *molle*


Type locality: "in Tennessee, circa Nashville."
An erect, much-branched perennial, about 6-7 dm. high, densely clothed with indument, grayish in color. Stem, 5 mm. thick at base, hirsute (hairs 1.1-2.3 mm. long, ascending-patent, moderate-abundant, falcate to straight) and hirtellous (hairs 0.9 mm. long, appressed, abundant, straight); hairs at base of stem sometimes deciduous, but leaving distinct scars. Leaves 4-8 cm. long, 1.4-2 cm. wide, lanceolate to ovate, acute, often 5-nerved, sometimes 7-nerved; upper surface hirsute (hairs 1.1-2.25 mm. long, ascending, moderate abundance, falcate) and strigulose (hairs 0.45 mm. long, very abundant and concealing the surface, straight); lower surface hirsute (hairs 0.5-1.0 mm. long, appressed-ascending, sparse, falcate) and strigulose (hairs about 0.5 mm. long, very abundant and concealing the surface, less hirsute). Veins hirsute (hairs 0.9-1.2 mm. long, ascending, sparse-moderate, falcate-straight) and abundantly strigose-strigulose (hairs about 0.7 mm. long). Inflorescence 4-7 cm. long. Bracts lanceolate, 6-8 mm. long, 2-2.3 mm. wide in flower, and 15-22 mm. long, 5-6.3 mm. wide in fruit. Sepals 3.7-6 mm. long, about 0.8 mm. wide, linear-oblong; outer surface hirsute (hairs 0.7-1.2 mm. long, ascending, sparse, falcate-straight), and strigulose (hairs 0.4 mm. long, very abundant); inner surface strigose-strigulose (hairs 0.4-0.7 mm. long, sparse at base, moderate-abundant towards apex). Corolla 7.7-10 mm. long; lobes 2.2-2.8 mm. long, 1.7-2 mm. wide, acute, white or greenish, externally hirsute (hairs 0.8-1.3 mm. long, ascending, sparse-moderate, more often flexuous, sometimes undulate), and strigulose (hairs about 0.3 mm. long, extending down the throat, moderate to abundant). Anthers 2-2.5 mm. long, style 12.5-16 mm. long, nutlet 2.7-3.6 mm. long, 2.5-2.7 mm. wide, ovoid, broadest in the middle, shallowly constricted at base, moderately pitted, brownish, slightly keeled ventrally.
Range and general ecology

It is limited in distribution to a smaller area than other varieties; mostly Tennessee, southern Illinois, and Kentucky; confined to limestone hills and barrens. Map 1.

Representative specimens

Kentucky

Logan Co.: thickets, limestone hills, near Russellville. E. J. Palmer 17745 (MO).

Illinois

Jackson Co.: dry rocky hillside, Grand Tower. H. A. Gleason 2578 (GH).

Tennessee


Rutherford Co.: dry hillside, near Laverygne. R. L. McGregor 17164 (KANU).

Discussion

Although the following specimens bear an overall resemblance to var. molle, they show tendencies towards other varieties.

The collection of McVaugh 4419 from Wilson Co., Tenn. (US) comes closer to var. subsetosum in the old stems being practically devoid of hairs; the scars of the hairs, however, are still recognisable. The basal discs of the long hairs are unusually prominent.

The specimens of Palmer 17745 from Logan Co., Ill. (MO); of Svenson 8831 from Giles Co., Tenn. (GH) and of Reverchon from Davidson Co., Tenn. (MO) show a faint look of var. occidentale.
The specimen of Gleason 2578 from Jackson Co., Ill. (GH) shows less dense hairs on leaves; the constriction on the nutlet is reminiscent of that of var. hispidissimum.

The collection of E. J. Palmer 8039 from Hempstead Co., Arkansas (MO, US), is intermediate between var. occidentale and var. molle. It is suggestive of var. molle in its indument on corolla lobes, on the lower surface of leaf and in the size of flower; it tends toward var. occidentale in the nutlet and in the slightly combed nature of indument on the upper surface of leaf. The general pattern of hairs on the upper surface of leaf tends toward var. hispidissimum.

The specimen of T. E. M. Donald, Aug. 2, 1893 from Peoria Co., Illinois (MICH), bears a look of var. molle in its indument on leaves and corolla lobes, while the hairs in their 'combed' orientation, are indicative of var. occidentale.

The collection of A. W. Brady, July 16, 1886 from Delaware Co., Indiana (UC), bears an overall resemblance to var. hispidissimum but the hairiness on leaves and corolla lobes are suggestive of var. molle.

1b. Onosmodium molle var. occidentale Johnst.


Based on O. carolinianum var. molle of A. Gray, not O. molle Michx.

Lectotype to be designated.

Plants 5-10 dm. tall, bushy, coarsely hairy, hairs whitish. Stems
thick, often branching from near the base, numerous, central stems erect, outer ones ascending, hirsute from the base upwards, hispid (hairs 1.8-2.0 mm. long, moderate, usually ascending, sometimes patent, especially in many specimens from northern latitudes, e.g. Minnesota, Illinois), and hirtellous (hairs 0.9 mm. long, appressed, abundant). Basal leaves in rosette, normally deciduous early. Cauline leaves 5-10 cm. long, 1.5-2 cm. wide, elliptic to ovate, 5-7 nerved, lower most usually deciduous by anthesis; upper surface hispid (hairs 1.6-2 mm. long, ascending, moderate to abundant, straight, very often the hairs between veins tend to converge towards apex and give a 'combed' appearance), and hispidulous (hairs 0.4-0.7 mm. long, appressed-ascending, sparse, but moderate-abundant along furrows); lower surface hirsute (hairs 1.4-1.8 mm. long, ascending, sparse) and hirtellous (hairs about 0.4-0.7 mm. long, appressed-ascending, moderate-abundant, straight-falcate); nerves hirsute (hairs 1.8-2 mm. long, appressed-ascending, moderate) and hirtellous (hairs about 0.8 mm. long, appressed-ascending, sparse). Inflorescence 12-20 cm. long. Bracts ovate-lanceolate, 7-9 mm. long, about 2.2 mm. wide in flower and 2.2-3.2 cm. long, about 0.8 mm. wide in fruit. Pedicel (1.1) 1.4-1.8 (2) mm. long in flower and (2.4) 3.4-4.9 (6.3) long in fruit. Sepals 8-9 mm. long, about 1.4 mm. wide, linear-lanceolate; outer surface hirsute (hairs 1.4-2 mm. long, ascending, abundant at base, sparse towards apex), and hispidulous (hairs about 0.4 mm. long, appressed, moderate in abundance); inner surface strigose (hairs 1.3-1.6 mm. long, abundant at base, sparse-moderate towards apex), and sparsely strigulose (hairs 0.5 mm. long). Corolla 11-15 mm. long, tube whitish; lobes 3-4 mm. long, 1.75-2.0 mm. wide at base, acute, sometimes acuminate, greenish, externally hirsute (hairs 1.8-2.0 mm. long, ascending, moderate-abundant,
straight or undulate), and hirtellous (hairs 0.5 mm. long or less, appressed-ascending, abundant, wavy). Anthers, 3-4 mm. long. Style, 18-19 mm. long. Nutlet 3.8-5 mm. long, 3.1-3.6 mm. wide, ovoid, smooth, not constricted at base, white or sometimes brownish.

Onosmodium molle var. occidentale can be recognized by its coarsely hairy appearance, pattern of indument on leaves, long corolla, greenish, often acute corolla lobes; and its large, glabrous nutlet without constriction.

Range and general ecology

This variety is the most widely distributed and the most frequently collected of the varieties. It occurs in grassy meadows, in open woods and sand hills; from Manitoba to Texas and from the foothills of the Rocky Mountains eastward through the plains and prairies to Illinois.

Representative specimens

Colorado


Lincoln Co.: Grassy meadow 5 mi. west of Hugo, on Hiway 40. L. Williams 2296 (UC, GH, US).

Illinois

Madison Co.: Near old Indian mound, Glencarbon, C. Heiser, Jr. 1760 (UC, MO).

Iowa

Harrison Co.: Dry Prairie on the crest of a loess bluff, Sect. 19, Raglan Twp., M. J. Fay 2436 (KANU, UC).

