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STUDIES IN THE BORAGINACEAE, XXVI
FURTHER REVALUATIONS OF THE GENERA OF THE LITHOSPERMEAE

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PREPARATORY TO A GENERAL DISCUSSION of the Lithospermeae to be published in the near future, seventeen genera of the tribe are given individual treatment in the present paper. These, along with six genera discussed previously, Jour. Arnold Arb. **34**: 258–299 (1953), include all the genera which can be referred to the tribe if that is to be a homogeneous division of the Boraginoideae. Of the seventeen genera here discussed only one, *Lithospermum*, has representatives native to both America and the Old World or has direct relations with genera in both regions. Since the distribution and relationships of all other genera are confined within one or the other of these major regions, the primary division in my key to the genera has been deliberately based on geography. For most uses this will be a convenience. Furthermore, it also has the advantage of permitting sharper contrasts of immediately related genera. A synopsis of all the genera of the tribe and technical keys for their identification will be provided in the following paper of this series.

KEY TO THE GENERA

PLANTS NATIVE TO AMERICA.

Anthers completely exserted from the throat; filaments elongate, 6–70 mm. long, exserted 1–65 mm. from the corolla mouth; corolla large, 39–90 mm. long, trumpet-shaped, lobes usually ascending or recurved or reflexed; pollen ellipsoidal to ovoid or ovoid-oblong, 23–33 $\times$ 15–28 μ . . . . 1. **Macromeria.**

Anthers completely included in the throat or only partially exserted from the corolla mouth; filaments at most 10 mm. long and usually very much shorter, completely included or exserted less than 1 mm.; corolla smaller, usually less than 25 mm. long and never more than 50 mm. in total length, tubular to salverform, lobes erect to spreading.

Flowers precociously sexual, corolla opening and exposing stamens and style before attaining full size; corolla-lobes erect, sharply acute or acute with an attenuate tip, very narrowly imbricate in the bud, usually evidently longer than broad; sinus between the corolla-lobes plicate and inflexed and thickened at the base; pollen ovoid, 16–24 $\times$ 13–22 μ. . . .2. **Onosmodium.**

Flowers not precociously sexual, corolla opening only when fully developed; corolla-lobes obtuse or rounded, frequently as broad as long or even broader than long, broadly imbricate in the bud; sinus between the corolla-lobes neither plicate nor thickened nor inflexed at the base.

Filaments about half the total length of the corolla, twice as long as the anthers, arising low in the corolla, towards the base shaggy with slender multicellular gland-tipped hairs; anthers borne high in the corolla-throat with its sterile tip exserted; tip of anther 1–2 mm. long; pollen ovoid, $25–28 \times 21–33\ \mu$. .... 3. **Nomosa.**

Filaments less than a third of the total length of the corolla and usually much shorter than the anther, usually arising at or above the middle of the tube, glabrous or bearing only a few inconspicuous stipitate glands; anthers without a sterile tip or the tip less than 1 mm. long.

Filaments broadening upwards from a narrow attachment; anthers with a small but definite sterile tip, with a well-developed sinus at the base.

Corolla lacking faucal appendages, corolla-lobes deltoid; filaments oblanceolate, almost as long as the anthers; anthers conspicuously hairy on the back, with an erect tip, thecae without darkened margins; pollen ovoid, $20–23 \times 16–20\ \mu$; coarse plant with broad strongly veined leaves .... 4. **Lasiarrhenum.**

Corolla with evident faucal appendages; corolla-lobes rounded; filaments triangular or obovate-triangular, half as long as the anther; anther glabrous, with a recurved tip, thecae with darkened margins; pollen ellipsoid, $24–25 \times 20\ \mu$; small slender-stemmed plant with very narrow veinless leaves .... 5. **Perittostema.**

Filaments linear or subulate or unguiculate; anther only very rarely bearing a sterile tip, base emarginate or rounded.

Corolla-throat angulate, externally with a small swelling directly below each sinus; corolla-lobes strictly ascending; filaments partially exserted from the throat; anthers one half to three fourths exserted from the throat; inside of corolla completely glabrous and bearing neither faucal appendanges nor stipitate glands; style exserted; pollen ellipsoid, $23–26 \times 16–22\ \mu$. .... 6. **Psilolaemus.**

Corolla-throat not angulate, not swollen externally below each sinus of the limb; corolla-lobes usually spreading; filaments and anthers always included in the throat; corolla inside with faucal appendages or stipitate glands or both and sometimes hairy; style usually included; pollen diverse as to size and form ... 12. **Lithospermum.**

Plants native to the Old World.