Palo Alto Co.: Prairie slopes, 5 mi. east of Ruthven, A. Hayden 9004 (MIN, GH, MO, UC).
Kansas

Ellis Co.: 3 mi. west and 2 mi. south of Hays. Shallow soil on limestone. S. Gibson and T. L. Das. (undistributed)

Geary Co.: 10 mi. south of Manhattan, T12S, R8E. John Poole Range. S. Gibson and T. L. Das. (undistributed)

Pottawatomie Co.: 3.8 mi. north of Belvue, deep soil, abundant. S. Gibson and T. L. Das. (undistributed)

Wilson Co.: Rocky prairie, hillslope, limestone surfacing in the area, growing among clumps of bluestem. 3 mi. N.W. Neodesha, R. L. McGregor 4299 (KANU, GH).

Minnesota

Nicollet Co.: Swan Lake, C. A. Ballard, June, 1892 (MIN, US, GH).

Pipestone Co.: Growing in pasture, 1/2 mi. east of Edgerton, J. W. Moore and G. B. Ownbey 22752 (KANU, MIN, TEX).

Missouri


Montana

Fergus Co.: Gravelly slope 6 mi. SE of Lewistown, C. L. Hitchcock 16020 (GH, UC).

Teton Co.: Low alkaline flat 1 mi. west of Choteau, C. L. Hitchcock 18112 (GH, UC, COLO).

Nebraska

Dawes Co.: 20 mi. south of Chadron. Rolling grassland, sandhills, common, C. L. Porter and M. W. Porter 8792 (UC).
Dixon Co.: Emerson, F. Clements 2515 (GH, US).

New Mexico

San Miguel Co.: Vicinity of Las Vegas, B. G. Arsene 18321 (GH).

Union Co.: Volcanic hills, on and near the Sierra Grande, altitude 2100-2925 meters, P. C. Standley 6093 (US).

North Dakota

Richland Co.: Sandy prairie, Kindred, O. A. Stevens 366 (GH, UC).


Oklahoma

Gimarron Co.: In arroyo running up the NW slopes of Black Mesa, 4 mi. N. of Kenton, U. T. Waterfall 7454 (TEX, MO, OKLA).

Comanche Co.: Wichita National Forest, Medicine Park, D. Demaree 12995A (MIN, MO, SMU, GH).

South Dakota

Lawrence Co.: High hillside, Deadwood, P. A. Rydberg 181 (MINN, GH).

Meade Co.: Rocky ground along creek, near Piedmont, Pennington Co., E. J. Palmer 37220 (GH, MO).

Texas

Collin Co.: Along railroad, near Plano, C. L. Lundell and A. A. Lundell 9294 (SMU, GH, MICH, UC).

Dallas Co.: Mountain creek, below Cedar Hill, in woodland, C. L. Lundell and A. A. Lundell 10610 (SMU, MO, MICH, GH, US, UC).

Wisconsin


Vernon Co.: Weedy opening on a rocky, wooded slope, Bergan Twp,

Wyoming


Canada


Discussion

Onosmodium molle var. occidentale shows clinal variation in hairiness on leaves from north to south. In the area of Oklahoma and Kansas, the long hairs on the upper surface of leaf are hispid and more or less appressed. Northwards, the hairs tend to be ascending and less hispid.

This variety intergrades with var. hispidissimum toward north and with var. bejariense toward the south. Intermediates between this variety and var. hispidissimum occur in regions where their ranges meet or overlap; this is especially so in the region from Illinois to Minnesota. Var. occidentale, however, can be distinguished from var. hispidissimum by its large-sized flowers and the absence of both pitting and constriction on the nutlet.

Intermediates between var. occidentale and var. bejariense are common. In the collection of D. Demaree 22660 (SMU, UC, MIN, MO, GH, OKLA) the indument on leaves is more or less intermediate between var. occidentale and var. bejariense; the nutlet resembles that of var. bejariense. It is
interesting to note that the indument on leaves in these intermediates tends towards var. *hispidissimum* in showing falcate, hirsute hairs with strigose hairs beneath. In the absence of flowers, nutlet and locality information, such specimens may be mistaken for var. *hispidissimum* or interpreted as a cross between var. *occidentale* and var. *hispidissimum*. It is noteworthy, however, that the var. *hispidissimum* is not found in Texas.

Var. *occidentale* can be distinguished from var. *bejariense* by the pattern of hairs on leaves and to some extent by the acute corolla lobes and the absence of pitting on nutlet.

The collection of A. P. Anderson, Aug. 1893 (MIN) Goodhue Co., Minnesota, resembles var. *occidentale* in sepals and nutlets but tends toward var. *hispidissimum* in hairiness on upper surface of leaf, though the 'combed' effect of the hispid hairs are suggestive of var. *occidentale*.

The collection of C. A. Ballard, June, 1892 (UC) from Nicollet Co., Minnesota, tends toward var. *occidentale* in the large size of corolla, acuminate corolla lobes, big sepals but tends toward var. *hispidissimum* in leaf hairiness.

The collection of A. Ruth 98 (US) from Tarrant Co., Texas, seems to be a hybrid between var. *occidentale* and var. *bejariense* as judged from the indument on leaves. It, however, tends toward var. *bejariense* in possessing thin sepals and in the duplex pattern of hairs on the upper surface of the leaves.

The collection of the Texas Highway Dept. 39139 (US) from Harris Co., Texas, resembles var. *occidentale*, but the long acuminate corolla lobes, the indument on them and on the leaves are remotely suggestive of var. *bejariense*. 
The collection of I. C. Martindale 6023 (?) (KANU) from Travis Co., Texas, resembles var. *occidentale*, though it is a little suggestive of var. *bejariense* in the spreading hispid hairs on the stem and the hispidulous hairs on the under surface of the leaves and the more or less acuminate corolla lobes. Similarly the collection of H. Eggert, 25 June 1899 (MO) from Dallas Co., Texas, resembles more var. *occidentale*; the likeness to var. *bejariense* is remote.

In the collection of R. A. Dixon 394 (GH) from Walker Co., Texas, the indument on the upper surface of the bracts tends towards var. *bejariense*, while that on the lower is towards var. *occidentale*. On the whole, the specimen resembles more var. *bejariense*.

Ic. *Onosmodium molle* var. *hispiddissimum* (Mack.) Cronq.


Based on *O. carolinianum* as used by American authors, not of A.DC. Lectotype to be designated.


Plants 9-12 cm. high, coarsely hairy, strongly branching above; branches ascending. Stem hispid (hairs 2-3.2 mm. long, spreading, sometimes ascending) and strigose (hairs 1.2 mm. long, moderate-abundant). Leaves 6-12 cm. long, 2-3 cm. wide, lanceolate, sometimes ovate, acute, 5-7
nerved, furrowed or not along nerves on upper side; upper surface hirsute (hairs 1.6-2.0 mm. long, distinctly ascending, moderate, falcate) and strigose-strigulose beneath the falcate hairs (hairs 0.6 mm. long, moderate-abundant); lower surface hirsute (hairs 1.3-1.6 mm. long, ascending, falcate-straight, sparse) and strigose-strigulose (hairs 0.6 mm. long, moderate); nerves hirsute (hairs 1.6-1.8 mm. long, ascending, falcate) and strigose (hairs 1 mm. long). Inflorescence 8-15 (20) cm. long. Bracts lanceolate, 11-14 mm. long, 1.8-2.0 mm. wide in flower and 1.6-3.6 cm. long, 0.7-1.5 cm. wide in fruit. Sepals 3.5-7.0 mm. long, 0.8-1.0 mm. wide, linear-lanceolate or weakly spatulate, acute or obtuse; outer surface hirsute (hairs 1.1-2.0 mm. long, ascending, moderate, hairs at base longer and abundant) and sparsely strigulose (hairs 0.4 mm. long); inner surface strigose-strigulose (hairs 0.4-1 mm. long, occasional to moderate towards apex, a few near apex ascending). Corolla 7-9 mm. long, tube whitish, lobes greenish, 2-2.7 mm. long, 1.5-2 mm. wide, acute; outer surface hirsute (hairs 1.4-1.6 mm. long, ascending, usually straight, sometimes wavy to flexuous, moderate) and hirtellous (hairs 0.5 mm. long or less, appressed-ascending, abundant, wavy-straight). Anthers 1.7-2.3 mm. long. Style 10.5-16 mm. long. Nutlet 3-3.4 (4) mm. long, 2.2-2.5 (2.9) mm. wide, ovoid, strongly constricted at base into a short neck, sparsely to moderately pitted, white or brownish.

*Onomodium molle* var. *hispidissimum* can be recognized by the duplex indument on the upper surface of leaf (i.e., the ascending, long, falcate hairs with short, strigose hairs underneath), short corolla with lobes acute, and nutlet with pitting and strong constriction.
Range and general ecology

This variety is distributed across the continent from New York to Minnesota, through Pennsylvania, Virginia, W. Virginia, Ohio, Indiana, Michigan, Illinois, Missouri, Iowa and Wisconsin, and in the lower part of Ontario between Toronto and Windsor. It occurs mostly in woods, meadows, creek and river bottoms, limestone cliffs and barrens, and overgrown fields. Map 3.

Representative material

Illinois

Hancock Co.: Augusta, S. B. Mead 1842 (?) (GH, MO).

Ogle Co.: Meadow Terrace at foot of sandstone hill, Oregon (MICH).

Indiana

Franklin Co.: Rocky wooded hillside 6 mi. S.E. of Brookville, C. C. Dean 16,060 (MIN).

Tippecanoe Co.: Dense shade, in low grounds, along Big Wab Creek, below Wabash railroad, 4 mi. S.W. of Lafayette, Charles M. Ek 6-17-1941 (UC).

Iowa

Delaware Co.: Alluvial woods, near spring N. end of Backbone State Park, Sept. 18, 1923 (GH).

Fayette Co.: Fayette, B. Fink, July, 1894 (GH).

Minnesota

Clearwater Co.: Edge of woodland, 3.0 straight-line miles north-northwest of Gonvick, G. E. Owmby and H. A. Anderson 2801 (MIN).

Missouri

St. Louis Co.: Dry rocky hillsides, Meramec Highlands, H. A. Gleason, June 25, 1904 (MICH, GH).

New York

Chymung Co.: Ashland, T. F. Lucy 2099 (MICH, KANU).
Herkimer Co.: Steep clay, stony banks and flats along west-Canada Creek, J. V. Haberer 622 (US, GH, UC, MO).

Ohio

Greene Co.: Open, dry bottom of little Miami River, John Bryan State Park, Yellow Springs, D. Demaree 11471 (US, UC, MO, MIN).
Lucas Co.: Maunee River bank, Toledo, H. A. Young, July 5, 1883.

Pennsylvania

Fayette Co.: Hillside near mouth of Brush Run, J. A. Shafer 172 (CKLA, UC).

Virginia

Wayne Co.: Overgrown field, Buffalo Creek, L. Plymale 721 (MIN, MO, US, MICH, GH).

West Virginia

—— Co.: Alleghenies, Iron Hill, alt. 667 meters, E. S. Steele and Mrs. Steele 192 (GH, MO).

Wisconsin

Rock Co.: Bariers rocks (?), S. C. Wadmond 3050 (MIN).

Ontario

Goderick, comte' de Huron . . . F. Marie-Victorin, F. Rolland-Germain, F. Dominique 45,901 (GH).

Wingham, J. A. Morton 22 Sept. 1891 - 12 July 1892 (MIN) and of 12 July 1892 (GH).

Discussion

The collection of A. W. Brady, July 16, 1886 (UC) from Delaware Co., Indiana, bears a look of var. molle in its color and the greater abundance of strigose hairs on the upper surface of leaf, but the specimen tends towards var. hispidissimum in its general pattern of indument on leaves and stem, and in the constriction of nutlet.

The collection of "S.F.P.," June 25-97 (MO) from Warren Co., Kentucky, consists of three specimens on the same sheet; they are numbered 1 to 3 (by me) so as to facilitate precise reference to them in the following discussion. In specimen 3, the pattern of hairs on leaves and stem in general resembles that of var. hispidissimum; the long straight hairs on the upper surface of leaf and the nearly acuminate corolla lobes bear resemblance to O. virginianum. Specimen No. 2 shows more or less the same features as specimen 3, except that the corolla lobes are distinctly triangular and acute. It is doubtful whether the strigose hairs on leaves involve var. molle parentage. Specimen No. 1 has no flowers, but it resembles specimen 3 in vegetative characters; the nutlet shows occasional pitting. The hispid hairs on the upper surface of leaf show 'combed' orientation in a few leaves. It is difficult to decide whether the above three specimens represent intraspecies variation or intermediates in segregating populations.
The collection of D. Demaree 11471 (SMU) from Greene Co., Ohio, seems to be intermediate between var. *hispidissimum* and var. *molle*. The indument on the upper surface of leaf and on corolla lobes tend towards var. *hispidissimum* while that on the lower surface of leaf is suggestive of var. *molle*.

Intermediates between this variety and var. *occidentale* are referred to in the discussion under the latter.

**Id.** *O. molle* var. *bejariense* (DC.) Cronq.


*O. bejariense* A.DC. *Prodr.* 10:70. 1846.

Type call.: Berlandier 1681, near Bejar, Río de la Trinidad, "Mexico boreali."

Plants 6-9 dm. tall, suffruticose, with a woody caudex, often branching above, sometimes from the base, branches ascending, coarsely hairy. Stems 8-10 mm. thick towards base, hispid (hairs: 2.9-4.1 mm. long, spreading, often retrorse or reflexed towards base, moderate, straight to falcate; sometimes hairs borne on elliptic, whitish, warty, raised bases on older stems), and hirsute-hirtellous (hairs: 0.5-0.9 mm. long, appressed, moderate, falcate to straight). Basal leaves crowded in rosette and begin to dry up at anthesis, 10-16 cm. long, 2-2.5 cm. broad, sessile, spatulate to oblanceolate; cauline leaves 5-10 cm. long, 1.5-2.5 (3.2) cm. broad, lower ones spatulate, upper ones linear-elliptic to lanceolate, acute, 5-7 nerved; upper surface hispid (hairs: 0.9-1.8 (2.7) mm. long, appressed,
sparse-moderate, straight) and hispidulous (hairs: 0.45 mm. long or less; ascending, sometimes upright, moderate-abundant, straight); under surface hirsute (hairs: 0.6 mm. or less, occasional to sparse, appressed, straight), and hirtellous (hairs: 0.4 mm. long or less, appressed, sometimes ascending, abundant to very abundant, falcate-straight); in many specimens the distinction between these two classes of hairs is not evident, all hairs are of small size; veins abundantly strigose (hairs 0.7-1.4 mm. long, some hairs are thicker than others). Inflorescence 8-20 (29) cm. long; bracts lanceolate, acuminate, 9-11.5 (14) mm. long, 2.5-3.2 mm. wide in flower and 1.8-2.5 (5) cm. long, 0.6-1 (2.5) cm. wide in fruit. Sepals 5.5-8 mm. long, 0.45-0.9 mm. broad toward the base, linear-lanceolate, acuminate; outer surface hispid (hairs: 0.7-2.5 mm. long, mostly confined to margins, with few or none on the midvein, ascending, moderate, bigger ones abundant at base forming a sort of 'whorl'.) and hirtellous (hairs: 0.6 mm. long or less, appressed, sparse at base, moderate towards apex, straight); inner surface strigulose (hairs 0.45 mm. long, moderate, less hirsute). Corolla (10) 12-15 (18) mm. long; tube whitish; lobes greenish or whitish, 3.5-4.5 mm. long, 2-2.75 mm. wide, broadly acuminate (attenuate), tip often abruptly bent outwards, hispid (hairs: 1.0-1.8 (2.7) mm. long, appressed-ascending, moderate-abundant, straight, sometimes weakly flexuous or undulate); and hirtellous (hairs: 0.45 mm. long or below, extends 3/4 down the corolla, appressed, moderate below, abundant above, straight-falcate). Anthers: 2.25-3.5 mm. long. Style 16-20.5 mm. long. Nutlet 2.9-3.8 mm. long, 2.5-3.15 mm. wide, ovoid, moderately pitted, whitish, sometimes faintly constricted at base, ventrally sulcate.
Range and general ecology

Confined to the region of San Antonio, Texas, where the Blackland Prairies, range lands of the Edwards Plateau, Post Oak Savannah, and South Texas Plains meet; sympatric with O. helleri. It occurs on flood plains, river banks, and in woods. Map 4.

Representative specimens

Texas

Bexar Co.: in woods, San Antonio, C. L. Lundell and A. A. Lundell 10268 (GH, MICH).
Bexar Co.: San Antonio, E. D. Schulz 2204 (MICH).
Brazos Co.: F. Lindheimer 1844 (MO, SMU).
Gillespie Co.: G. Jermy (MO).
Gonzales Co.: Ottine, B. C. Tharp 5-1-41 (TEX).
Hays Co.: San Marcos, B. Baker 4-21-28 (TEX, UC, MO).
Hays Co.: infrequent in deep shade of live oak and undershrub, Kyle, J. C. Johnson 495 (TEX, KANU).
Kimble Co.: River banks, Junction, E. J. Palmer 10919 (US, MO).
Travis Co.: Little Walnut Creek, N. E. Austin, C. L. York 46053 (TEX, UC).
Uvalde Co.: Nueces River, rocky limestone soil, Uvalde, E. Whitehouse 11728 (MICH).
Wilson Co.: Southerland Springs, Marcus E. Jones. A.M. (?) 29532 (MO, UC).