Anthers without a sterile tip or with the tip small and inconspicuous and rising abruptly from the emarginate, truncate or rounded summit of the anther; base of anther usually rounded or simply emarginate; base of theca not pointed, usually rounded; anthers always distinct, never joined together; pollen inconspicuously if at all colpate, pores in one or sometimes two rows, 6–9 or more.

Nutlets narrowed upwards into a prolonged beak, conspicuously rostrate with the apex hamate; cymes bractless above the base; upper leaves very ample and evidently veined; corolla-throat inside abundantly and antrorsely villose-strigose; Japan .... 7. **Ancistrocarya.**

Nutlets not conspicuously rostrate, apex not hamate; cymes bracted throughout; upper cauline leaves not conspicuously ample, usually veinless; corolla-throat inside not villose-strigose.

Corolla-throat inside bearing 5 well-developed elongate vertical guide-lines for insect visitors; guides consisting of vertical inflexed plaits bearing hairs or stipitate glands or both, or consisting merely of elongate vertical bands of crowded hairs and stipitate glands; anthers usually with small sterile tips; style usually with a prolonged bilobed sterile apex, always short, always shorter than the mature nutlets . . . . 8. **Buglossoides.**

Corolla-throat lacking guide-lines, bearing localized faucal appendages or bearing stipitate glands which are scattered or are in localized congregations, or sometimes naked; anthers only very rarely bearing a minute sterile tip; style only very rarely with a prolonged bilobed sterile apex, short to elongate, usually becoming much longer than the nutlets.

. Nutlet attachment not on the true base of the nutlet, borne ventral to the nutlet base at the lower end of a stipe which is directed downward from the ventral side of the ascending nutlet-body; pollen with biseriate pores; Mongolian . . . . 9. **Stenosolenium.**

Nutlet attachment on the base of the erect nutlet-body.

Pollen bearing 2 rows of pores, one about each end of the elongate grain, grains oblong or medially constricted, upper and lower halves of the same size and configuration; corolla without faucal appendages, its inner surfaces prevailingly devoid of stipitate glands, such glands when present scanty, inconspicuous, and confined to the corolla mouth; flowers heterostylic or monomorphic; stamens usually whorled, affixed at unequal heights above the corolla base only in one monomorphic species; Asia extending into Africa . . . . 10. **Arnebia.**

Pollen bearing a single row of pores either about the equator or below the equator about the lower half of the grain; grains globose, oblong-ellipsoidal or with the upper and lower halves dissimilar in size and configuration.

Corolla inside without faucal appendages or stipitate glands; annulus absent; stamens borne at very unequal heights on the corolla-tube; flowers heterostylic; Caucasus, Armenia, and adjacent Iran . . . . 11. **Echioides.**

Corolla inside with faucal appendages or stipitate glands or both; annulus present; stamens whorled, all borne at the same level above the corolla base; flowers heterostylic or monomorphic; Eurasia, Africa, and America . . . . 12. **Lithospermum.**

Anthers narrowed into a prolonged evident sterile tip; base of anther usually with an open sinus and hence somewhat sagittate; basal tip of theca usually pointed or narrowly prolonged; anthers usually joined to form a synandrium; pollen evidently colpate, pores in a single row.

Nutlets bilocular; calyx-lobes very unequal, strongly imbricate; anthers distinct or joined by the entangling of the tail-like appendages borne at the base of the theca; pollen barrel-shaped or ellipsoidal, pores 8, borne in a well-developed equatorial groove; plant nearly glabrous, leaves with a cordate-amplexicaul base . . . . 13. **Cerinthe.**

Nutlets unilocular; calyx-lobes equal or practically so, not imbricate; anthers usually coherent at the base or along the sides or both; pollen ovoid or globose or cylindric or ellipsoidal, pores 3, suprabasal or equatorial, not in an equatorial groove; plants evidently hairy, middle or lower leaves never with a cordate-amplexicaul base.

Nutlets bent 90° below the middle, strongly incurved, attachment small and substipitate appearing to be lateral but actually basal on the short erect lower section of the nutlet; gynobase with elevated pulvinate lobes each bearing a small attachment face; indument on herbage with intermixed slender gland-tipped hairs; bracts becoming large and foliaceous; fruiting calyx frequently on decurved pedicels . . . . 14. **Podonosma.**

Nutlets straight and erect or nearly so, with a usually broad and evidently basal attachment; gynobase not bearing the attachment faces on elevated pulvinate lobes; indument containing no gland-tipped hairs; bracts rarely becoming conspicuous and foliaceous; fruiting calyx borne on erect or ascending pedicels.

Corolla-lobes well developed, as long as or much longer than the tube, spreading or decurved; anthers coherent only along the margins of the terminal appendage, the appendage evidently longer than the theca; filaments very short and usually bearing a hairy basal appendage; throat of corolla frequently hairy; southern Arabia, Socotra, Somaliland to Angola . . . . 15. **Cystistemon.**
15a. **Vaupelia.**

Corolla-lobes short, commonly about as long as broad, conspicuously much shorter than the tubular part of the corolla, erect or loosely recurved (or, in one species, *Onosma longilobum*, with the lobes elongate, longer than the tube, but erect); anthers usually coherent at the base and frequently also along the margins of the thecae and the appendages, the appendage almost always shorter than the theca; filaments usually elongate, not appendaged at the base; throat of corolla never with spreading hairs; North Africa and Europe to eastern Asia.

Calyx-lobes narrow and elongate, more or less parallel, separated by a very narrow or closed sinus; corolla having no puffed-out ribs projecting between the calyx-lobes; filaments within a corolla all similar; anthers included to completely exserted from the corolla; nutlets smooth to rough with the surface only very rarely evidently papillate or muriculate; pollen ovoid to spheric or transversely ellipsoid . . . . 16. **Onosma.**

Calyx-lobes more or less triangular, ascending, separated by an open triangular sinus; corolla with puffed-out ribs projecting between the calyx-lobes; filaments within a corolla differing in the shape of their base and in the orientation of their attachment on the corolla; anthers included; nutlets roughened and with the surface abundantly and minutely papillate or muriculate; pollen cylindric or vertically ellipsoid; Himalaya and mountains of southwest China. . . . . 17. **Maharanga.**

1. **Macromeria** D. Don, New Edinb. Philos. Jour. **13**: 239 (1832). Based upon *M. longiflora* Don and *M. exserta* Don.

Philonomia DC. in Steud. Nom. ed. 2, **2**: 320 (1841); Meisner, Pl. Vasc. Gen. **2**: 189 (1836–43), in synom.

Onosmodium § *Macromerioides* Gray, Synop. Fl. N. Am. 2[1]: 205 (1878). Type species, *Macromeria viridiflora* A. DC.

Macromeria § *Macromerioides* (Gray) Johnston, Contr. Gray Herb. **70:** 13 (1924).