Discussion

Intermediates between var. *occidentale* and var. *bejariense* are frequent.

Out of the specimens of B. C. Tharp 7-9-27 (MICH, GH, MO, UC, TEX) from Burton, Washington Co., Tex., the first one (MICH) is distinctly var. *bejariense*; the rest resemble var. *occidentale* in having big (3.8-4.1 mm. long, 3.15-3.6 mm. wide) and nonpitted nutlets, however the hair pattern on leaves, though tending toward var. *occidentale*, is not typical of it and suggests var. *bejariense*.

The collection of J. Reverchon 3897 (MO) from Dallas, Dallas Co., resembles var. *bejariense* in the acuminate corolla lobes, but is intermediate between this variety and var. *occidentale* in hairiness on leaves, especially the under surface, and pitting on nutlet is occasional to sparse.

The collection of E. J. Palmer 7890 (MO, US) from San Augustine, San Augustine Co., Texas, resembles var. *bejariense* in nutlets; is near var. *hispidissimum* in flowers and is intermediate between these two varieties in hairiness on leaves.

The collection of C. Mohr, July 3, 1885 (US) from Alabama has the nutlets of one specimen (marked 1) typical of var. *bejariense* but appearing intermediate between this variety and *O. virginianum* in the great reduction of the small hairs on the upper surface of the leaves. The nature of the other specimen (marked 2) is still more obscure. The corolla is 7.5 mm. long, corolla lobes more or less acuminate. The hair pattern on leaves is a little suggestive of var. *bejariense* and var. *hispidissimum*.

The collections of "B.V.G." 303 (GH) from Texas and of R. C. Reeves 925
(SMU) from Brazos Co. in Texas, nearly agree with var. bejariense, but the indument on the upper surface of leaf is not typical in that the hispidulous hairs are absent and instead there are occasional strigose-strigulose hairs.

In the collection of E. Whitehouse 18402 (SMU) from Bexar Co. in Texas, the nutlet tends toward that of *O. dodrantale*.


Type call.: Bush 135, Eagle Rock, Mo.

Plants 6-10 dm. high, branching above, branches ascending. Stems about 6 mm. thick at base, main stem glabrous at base, often upwards to the point where the first branch arises, more or less lustrous, scars of hairs not visible; occasionally a few hairs present right at the base of the stem; upper stem strigose (hairs 0.7-1.1 mm. long, moderate, hirsute) and hirtellous (hairs 0.4 mm. long, appressed, moderate, often falcate, sometimes straight). Leaves 4-10 cm. long, 0.8-1.8 (3.4) mm. wide, 5-7 nerved; basal leaves in rosette, smaller, oblanceolate; cauline leaves lanceolate to narrowly lanceolate or elliptic, acute; upper surface strigose (hairs 0.7-1 mm. long, moderate, leaf area in between hairs distinctly visible, hirsute, often show 'combed' orientation as var. *occidentale*) and strigulose (hairs 0.45 mm. long, sparse-moderate, less hirsute); under surface hirsute-hirtellous, not clearly distinguishable into long and short hairs (hairs 0.7 mm. long or less, appressed-ascending, abundant, falcate, sometimes
straight); veins hirsute (hairs 0.4-0.7 mm. long, appressed-ascending, moderate-abundant, straight). Inflorescence: 6-9 cm. long; flowering bracts 8-10.5 mm. long, 2-2.5 mm. wide, oblanceolate to elliptic; fruiting bracts 2-3 cm. long, 0.5-0.9 mm. wide, lanceolate-elliptic. Sepals 5-7.5 mm. long, oblong-oblanceolate, obtuse-acute, 1.2 (1.4) mm. wide; outer surface hirsute (hairs: 0.9-1.8 mm. long, appressed-ascending, moderate, falcate-straight, longer hairs abundant at the base) and hirtellous (hairs 0.45 mm. long, appressed, moderate, falcate); inner surface strigose (hairs 0.6-0.9 mm. long, moderate but sparse at base, nearly straight, less hirsute). Corolla: 7-12 mm. long; lobes 2-2.25 (3.25) mm. long, 1.5-2 (3) mm. wide, triangular, acute to obtuse, greenish; outer surface hirsute (hairs 0.7-1.6 mm. long, appressed-ascending, sparse-moderate, undulate-flexuous) and hirtellous (hairs 0.5 mm. long or below, extend a little down the throat, appressed, moderate-abundant, falcate-straight). Anthers 2-3.5 mm. long, linear-lanceolate. Style 13.5-17.5 mm. long. Fruit stalk 4.1 mm. long. Nutlet: 2.8-3 (3.4) mm. long, 2.2-2.7 mm. wide, broadest just below the middle, ovoid, little if at all constricted at base, moderately pitted, pale brownish to whitish.

Range and general ecology

Ozarks of Missouri, Oklahoma, and Arkansas. Dry woods, limestone and rocky barrens, limestone glades on wooded bluffs, and river bottoms. Map 5. Representative specimens

Arkansas

Hot Springs Co.: Novaculite ridges, Magnet Cove, D. Demaree 17888 (GH, MIN, SMU).

Izard Co.: Penters Bluff, Croker Springs, D. Demaree 17022 (SMU, GH, MO).

Missouri


Cooper Co.: Wooded limestone upland and slopes, 2 mi. NW Otterville, J. A. Steyermark (MO).

Jasper Co.: rocky woods, dry woods, Webb City, E. J. Palmer 2050 (MO).

Ozark Co.: limestone ledges along bluffs, 4 mi. NE of Dormis, J. A. Steyermark 15576 (MO).


St. Francois Co.: rocky hills, H. Eggert, 5 June - 3 July 1892 (MO, GH, US).

Oklahoma

Adair Co.: Oak-hickory woods, 23 mi. NE of Tahlequah, C. S. Wallis 7386 (SMU, OKLA, KANU, TEX).

McCurtain Co.: Glades, Garvin D. Demaree 12626 (SMU, MIN).

Discussion

Stems in some cases bear occasional to sparse hairs instead of being typically glabrous (Bush 2050 (MO) Webb City, Jasper Co., Missouri; and Palmer 2140 (MO) Carterville, Jasper Co., Missouri). Plants with these two types of stems seem to occur together in some localities as indicated by Steyermark in his collection of var. subsetosum (73999, Otterville, Cooper
Co., Missouri (MO), "but stems hispid, occurring with glabrous stemmed type"). A similar situation is observed in the collections of D. Demaree 1702 (SMU, GH, MO) from Croker Springs, Izard Co., Arkansas. The stems in the first specimen (SMU) are glabrous and the long hairs on leaves are hirsute; in the other two specimens (GH, MO) the stems bear scattered hairs and the long hairs on leaves are less distinctly hirsute.

The collection of C. S. Wallis 626 (OKLA) from Cherokee, Oklahoma, tends toward var. subsetosum, but shows a few characteristics of var. occidentale in having hirsute stems, ascending long hairs, bigger nutlets (3.4-3.6 mm. long, 2.2 mm. wide) which are whitish and almost ovoid of pitting. The hairiness on the under surface of the leaves is not typical of var. subsetosum.

The collection of J. Davis, June 24, 1916 (MO) from Eolia, Pike Co., Missouri, is intermediate between var. occidentale and var. subsetosum in hairiness; the flowers tend to be more toward var. subsetosum.

The collection of L. D. Smith 906 (TEX) from Blue Bonnet Hills, McLennan Co., Texas, has hairs on upper surface of leaf more or less typical of var. subsetosum; but the hispid nature of the stem even from the base and the pattern of hairs on the lower surface of leaf are not at all typical of var. subsetosum.

In the collection of A. Winchell (US) from Alabama, two of the individual plants (marked 2 and 3 on the herbarium sheet) tend toward var. occidentale in nutlet; the indument on both sides of leaf and the color of the leaves tend toward var. subsetosum.
2. *O. virginianum* (L) A. DC.

*O. virginianum* (Linn.) A. DC. Prodr. 10:70. 1846.