Plant perennial. Stems coarse, erect, simple or bearing a few leafy fertile branchlets in the upper axils, hispid or sometimes hispid-villose or strigose. Leaves well developed, all cauline, lowest ones smaller than the upper, hispid, velvety or strigose (hairs on upper surface usually with discoid or bulbose bases), with evident midrib and usually two or more pairs of well-developed evident assurgent veins. Cymes scorpioid, simple or sometimes geminate, terminating the main stems and frequently also arising directly from the uppermost leaf-axils and sometimes terminating leafy branchlets arising from the upper axils, relatively loose, with the flowers not evidently biseriate, after anthesis becoming straight, very loosely flowered, and very elongate; bracts numerous, conspicuous and foliaceous, usually somewhat accrescent in age, lanceolate to broadly ovate. Flowers at anthesis borne on strict pedicels at the summit of the straightened portion of the cyme and hence erect, or borne on the still curved portion of the cyme and directed backwards over the top of the cyme with the abaxial side uppermost and the corolla accordingly resupinate. Calyx 5-fid, the lobes elongate, usually evidently unequal, linear to narrowly lanceolate; pedicels elongating at maturity, strict or ascending. Corolla yellow, yellowish or greenish, straight and regular or curved and having the throat prolonged on the two-lobed adaxial side, elongate, somewhat trumpet-shaped, having a slender tube which gradually or abruptly expands into an elongate, subcylindric or conic-cylindric throat once to twice as long as the tube, the outer surface always evidently hairy, the inner surface glabrous or rarely inconspicuously hairy in the tube and on the lobes and along the veins in the throat, usually glanduliferous in the throat and sometimes on the lobes; faucal invaginations evident in one species but usually absent or only very obscurely developed, when present decorated with glands. Annulus absent or represented by a very narrow, continuous or interrupted lineate ridge just above the base of the tube, glabrous, or in one species with very inconspicuous tufts of minute hairs. Corolla-lobes equal, elliptic to deltoid, erect to ascending or reflexed at the base or rarely loosely recurved, shorter than the throat, imbricate, apex tending to be acute. Filaments equal, terete or distinctly flattened or even strap-shaped, glabrous or somewhat hairy in one species, arising well above the middle of the corolla-throat and always exserted from it but in only one species extruded more than the length of the corolla-lobes, affixed all at the same altitude on the corolla or at three superimposed levels with the medial adaxial one highest, the abaxial pair lowest, and the adaxial laterals at an intermediate level. Anthers straight or sometimes weakly falcate, elongate, oblong or oblong-linear, several to many times shorter than the filaments, affixed at or slightly below the middle, commonly in a groove in the connective, strict and erect or becoming horizontal by a subapical bend of the filament or sometimes versatile, apex usually rounded or obtusish and with a small inconspicuous tip formed by the prolongation of the connective tissue, but in one species emarginate and bearing a subapical gland; thecae parallel but unjoined for a short distance above the unappendaged, apparently emarginate base of the anther; connective evident on the back of the anther, especially above the middle, glabrous or in one species bearing short stout hairs above the middle. Pollen broadly to narrowly ellipsoidal or somewhat ovoid or ovoid-oblong, 25–33 $\times$ 15–28 μ, sometimes constricted near the middle, upper and lower half of the grain equal or more or less dissimilar, pores borne eight or nine in a single row at the equator or below it and sometimes very low on the grain just above its rounded base, grain in polar profile circular or obscurely polyhedral. Style filiform, glabrous, longer than the corolla and becoming evidently exserted; stigmas two, very small, juxtaposed and terminal on the tip of the style or subterminal and separated (though scarcely if at all surpassed) by an apical prolongation of the style. Nutlets smooth, ovoid or ellipsoidal, usually smooth, lustrous and white, straight, erect or more commonly diverging from the pyramidal gynobase; ventral keel weak or absent, suture completely closed or represented (sometimes only on the upper half of the nutlet body) by a lineate groove; attachment scar broad, basal, flat or convex, usually bearing the projecting end of the tubular bony funicular canal. Gynobase somewhat pyramidal, usually broadly so and commonly terminated by the thickened four-angulate base of the style; attachment faces nearly as broad as long, at maturity each surrounded by an elevated cartilaginous margin, usually sloping and the basifixed nutlets borne upon them usually divergent.

A genus obviously related to *Lithospermum* and most closely so to its Mexican species. It is distinguished only by the form and large size of its corollas and by having filaments elongate and exserted from the corolla-throat. Its eight species are well marked and form a very natural assemblage. They range between northern Guatemala and Arizona and New Mexico in southwestern United States, with most of them confined to very restricted areas in the mountains of Mexico.

Macromeria, as originally defined and established by David Don, included two species, *M. longiflora* and *M. exserta*. The most detailed subsequent treatments of the genus have been by De Candolle, Prodr. **10**: 68 (1846) and by Johnston, Contr. Gray Herb. **70**: 13 (1924). Of the species which have been referred to the genus, only *M. cinerascens* DC. (1846) is to be excluded, that being a species of *Lithospermum*. Both Gray, Synop. Fl. N. Am. 2^1: 205 (1878), and Macbride, Contr. Gray Herb. **49**: 19 (1917), have suggested that the genus should be reduced to one species, *M. exserta*, and that the remaining species be treated as a section of *Onosmodium*. As previously noted by me, Contr. Gray Herb. **75**: 16 (1924), such procedure would do violence to natural relationships by separating *M. exserta* from its evident relative *M. hispida*. It would also destroy the homogeneity of *Onosmodium*. The eight species of *Macromeria* are obviously more closely related to one another than any of them are to any species of *Lithospermum* or *Onosmodium*. From the latter genus they differ in size and form of the corolla, length of filaments, shape of the anthers, and tardily exserted style.

The species of this genus are coarse perennials having few to numerous stems usually over half a meter tall and frequently approaching and rarely even surpassing a meter in height. The leaves are all cauline, the lowermost being smaller and proportionately more elongate than those on middle sections of the stem. The leaf-blades have a strong midrib and also several well-developed assurgent lateral veins. In foliage, as well as in general habit, *Macromeria* is suggestive of *Onosmodium* and *Lasiarrhenum*, and to a somewhat less degree also of such American species of *Lithospermum* as *L. viride*, *L. oblongifolium*, *L. guatemalense*, and *L. cinerascens*.