Type: Earle and Baker, 29 May 1897, Auburn, Lee Co., Alabama (MIN, MO)

Plant erect, 3-4 dm. tall. Stems 1-few arising from the rootstock, 3-5 mm. in diameter, moderately strigose (hairs 0.4-1 mm. long), often branching above the middle; branches ascending. Basal leaves forming a rosette, 3.5-9.5 cm. long, 1.5-2 (3.4) cm. wide, 3-5 nerved, oblanceolate to spatulate with a caudate base and with a round or obtuse apex, beginning to dry-up at anthesis. Cauline leaves 5.5-8 cm. long (1) 1.4-1.6 (3) cm. wide, middle ones longer, 3-5 nerved, sulcate-striate along nerves on the upper surface, ridged on the lower surface, oblanceolate, sometimes upper leaves elliptic, obtuse or apiculate-acute, moderately strigose-strigulose on both sides (hairs 0.2) 0.5-1 mm. long), hairs rarely ascending. Inflorescence branched, each branch 7-15 cm. long. Bracts 4.5-5.8 mm. long, 2.2-3.4 mm. wide in flower and 12-20 mm. long, 3-7 mm. wide in fruit. Pedicel about 1 mm. long in flower and 1.8-3.5 mm. long in fruit. Sepals 4-6.5 mm. long, 0.5-1.3 mm. wide, linear-lanceolate, acuminate, sparsely strigose-strigulose outside (hairs 1.0 mm. or below), sparsely strigulose within; margins ciliate (hairs 1.0 mm. long, ascending). Corolla 7.5-12.5 (14.4) mm. long; tube whitish, lobes usually yellowish, rarely pale greenish,
1.8-2.7 (4.9) mm. long, 1-1.3 mm. wide, linearly (rarely broadly) acuminate, sparsely hirsute outside (hairs 0.9-2 mm. long, ascending, usually straight, sometimes undulate towards tip) and also sparsely-moderately hirtellous (hairs about 0.5 mm. long, ascending-appressed, and extending down to the middle of the corolla). Anthers 1.8-2.8 mm. long, apex of the anthers often a little below the corolla sinuses. Style 13.5-18.5 cm. long. Nutlet 2.5-3 mm. long, 1.6-2.1 mm. broad, ovoid, broadest near the middle, usually moderately-abundantly pitted, whitish with brownish tinge toward the tip.

Range and general ecology

Along the eastern coastal plain from Massachusetts southward to Florida, and westwards to Alabama, Mississippi and Louisiana.

Largely confined to clearings on sandy (light) soils. Map 6.

Representative specimens

Alabama

Baldwin Co.: Gateswood, S. M. Tracy 8400 (MO, MIN).


Connecticut

Litchfield Co.: on a dry lightly shaded bank of the Housatonic River, Kentucky, Austin, James and Godfrey 322 (SMU).


Dist. of Columbia

Dry woods, cabin John, Washington, F. H. Sargent 7892 (SMU).


Florida

Dixie Co.: Railroad Savanna, near Old Town, R. K. Godfrey 56496 (SMU, GH).


Walton Co.: DeFuniak, S. M. Tracy 9187 (GH, MIN, TEX, US, MO).

Georgia


Louisiana

Ouachita Co.: Sandy loam of cut-over pine woods, 10 mi. S.W. West Monroe, R. Kral 8747 (SMU).

St. Tammany Co.: Covington, B. G. Arsene 11821 (US).

Maryland

Prince Georges Co.: Dry sandy woods, Riverdale, A. Chase 2376 (MICH, MIN).


Massachusetts

Barnstable Co.: Cape cod, J. M. Greenman 450 (MO, GH).

Nantucket Co.: Nantucket, J. R. Churchill, July 12, 1884 (MO).

Mississippi

Harrison Co.: Sandy ridges, Handsboro, D. Demaree 34997 (SMU, OKLA).

Lamar Co.: Sandy hillsides, longleaf pine area along Mississippi route 24, 13.5 miles W. of Hattiesburg, R. McVaugh and A. M. Harvill, Jr.
8529 (TEX, MICH, GH, SMU).

North Carolina

Cleveland Co.: Sandy bottom on the Broad River, about 4.5 mi. S. of Boiling Springs on NC. Rt. 150, H. E. Ahles and R. S. Leisner 15362 (GH).


New Jersey

Camden Co.: Swamps, Lindenwold, H. B. Meredith, June 8, 1921 (UC, GH).


New York

Albany Co.: Sandy soil, along "water-pipes" from Pine Hills, Albany to Rensselaer Lake, S. H. Burnham, July 22, 1911 (GH).

Suffolk Co.: River Head., L. I., E. S. Miller, June 19, 1872 (MICH).

Pennsylvania


Rhode Island

Providence Co.: Smithfield, G. Thurber, June, 1846 (GH).

S. Carolina


Virginia

Roanoke Co.: Dry soil, grassy clearing, S. slope of Catawba Mt. 3½ mi. N.W. of Hanging Rock, C. E. Wood, Jr. 5867 (US, GH).

Discussion

Clear intermediates between *O. virginianum* and other taxa are not noticed. The following specimens, however, show deviations from typical characters of the species. Whether these deviations represent variation within the species or the involvement of any related taxon is not known.

The collection of A. Winchell (US) (marked 1) from Alabama and of E. C. Almendinger 1870 (MICH) from Cobb Co. in Georgia, show spreading hairs on stem and ascending hairs on leaves.

The collection of J. D. Smith, March 20, 1886 (US) from Orange Co. in Florida, shows a long corolla (14.8 mm.) with long corolla lobes (4.7 mm.).

The collection of J. H. Wibbe, July, 1891 (UC, WIN) from Albany Co. in New York shows broadly acuminate corolla lobes (2.9 mm. long, 1.6 mm. wide, length of corolla 9.4 mm.). Leaves mostly elliptic. It approaches var. *bejariense*, *O. dodrantale* and *O. unicum* in the shape of corolla lobe.

The collections of J. P. Gillespie 757 (GH) and 55461 (SMU) from Leon Co. in Florida resemble *O. virginianum* but the corolla lobes are greenish and the hairs are ascending.

3. *O. helleri* Small

*O. helleri* Small, Fl. S.E. U.S. 1000. 19. 1000. 1337. 1903.  
Type coll.: "Heller, Pl. So. Tex. 1682, in Herb C.U." (NY).

Plant 3-4 dm. tall, suffrutescent at base, branching above, branches ascending. Stems usually single, erect, terete or slightly angular, usually glaucous, hispid (hairs 1-2.3 (3.6) mm. long, spreading, retrorse or reflexed on old stem, moderate, falcate-straight) and also hispidulous
(hairs 0.7 mm. long, appressed, moderate, markedly falcate). Leaves highly variable in shape, size and color on drying, often brown or black on drying, glaucous, 5-7 (9)-nerved, cross nerves nearly perpendicular to the longitudinal ones; basal leaves in a rosette, 8-15 cm. long, 2-3.2 cm. broad, spathulate with caudate base, obtuse. Cauline leaves 7-10 (14) cm. long, 2-5 (7.6) cm. broad; lower leaves smaller, spathulate, middle ones biggest, elliptic to lanceolate, sometimes broadly ovate-rarely cordate. Upper surface hispid (hairs 0.9-2.2 (3.4) mm. long, stiff ascending, moderate, falcate, the whitish basal discs, often prominent against the brownish black color of the leaf in dried specimens). Lower surface hispid (hairs 0.8-1 mm. long, upright-ascending, moderate, falcate). Veins moderately hispidulous (hairs 0.9-1.2 mm. long, spreading, falcate). Inflorescence 3-6 (10) cm. long, not spirally coiled toward apex, flowers not secund. Flowering bracts 10-15 mm. long, 3.2-4.1 mm. broad. Fruiting bracts 4-6.5 cm. long, 1.7-3.5 cm. broad, lower bracts broadly ovate to lanceolate, upper ones ovate to elliptic. Pedicel 4-6.3 (9.4) mm. long in flower, (5.1) 7-11 (13.5) mm. long in fruit. Sepals 6-7 mm. long, 0.9 mm. broad, spatulate-oblong, obtuse, hispid outside, (hairs 0.9-1.4 mm. long, mainly restricted to midvein and margins, ascending-spreading, moderate, falcate-straight), and also sparsely strigulose with hairs 0.4 mm. long all the sepal; inner surface strigose (hairs 0.7 mm. long, very sparse at base, sparse towards apex). Corolla 9-11 mm. long; sinuses not thickened; lobes 3.2-5 mm. long, 2-3 mm. wide at base, acuminate, hirsute outside (hairs 1.3-2.5 mm. long, appressed-ascending, moderately abundant, undulate at apex of the hair), also sparsely villulose-hispidulous with hairs 0.4 mm. long or below. Anthers 2.7-3.4 mm. long, oblong, 1/3-1/2 of the anther above the
corolla sinuses. Style 14.5-16 mm. long. Nutlet (2.8) 3.2-3.8 mm. long, 2.8-3.2 mm. wide, globular-ovoid, moderately pitted, sometimes grooved length-wise on the ventral side, whitish, not constricted at base.

Range and general ecology

Confined to the region of San Antonio, Texas, where it is sympatric with *Q. molle* var. *bejariense*. Near rivers, creeks, on flood plain, under shade, in woods, on rocky limestone soil. Map 7.

Representative specimens

Bandera Co.: 2 mi. SE. of Bandera, Hugh C. Cutler 872 (MO); Bandera Pass, J. Reverchon 1564 (SMU).

Comal Co.: Comanche Spring, New Braunfels, Lindheimer 1025 (MO, US, UC, GH, TEX).


Kendall Co.: Spanish Pass, Mr. and Mrs. Clements 307 (MO); Thickets, Calcareous hillsides, E. J. Palmer 9869 (US, MO).

Kerr Co.: Lacey's ranch, rich hillside woods, E. J. Palmer 9281 (US, MO); Turtle Creek, 13½ mi. SW. of Kerrville, V. L. Cory 23982 (GH); Kerrville, A. A. Heller 1682, June 2, 1894 (US); Bear Creek, A. A. Heller 1682, April 30, 1894 (UC).

Travis Co.: Disintegrating limestone in oak-cedar woodland, 12 mi. west of Austin, Lee and Fred A. Barkley 16T516 (MO, TEX); Austin, B. C. Tharp 3/30/30 (UC, MO, SMU, GH); Upper Bull Creek, B. Q. Tharp 50-1 (MIN, COLO, TEX, KSC).


Discussion

Considering the relatively small range of its distribution and the few
available specimens, *O. helleri* shows great variation in many characters such as leaf shape and size, furrowing along veins, basal discs of hairs on the upper surface of leaf, glaucousness, degree of darkening on drying. Based on the gross morphology, leaf shape, size and color (in dried specimens), the plants are readily separable into two groups. In the first group, the leaves are bigger in size (about 9.5 cm. long and 5 cm. wide) broadly ovate, sometimes slightly cordate at base, upper surface of leaf dark brown on drying and the basal discs of hairs are prominent as white specks. (Comal Co.: Comanche Spring, New Braunfels, F. Lindheimer 1025 (MO, US, UC, GH, TEX).) In the second group, the leaves are smaller (about 9 cm. long and 2 cm. wide), elliptic or faintly ovate, not cordate at base, upper surface of leaf light brown on drying, and the basal discs of hairs not so prominent. (Travis Co.: upper Bull Creek, B. C. Tharp 50-1 (MIN, COLO, TEX, KSC).) Floral and nutlet characters do not seem to show such variability.

Intermediates between this variety and others seem to be rare. The only one noticed is the collection of D. Demearee 20546 (SMU, MIN) from Mount Nebo State Park, Yell Co., Texas, which resembles *O. molle* var. *subsetosum* in hair pattern on the upper surface of leaf. However, the hairs on the lower surface of leaf, the presence of petioles, the dark color and the faint glaucous nature of the leaves, the big size of the basal discs (0.3-0.4 mm. in diameter) of hairs on upper surface of leaf, and the general appearance of the plant are typical of *O. helleri*.

Most of the plants in *O. helleri* bloom in the last week of March and the first week of April, while those of *O. molle* var. *bejariense* bloom in the first week to third week of April. Thus there is an overlap of
flowering for about a week. Even then, intermediates between these two taxa seem to be rare.

The nature of variability of *O. helleri* and the isolation mechanism that apparently keeps these two taxa separate are difficult to explain without field study.

In the absence of clear intermediates and from the fact that *O. helleri* maintains its distinctiveness though occurring sympatrically with *O. molle* var. *bejariense*, it seems justifiable to continue to treat *O. helleri* as a distinct species.


Type coll.: C. H. Mueller 2259, Cerro Potosi, Galeana, Nuevo Leon (Mexico), July 21, 1935 (GH).

Plants rhizomatous, 1.5-2.5 dm. tall, erect with 1-few clustered stems arising from a small subcaudex, stems usually unbranched above; herbage finely hairy, hairs conspicuously bulbous at base. Stems 1.3-2.7 mm. in diameter at base, hirsute (hairs 1-1.6 mm. long, ascending or spreading, moderate, straight-falcate), also strigose-strigulose (hairs 0.4-1 mm. long, moderate, less hirsute). Basal leaves not seen, presumably deciduous at anthesis, apparently in a rosette as inferred from the persisting leaf bases. Cauline leaves 1.6-4.5 cm. long, 0.5-1.5 cm. broad, 3-nerved; lower cauline leaves smaller, oblanceolate-elliptic-oblong, obtuse, deciduous at flowering stage; upper cauline leaves biggest, elliptic to linear-lanceolate, acute. Leaves hirsute on both surfaces (hairs
0.5-1.4 mm. long, whitish or chalky white, appressed or ascending, moderate, falcate) also sometimes sparsely or very sparsely hispidulous especially along veins (hairs 0.4 mm. long or below, appressed-ascending); veins on the lower surface abundantly hirsute. Inflorescence about 5 cm. long, unbranched, flowers few and more or less congested. Flowering bracts 1.2-2.5 cm. long, 0.3-1 cm. wide, elliptic-lanceolate, fruiting bracts 1.5-3.4 cm. long, 6.2-8 mm. wide. Pedicel 2-3.5 mm. long in flower, 5.4-7 mm. long in fruit. Sepal 7.5-11.2 mm. long, 1.3-1.7 mm. wide, linear-lanceolate with attenuated apex; outer surface hirsute (hairs (0.7) 2.3 mm. long, appressed-ascending, falcate-straight, moderate-abundant, longer hairs clustered at base), and also sparsely strigulose (hairs 0.5 mm. long or less); inner surface strigose, (hairs 0.7 mm. long or less, sparse-moderate). Corolla 13-17 mm. long, with yellowish tube; lobes greenish, 2.8-3.3 mm. long, 2-2.7 mm. wide, acuminate with tip often recurved a little outward, hirsute-hirtellous outside, hairs 0.3-1.6 mm. long, not readily separable into short and long, hairs appressed, but the longer hairs ascending; shorter hairs extending 3/4 down the tube sparsely. Inner surface of corolla lobes strigose-strigulose, hairs 0.2-0.7 mm. long, moderate-abundant on the upper half extending down to the base of the lobes along the margins sparsely. Style 15.5-20 mm. long. Nutlet 3.8 mm. long, 3 mm. in diameter, ovoid with conical apex, sulcate along the ventral suture, sparsely pitted only on either side of the suture, brownish, not constricted at base, pale brownish.

**Range and general ecology**

Central Mexico: Nuevo Leon, Tamaulipas. Forest floor, pine forests on mountains, alt. 9-10,000 ft. Map 8.
Specimens examined

State of Nuevo Leon


Sierra Madre Oriental, ascent of Infernillo, 15 mi. S.W. of Galeana, alt. 9-10,000 ft. common about the peak, C. H. and M. T. Mueller 923 (TEX, MICH, GH).


State of Tamaulipas

On mountain top 7 kilo. S.W. of Miquihuana in forest of large pines; forest floor of low vegetation, alt. 3600 m. L. R. Stanford, K. L. Rutherford, and R. D. Northcraft 909 (MO, GH).

Discussion

The simple type of indument recalls a similar sort in O. virginianum. O. dodrantale closely resembles O. molle var. bejarierse and O. unicum in its broadly acuminate corolla lobes, and to some degree O. virginianum in its acuminate lobes. The yellow corolla tube and apex of the nutlet are more or less similar to those of O. unicum.

Onosmodium dodrantale, however, differs from the rest of the species in its small stature, thin stems, small size of leaves, short inflorescence with few flowers, and indument on the inner face of corolla lobes. No intermediates were noticed. On the whole it is sufficiently well marked to be considered a distinct species.
5. *O. unicum* Macbride


*Type call.:* Palmer 185 Alvarez, San Luis Potosi, July 13-23, 1904 (GH).