The corollas, 35–90 mm. long, are among the largest in the Boraginaceae, with those of *M. exserta* the very largest in the family. They are more or less trumpet-like in form, having an elongate subcylindric or conic-cylindric throat usually several times longer than thick and commonly about as long as the slender tubular portion of the corolla supporting it. The equal, relatively short lobes are ellipsoidal, deltoid, or triangular ovate and commonly pointed. They may be straight and ascending or loosely recurving or abruptly reflexed at the base. In most of the species the corolla is regular or practically so, but in *M. hispida* and *M. exserta* it is curved, the throat is oblique and evidently prolonged on the adaxial side, and the stamens are affixed at superimposed levels in the throat, with the adaxial medial member highest. The corolla in these two species having a very distinct bilateral symmetry is clearly zygomorphic. This condition is usually most obvious in the bud of the corolla just before it opens. For most of its length the bud is gracefully curved adaxially, but in the thickened apical portion it becomes curved in the reverse direction. The outer thickened portion of the bud, formed of the unexpanded lobes, is evidently swollen on the two-lobed adaxial side. The bud has its tip not central but closest to its abaxial side. These zygomorphic corollas of *M. exserta* and *M. hispida* have their two-lobed lip and their medial stamen both on the adaxial side of the flower.

In most species of the genus, both before and after anthesis, the corolla stands erect, being borne on strict pedicels at the summit of the straightened portion of the cyme. In *M. hispida* and *M. exserta* the corolla at anthesis, and also as a mature bud, is borne at a relatively higher position on the scorpioid cyme, mostly developing on the curve between its arched summit and the point at which it becomes straight and vertical. Since the pedicels are strict and borne on the curved portion of the cyme, the flowers are directed ascendingly backwards over the arched top of the cyme. The backward direction of the flowers in *M. exserta* is given further accentuation by the marked adaxial curving of the throat and tube. As a combined result of all this, at anthesis the outer parts of the corolla achieve a nearly horizontal position. By leaning backwards over the tip of the cyme the corolla has become resupinate.

The corolla in all species except *M. viridiflora* bears at least scattered stiped glands in the upper parts of the throat and usually also on the adjacent portions of the lobes as well. In *M. leonotis* the salient mouth of the corolla is encircled by a band of glands. In species such as *M. barbigera, M. hispida,* and *M. exserta,* the glands are more scattered, less evident, and may be distributed from above the level of the filament attachments upward onto the lower half of the corolla-lobes. In *M. Pringlei* and less clearly in *M. longiflora* the glands are restricted to obscure congregations associated with small, weak, ill-defined circular or elliptic convexities, one located at or slightly below each of the corolla-lobes. In *M. notata* the association of glands and invaginations is much clearer. In that species there are five inflexed plaits, cuneate in outline, which have their broad end (1–1.5 mm. wide) about 2 mm. below the summit of the throat, and from thence, gradually narrowing, extend outward along the midline of each corolla-lobe with their pointed end about 2 mm. below the lobe apex. Stipitate glands are abundant on these elongate swollen areas but practically absent elsewhere on the corolla. A unique feature of *M. viridiflora* is the presence of minute hairs on the inner surface of the corolla. The corolla is villulose inside the slender tube and may be scantily and minutely strigulose below the middle of the throat along the vein leading from each corolla-lobe. Though hairy the corolla bears no glands.

The corollas of *Macromeria* have no annulus or at most only a weakly developed one ca. 0.5 mm. above the base of the tube. In *M. notata* the annulus is represented by an inconspicuous narrow encircling ridge, and in *M. barbigera* by an obscurely five-lobed one, but in all other species it is obscure or absent. Hairs, these very minute and inconspicuous, were noted in association with the annulus only in *M. leonotis.*

The stamens are affixed in the corolla-throat and within an individual flower are all at about the same distance (4–10 mm.) below the base of the corolla-lobes. In regular corollas the filaments arise at equal distances above the corolla-base. In zygomorphic corollas, however, the throat is prolonged on the adaxial side and the mouth of the throat is oblique. Because the stamen attachments have a fixed relation with the summit of the throat, those on the prolonged adaxial side of the corolla accordingly have a position at a greater distance above the corolla-base than those on the abaxial side. This is the condition in *M. exserta* and *M. hispida.*

The filaments are well developed. In *M. exserta* they may become 70 mm. long, and accordingly are very conspicuously long-exserted from the corolla. The shortest ones (6–9 mm.) occur in *M. notata.* In other species, however, the filaments are mostly 10–20 mm. long. They are clearly exserted from the corolla-throat but do not surpass the corolla-lobes when the latter are in an erect position. In most species the filaments are slightly compressed. In *M. viridiflora,* however, they are strongly so, being strap-shaped, 1.2–1.5 mm. broad just above their base, and then gradually narrowed upwards to become 0.5–1 mm. wide at the apex. In *M. leonotis* the filaments may be sparsely hairy below their middle and sometimes also on their decurrent bases, but in all other species they are always glabrous.

The anthers are elongate and have an oblong outline. They are affixed to the filament at or perceptibly below the middle, usually in an elongate depression in the connective. Although past authors have stated that they are usually versatile, that condition exists, if at all, only in *M. exserta.* In *M. hispida, M. longiflora, M. Pringlei,* and probably *M. leonotis* also, the anther may assume a position at right angles to the filament, but that appears to be the result of a ninety-degree bend of the filament just below its apex. In *M. viridiflora* and apparently also in *M. barbigera* the anthers are strictly and firmly affixed to the filament and are erect. The connective is glabrous in most species, but in *M. viridiflora,* in which the structure reaches its maximum development, it may bear numerous stout hairs on the back side of the anther above the middle. In most species the connective is slightly prolonged to form a minute, usually thickish, truncate or subulate apicule on the broad summit of the anther. In *M. viridiflora* the connective is thickened, apparently glandular, and locally very hairy just below the anther tip. It is not prolonged beyond the thecae. The anthers in this species, accordingly, are emarginate at the tip.

The connective is not only broadest but also most readily observed in *M. viridiflora, M. Pringlei,* and *M. longiflora.* In these species the thecae, after shedding pollen and becoming explanate, are displayed obliquely on the ventral side of the anther. The back side of the anther is nearly plane, and the broad connective and the filament attachment are fully exposed to view. In the five other species of the genus, however, the explanate thecae have reflexed lower halves, and their surfaces become parallel and face left and right in opposite directions. Such mature anthers are strongly compressed laterally. Their back appears to be strongly conduplicate with the narrow connective and the filament attachment hidden in the depth of the fold.

The style is filiform and sufficiently elongate to bear its stigmas commonly about 5 mm. beyond the anthers. The minute stigmas are subterminal, being separated and surpassed by the tip of the style in *M. Pringlei, M. leonotis,* and *M. notata,* but in the other species they are terminal and juxtaposed upon the apex of the style.

As in most other genera of the Lithospermeae, in herbarium specimens I have found the anthers of *Macromeria* dehiscent and the pollen shed in those flower-buds in which the corolla is nearly ready to open. Just previous to the opening of the corolla, the stigma in seven of the eight species is pushing against the very top of the bud-cavity, and hence is above the anthers. The stamens have attained almost full development before the corolla opens. In *M. exserta,* however, the very elongate, eventually long-exserted filaments and style are not completely lengthened before the corolla expands. The filaments have their middle portion lying pressed against the curve of the swollen adaxial side of the outer half of the bud. At the tip of the bud cavity the distal portion of the filaments curves backwards for 180° to 360°. The anthers usually lie within the adaxial half of the most ample part of the bud cavity. The style, shortened by undulate contortions, bears its stigmas appressed against the tip of the bud cavity or against the abaxial side of the cavity close to the tip. In *Echium,* in which elongate filaments and style are also curved and contorted inside the flower bud, the stigmas before the corolla opens may have a position amidst the clustered dehiscent anthers. In the bud of *Macromeria*, however, the stigmas have a position above or beyond the anthers and so decidedly less accessible to any pollen set free in the bud. The stigma is not precociously exserted. It escapes from the flower bud only when the imbricate corolla lobes have begun to loosen — just before the corolla opens, or, in many cases, not until the corolla is almost completely open.

Macromeria has pollen similar to that of *Lithospermum*, and especially like that of the Mexican members of that genus. Each species of *Macromeria* has distinctive pollen with the grains recognizable if not by shape at least by size. Related species agree more closely in the length of their grains than in the form of them.