Plants rhizomatous, 4-5 dm. tall, often more ashy towards base because of cineraceous indument, usually single-stemmed, branching above; branches few, ascending. Herbage glanduliferous; glandular hairs 0.5 mm. long, spreading, present on stem, leaves, bracts, pedicels and calyx; gland at the tip of a multicellular flattened stalk, globular, orangish. Stems 5.5 mm. thick at base, hirsute (hairs 0.7-1.4 mm. long, appressed-ascending, falcate-straight), also abundantly hirtellous (hairs 0.5 mm. long or below, falcate, appressed, a few hairs retrorse, especially the smaller ones). Leaves 3-9.5 cm. long, 0.9-2.8 cm. wide, 3-5 nerved. Basal leaves not seen and presumed to be deciduous by anthesis. Lower cauline leaves narrowly oblanceolate to elliptic; upper surface hirsute (hairs 0.7) 0.9-1.2 (2.5) mm. long, appressed-ascending, falcate-straight), also finely hirtellous (hairs 0.3 (0.5) mm. long, abundant-very abundant, appressed, a few ascending, antrorse, a few laterally pointing especially those along the nerves); lower surface hirsute (hairs 1-2 mm. long, moderate-abundant, appressed-ascending, straight-falcate), also hirtellous (hairs 0.5 mm. long or below, very abundant, straight to flexuous, appressed to spreading, antrorse to retrorse, giving a tomentose appearance because of the last two features). Nerves very abundantly hirtellous and sparsely hirsute. Middle cauline leaves biggest, elliptic to oblanceolate, sometimes lanceolate, acute; upper surface moderately hirsute (hairs 0.4) 0.8-1.2 mm. long, moderate,
appressed-ascending, falcate-straight, usually whitish, sometimes a few hairs chalky white), also finely hirtellous (hairs 0.2-0.35 mm. long, abundant, mostly appressed), glanduliferous all over the surface; lower surface hirsute (hairs 0.7) 1-1.2 (1.6) mm. long, moderate-abundant, appressed-ascending, antrorse, falcate-straight) also hirtellous (hairs 0.2-0.35 mm. long, abundant, mostly straight, many appressed, some spreading, antrorse, retrorse and some laterally pointing). Nerves abundantly hirsute, moderately hirtellous, glands restricted to nerves. The pattern of hairs on lower and upper cauline leaves is essentially similar except that in the latter the hairs are less dense. Lower surface of leaf paler in color than the upper surface; lower cauline leaves usually distinctly more ashy gray because of cinereous and denser indument. Most hispid hairs on the upper surface of leaf are bulbous at base and arising from discoid base; the hairs on the lower surface show these features less evidently. Inflorescence 10-29 cm. long, little or not branched, few flowered. Flowering bracts 9.5-25 mm. long, 1.8-4.5 mm. wide, elliptic-lanceolate; fruiting bracts 1.3-5 cm. long, 0.4-1.5 cm. wide. Pedicel 1.8-3.8 mm. in flower, 4-9 mm. long in fruit. Sepals 7-11 mm. long, 0.5-1.3 mm. wide, linear-lanceolate, attenuated towards apex; outer surface hirsute (hairs 0.7-1.1 mm. long, ascending, moderate-abundant) also strigulose (hairs 0.5 mm. long or below, appressed, sparse-moderate) moderately glanduliferous; inner surface sparsely strigose, a few hairs near apex ascending, glands absent. Corolla 13.5-15 mm. long, tube cream yellow, lobes greenish, 3.2-4.3 mm. long, broadly acuminate, sometimes more or less caudate with outwardly recurved tips; outer surface hirtellous (hairs 0.6-0.9 mm. long, appressed, sparse-moderate, straight-falcate) also strigulose (hairs 0.4 mm. long or below,
abundant to very abundant, extending 3/4 down the tube sparsely). Anthers 2.7-3.4 mm. long. Style about 17 mm. long. Nutlet 3.7-4.4 mm. long, 2.8-3.2 mm. in diameter, ovoid with conical apex, sulcate along the ventral suture, occasionally pitted on either side of the suture, strongly constricted at base, brownish.

Range and general ecology

Occurring in central Mexico in the states of Hidalgo, Nuevo Leon, San Luis Potosi.

Dry woods, moist mixed woods, ravines, rocky crevices of limestone, at higher altitudes of about 5000-8000 ft. Map 9.

Specimens examined

State of Hidalgo


Zacualtipan District, dry woods, trailsides, slopes and ravines by Rio Panotlan between Zacualtipan and Olotla on road to Metztitlan, 1600-2000 m., H. E. Moore, Jr. 3271 (UC).

Zimapan District, rocky walls and floor, upper end of Barranca de San Vicente, Alt. 2000 m., H. E. Moore, Jr. (GH).

Zimapan District, moist mixed woods, Barranca de las Verduras, N. of El Monte, on trail from Zimapan to mines of El Monte, Alt. 7500-8400 ft., H. E. Moore, Jr. and C. E. Wood, Jr. 4503 (GH).

State of Nuevo Leon

Dense fog forest, alt. 1800 m., Dulces Nombres and just east of border into Tamaulipas (State), F. G. Meyer and D. J. Rogers 2775 (MO).
State of San Luis Potosí

Alvarez, E. Palmer 185 (US).

Rocky crevices of limestone, alt. 2200-2400 m. Alvarez, Sierra de Alvarez, F. W. Pennell 17861 (GH, US).

Discussion

No intermediates were noted among the specimens at hand. The leaves seen show variation in indument and size on the same plant, and in size and shape between individuals (populations?).

This species resembles O. molle var. bejariense in the indument on the upper surface of leaf and the broadly acuminate corolla lobes; it resembles var. hispidissimum in the constriction of the nutlet. This taxon differs from others in being glanduliferous and in the indument on the lower surface of leaf, and the ashy gray basal leaves which together, no doubt, justify treating it as a distinct species. However, the unique presence of glandular hairs is so distinctive of this taxon, that one may be even tempted to treat this species as a separate genus.

It would be interesting to ascertain the phylogenetic significance and the adaptive value, if any, of the glandular hairs.

DISCUSSION

DISTRIBUTION AND ECOLOGY: The genus Onosmodium is confined to North America and is mainly temperate in distribution. It occurs from about 400 ft. elevation (var. bejariense, O. helleri in Texas, U.S.A.) to about 10,000 ft. elevation (O. dodrantale in Mexico); from humid region in east coast (O. virginianum) to arid regions in the west (part of O. molle var.
occidentale in New Mexico).

Onosmodium molle var. occidentale, var. hispidissimum, and O. virginianum have extensive ranges; the rest of the taxa are confined to smaller areas and are endemic or local in distribution. The pattern of distribution shows remarkable correlation with ecological zones. Var. occidentale, a continental species, is mainly confined to the central prairies extending from Manitoba to Texas. O. virginianum, a coastal species, is restricted mostly to pine lands or grassy clearings on sandy (light) soils along the east coast from New York southward to Florida and westwards along the Gulf Coast to Alabama and Mississippi. Var. hispidissimum extends across the continent from the Appalachian Mountains between New York and Virginia of the east coast to a Minnesota-Missouri axis on the west. Its range is mainly confined to central low lands, its southern border more or less coincides with the southern limits of Pleistocene glaciation. Var. molle occurs mostly in the dry limestone glades in the central (Nashville) basin of Tennessee and adjacent areas. Var. subsetosum is restricted to the Ozark Plateau and Cuchita mountains in Missouri, Arkansas, and Oklahoma. It occurs in limestone glades, barrens and oak-hickory woods. Var. bejariense and O. helleri occur together in central Texas. This area represents a meeting place of different vegetational areas, viz., cross timbers and prairies, Edwards plateau, post oak savannah, blackland prairies and south Texas plains. The exact habitats for these two taxa could not be determined from the field notes on the specimens. O. helleri is found in limestone hills and on disintegrating limestone in oak-cedar woodland. Var. bejariense is more widely distributed than the above taxa. It seems to occur mostly in prairies; also in open woods and margins of woods, and flood plains
(clay soil).

The material available on the Mexican species, viz., O. dodrantale and O. unicum is too little to permit drawing a tangible conclusion. Both these taxa, which seem to be local in distribution, are high altitude mountain species occurring at 5000-10,000 foot elevations in central Mexico. O. dodrantale appears to occur at higher elevations in pine woods on mountain peaks between 9000 to 10,000 feet elevation; while O. unicum occurs at elevations of 5000 to 8600 feet in moist mixed woods and limestone ledges.

In the following two sections an attempt is made to draw certain tentative conclusions on the variability and evolutionary tendencies in this group. These are arrived at without adequate field or cytological studies or breeding experiments. They are based on assumptions and are purely speculative, especially so with regard to evolutionary tendencies. In spite of this, I desire to put down my impressions about this group gained through my study of this material.