The pollen bears eight or nine pores in a single row. Its pores are frequently detectable as minute swellings on the outline of the grains when the latter are viewed in lateral profile. Frequently they are sufficiently prominent to give the sides of the grains a somewhat obtusely angled silhouette. The polar profile of the grain is usually circular, and only very rarely are the pores sufficiently evident to produce a vaguely polyhedral outline. Evidences of possible shallow furrows on the grain have been detected only in *M. barbigera*. The pores are equatorial, and the upper and lower halves of the grain are equal in *M. leonotis* (grains globose ellipsoidal, sides angulate, 25–26 × 23 μ), *M. barbigera* (ellipsoidal, sides rounded or angled, 30–33 × 25–28 μ), *M. notata* (ellipsoidal, sides tending to be angled, 28–30 × 23–25 μ), and *M. Pringlei* (ellipsoidal, sides rounded to nearly parallel, 25–26 × 15–18 μ). In two species, *M. exserta* and *M. hispida*, the grains bear the pores very slightly but still perceptibly below the middle. The lower half of the grain has a more evenly and broadly rounded curve than the upper half. *Macromeria exserta* has ovoid-ellipsoid grains (38–41 × 25–28 μ), and *M. hispida* globose-ovoid grains (38–41 × 33–37 μ). The pollen of the two remaining species of the genus is elongate, perceptibly constricted below the middle, and bears its row of pores above its broad rounded base, where its diameter is greatest. Constrictions of the grain begin directly above the row of pores and form "shoulders" of a type previously noted in grains of a similar type in *Lithospermum*, cf. Jour. Arnold Arb. 33: 310 (1952). Such elongate, medially constricted grains are characteristic of *M. longiflora* (25–28 × 16–18 μ) and *M. viridiflora* (28–33 × 18–22 μ). Of these two species with constricted pollen, *M. viridiflora* has no close relatives. *Macromeria longiflora*, however, is obviously most closely related to *M. Pringlei* and species having ellipsoidal grains with equatorial pores. The only agreement is in the length of the grains.

The nutlets of *Macromeria* are smooth, shiny, and usually white, and are symmetric or nearly so and nearly circular in transverse section. In general appearance they closely resemble those of most American species of *Lithospermum*. The venter of the nutlet is only obscurely if at all keeled. The ventral suture may be represented by a very narrow lineate groove (sometimes not half the length of the nutlet) or it may be completely fused and obliterated. It may be present or absent or vary in length not only within the species but also among the nutlets produced by a single plant. The large, nearly circular attachment scar, horizontal or very slightly oblique, is flat or slightly convex and is always distinctly basal. In all species towards its ventral margin the scar bears a prominence composed of the slightly protruding broken end of the well-developed bony tubular funicular canal. In the detached nutlets of *M. viridiflora, M. barbigera,* and *M. notata,* the scar also bears another process, this small and obliquely ascending and apparently representing protrudent tissue about the base of one of the vascular traces leading to the dorsum of the nutlet body. This dorsal prominence on the scar appears to be absent on the nutlets of *M. exserta.* Since thoroughly mature, self-detached nutlets of *M. longiflora, M. Pringlei, M. hispida,* and *M. leonotis* have not been seen, the nature of the scar in these species is unknown. The gynobase in all species is well developed, broadly pyramidal, and terminated by a persisting, more or less thickened four-angulate base of the style. The attachment surfaces of the mature gynobase are usually each encircled by a coarse thickened and elevated cartilaginous margin. When all four nutlets are matured, the gynobase has more or less distinctly sloping attachment faces, and the nutlets they bear, being straight and basifixed, are accordingly divergent.

KEY TO THE SPECIES

Corolla with erect or ascending lobes.
  Back of anthers hairy above the middle; filaments strap-shaped; corolla without glands on the inner surface, villulose in the tube; stigmas terminal on the style .... 1. *M. viridiflora.*
  Back of anthers glabrous; filaments not strap-shaped; corolla glanduliferous in the throat, tube glabrous inside; stigmas usually subterminal, separated by the sterile tip of the style.
    Corolla bearing 5 evident cuneiform plaits, these glanduliferous and extending from below the corolla-lobes upward upon the lobes to beyond their middle .... 2. *M. notata.*
    Corolla without cuneiform glanduliferous plaits, bearing only inconspicuous small circular or elliptical congregations of glands at or below the base of each corolla-lobe; upper face of lobes glandless.
      Upper surface of leaves without evident hairs, abundantly and very minutely verrucose or muriculate and hence at most scabrellous; pollen constricted below the middle and bearing the pores above the rounded base .... 3. *M. longiflora.*
      Upper surface of leaves bearing evident stiff appressed hairs usually arising from evident pallid dot-like bulbose or discoid bases, surface scabrous; pollen ellipsoidal, broadest at the middle, pores equatorial. 4. *M. Pringlei.*