VARIABILITY: Variation in Onosmodium is of two types. The first is clinal variation which is normally associated with wide distribution of a species and with some regularly changing environmental factors in the area of its distribution. Var. occidentale meets these two requirements and shows variation in hairiness on leaves from North to South. However, such variation could not always be correlated with area of distribution. Thus, O. virginianum, though extensive in range, does not seem to show corresponding variation. On the other hand, O. helleri which is local in distribution in Texas shows relatively high variation in leaf characters; it is likely that the samples examined represent local populations or aggregates occurring in contrasting habitats.
The second type of variation is apparently due to hybridization. Var. *occidentale* intergrades with var. *hispidissimum* in its northern range, i.e., north of Missouri, and with var. *bejariense* in Texas. Judging from the intermediacy in the morphological characters and from the occurrence of these intermediates in zones of overlap, it is likely that the intermediates are the result of hybridization. Similar intermediates, though few in number, were noticed between var. *molle*, var. *subsetosum*, var. *occidentale* and var. *hispidissimum*, but intermediates between var. *bejariense* and var. *hispidissimum*, var. *molle* and var. *subsetosum* were not noticed. The varieties, however, are knit together through var. *occidentale* and var. *hispidissimum*. All these tend to show that introgression is taking place in nature, especially between var. *occidentale* and each of var. *hispidissimum* and var. *bejariense*. It is probable that the wide ecological tolerance of var. *occidentale* is at least partly due to introgression with var. *subsetosum* and var. *hispidissimum*.

The absence of reproductive barriers between these taxa may be explained by assuming that the nature of isolation mechanisms is seasonal and/or ecological. In the case of var. *occidentale* and var. *hispidissimum*, the uniform environmental conditions in the region of overlap might stimulate convergence in flowering time and thus abolish a good part of seasonal isolation. With regard to var. *occidentale* and var. *bejariense* in Texas, the disturbance of the local habitats by man might be a chief factor in not only promoting hybridization but also in providing a suitable habitat for the establishment of the hybrids and their segregates. The fact that var. *bejariense* and var. *occidentale* still maintain their distinctiveness and persist in their respective zones indicates that the
hybrids are inferior in competition with the parents. The apparent failure of *O. helleri* to hybridize with var. *bejariense* may be due to an intrinsic isolation mechanism or due to the existence of different pollinating insects as required by the differences in the flower structure of the two taxa.

**EVOLUTIONARY TENDENCIES:** An attempt is made to explain the speciation in *Onosmodium* on the basis of allopatric or sympatric speciation or colonization.

The ranges of all the taxa (except those of the Mexican species) occur or meet in the Texas-Missouri-Tennessee area which represents the center of diversity for the genus. The same area was protected from glaciation. These two facts tempt one to postulate that this 'refugium' is the center of preservation which has become the (secondary) center of dispersal in the post glacial period. This postulate involves the assumption that the genus was differentiated even prior to glaciation. This seems to be likely from the following three evidences: (1) the area of 'refugium' coincides with the center of diversity, (2) the varieties *occidentale* and *hispidissimum*, which now occupy the glaciated area, are not yet fully differentiated as judged from the degree of development of reproductive barriers, whereas the varieties *bejariense*, *subsetosum*, and *melle* are relatively more differentiated, (3) the latter three varieties are of narrow distribution. The var. *occidentale* might have spread from the Oklahoma-Kansas area, and var. *hispidissimum* from the Ozark-Tennessee region northwards or eastwards through the 'prairie-peninsula' (Northern Illinois, Indiana, Ohio, and Southern Michigan). Another feature that lends support to this viewpoint is that it is possible to visualize the derivation of varieties *occidentale*
and *hispidissimum* from varieties *bejariense* and *molle* respectively.

The contiguous but distinctive ranges of these taxa, the presence of clear-cut morphological discontinuities, and the occurrence of 'hybrid' intermediates between them suggest that the manner of speciation is allopatric and that they should be treated as varieties (of a polytypic species). *O. virginianum* also may have originated through a similar process.

The occurrence of var. *bejariense* and *O. helleri* together in central Texas might be an example of sympatric speciation. The existence of diversified and sharply differentiated habitats or vegetations in this zone lends support to this assumption.

With regard to the Mexican species (*O. dodrantale* and *O. unicum*) it is more difficult to account for their origin. They show disjunct distribution from the rest of the group; both these taxa differ from others in distinctive ways. Thus, *O. dodrantale* is a short herb with indument on the inner surface of corolla lobes. *O. unicum* is unique in possessing glandular hairs. Both are local in distribution. It might be that they have originated in isolation, from nutlets being disseminated from northern territory by the migrating birds. There is no evidence, however, that the birds could be the dispersal agents for this genus.

With regard to the interrelationships of the group and on the basis of morphological characters I am inclined to think the taxa (except for *O. helleri*) seem to be closely related (monophyletic ?); *O. helleri* appears to be related to this group through convergent evolution with regard to the flower, but not necessarily the nutlet.
SUMMARY

This study is a revision of the infrageneric taxa of the genus Onosmodium (Boraginaceae). The genus is mainly temperate in distribution and is confined to North America east of the Rocky Mountains, extending from the southern border of Canada to Central Mexico.

The genus concept is based mainly on floral characters (Mackenzie, 1905). The species concept adopted is the traditional taxonomic species concept. Varieties are based mainly on the occurrence of morphological intermediates.

No new species or varieties are recognized. Five species and five varieties are recognized; their full descriptions are given. Two of the species, viz., O. dodrantale and O. unicum occur in Central Mexico; the remaining in the U.S.A. and Canada. Only two species, viz., O. bejariense and O. helleri occur sympatrically, and these are in Central Texas.

The center of diversity for the genus is indicated as the Texas-Missouri-Tennessee region. The pattern of distribution is correlated with ecological regions. Variation in the genus is clinal or due to hybridization. The process of speciation is attributed to allopatric or sympatric speciation or to colonization.

Illustrations of flower parts and nutlets, and distributional maps of all the taxa are included. A key for all the taxa is provided.
DOUBTFUL AND EXCLUDED NAMES


Onosmodium carolinianum (Lam.) A.DC. Prodr. 10:70. 1846. Apparently based on Lithospermum carolinum Lam. Table Encyc. 1:367. 1791. No specimens seen (cf. the discussion in Mackenzie's revision).


---Macromeria discolor Benth. Pl. Harw. 49. 1840.

Onosmodium eriocalon A.DC. Prodr. 10:70. 1846. No specimens seen.


Onosmodium scabrum Roem. & Schult. Syst. 4:57. 1819. "Ad in virginia?". No specimens seen.


LITERATURE CITED


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PLATE I

Fig. 1. Flower showing the shape and orientation of corolla lobes and the exerted style.

Fig. 2. Corolla split open to show the included stamens (diagrammatic).

Figs. 3-8. Hair abundance classes:

Fig. 3. Glabrous
Fig. 4. Occasional
Fig. 5. Sparse
Fig. 6. Moderate
Fig. 7. Abundant
Fig. 8. Very abundant

Figs. 9-11. Hair orientation classes.
0-30° APPRESSED UPWARDS

30-60° ASCENDING

60-120° PATENT

120-150° DESCENDING

150-180° APPRESSED DOWNWARDS

SPREADING

RETRORSE
PLATE II

Figs. 1-9. Anthers in Onosmodium. The arrows indicate the attachment of the filaments to the anthers.

Figs. 10-18. Sepals in Onosmodium.

1 and 10 Onosmodium molle var. molle
2 and 11 " " var. occidentale
3 and 12 " " var. hispidissimum
4 and 13 " " var. bejariense
5 and 14 " " var. subsetosum
6 and 15 " " virginianum
7 and 16 " " helleri
8 and 17 " " dodrantale
9 and 18 " " unicum
Corolla lobes in *Onosmodium*

1. *Onosmodium molle* var. *molle*
2. " " var. *occidentale*
3. " " var. *hispidissimum*
4. " " var. *bejariense*
5. " " var. *subsetosum*
6. " " *virginianum*
7. " " *helleri*
8. " " *dodrantale*
9. " " *unicum*
PLATE IV

Nutlets in Onosmodium

1. Onosmodium molle var. molle
2. " " " var. occidentale
3. " " " var. hispidissimum
4. " " " var. bejariense
5. " " " var. subsetosum
6. " " virginianum
7. " " hollori
8. " " dodrantale
9. " " unicum
Map 1. Distribution of *Q. molle* var. *molle*. 
Map 4. Distribution of *O. molle* var. *bejariense*.
Map 5. Distribution of *O. molle* var. *subsetosum*. 
Map 6. Distribution of O. virginianum.
Map 7. Distribution of *O. helleri*.
Map 8. Distribution of *O. dodrantale* in Mexico.
Map 9. Distribution of *O. unicum* in Mexico.
A TAXONOMIC REVISION OF THE GENUS ONOSMIDIUM

by

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B. Sc., Andhra University (South India), 1946

AN ABSTRACT OF A MASTER'S THESIS

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MASTER OF SCIENCE

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