Corolla with lobes reflexed or (in no. 6) loosely recurved.
  Mouth of corolla densely glanduliferous in a continuous band; stigmas subterminal, separated and surpassed by the short sterile apical prolongation of the style .... 5. *M. leonotis.*
  Mouth of corolla not conspicuously glanduliferous; stigmas terminal.
    Corolla-lobes loosely recurved, deltoid, about as long as broad; corolla

regular, symmetric in the bud, stamens all affixed at the same distance above the corolla-base; pollen ellipsoidal, pores equatorial ....6. *M. barbigera.*

Corolla-lobes becoming reflexed, elongate; corolla zygomorphic, asymmetric in the bud, throat oblique, stamens on adaxial side affixed higher than those on the opposite side of corolla; pollen bearing the row of pores slightly below the middle of the grain.

Filaments 10–15 mm. long; corolla 50–55 mm. long; middle stem leaves usually lanceolate; pollen globose-ovoid ....7. *M. hispida.*

Filaments 55–70 mm. long, conspicuously long-exserted; corolla very large, 60–90 mm. long; middle stem leaves oblanceolate; pollen ovoid-ellipsoidal ....8. *M. exserta.*

1. **Macromeria viridiflora** DC. Prodr. **10:** 68 (1846); Sessé & Moc. Calq. Fl. Mex. t. 904 (1874); Johnston, Jour. Arnold Arb. **30:** 110 (1949). Type from Mexico, *Sessé & Mociño.*

Macromeria longiflora sensu Johnston, Contr. Gray Herb. **70:** 14 (1924).

Stems 5–10 dm. tall. Cymes terminal on the stems and frequently geminate and commonly borne also on short leafy branchlets arising from the uppermost axils. Calyx becoming 25 mm. long, largest lobe up to 2.5 mm. broad and the smallest 1–1.5 mm. broad. Corolla greenish yellow, 65–80 (usually 70–75) mm. long, regular or nearly so, outside with abundant appressed and scattered spreading hairs 0.7–2 mm. long, inside sparsely and inconspicuously strigulose along the veins below the lobes and villulose inside the narrow tube, stipitate glands very few or absent, annulus absent or very imperfectly developed. Corolla-lobes triangular-ovate, acute, ascending, 8–10 mm. long, 5–7 mm. broad above the base, usually greenish and sometimes strigose along the middle of the upper surface. Filaments equal, 16–20 mm. long, borne 8–10 mm. below the base of the corolla sinus, broad and strongly compressed, strap-shaped, broadest (ad 1.5 mm.) slightly above the base and then very gradually narrowed towards the apex (ca. 1 mm. wide). Anthers 4–5.5 mm. long, affixed at or slightly below the middle, strictly erect, apex emarginate, base shallowly lobed; connective on upper half of dorsum broad and bearing scattered coarse appressed hairs usually most abundant below the gland at its summit. Pollen elongate, 28–33 $\times$ 18–22 μ, somewhat constricted below the middle, bearing the row of pores where broadest 8–10 μ above the base of the grain. Stigmas two, distinctly terminal. Nutlets 3–3.5 mm. long, with an obscure ventral keel, suture absent or represented by a lineate groove.

Mountains of northern Mexico, in the states of Chihuahua and adjacent Durango, Sinaloa, and Sonora, and extending north into the United States only in the mountains (Chiricahua and Huachuca Mts.) of southeastern Arizona.

1a. **Macromeria viridiflora** var. **Thurberi** (Gray), comb. nov.

Onosmodium Thurberi Gray, Synop. Fl. N. Am. **2**[1]**:** 205 (1878). Type from western New Mexico.

Macromeria Thurberi (Gray) Mack. Bull. Torr. Bot. Cl. **32:** 496 (1905).

Flower smaller than in typical *M. viridiflora.* Calyx becoming 20 mm. long, lobes 1–1.5 mm. broad; corolla 35–50 (usually 40–45) mm. long; filaments 12–14 mm. long, borne 6–8 mm. below the corolla sinus; anthers 3–4.5 mm. long.

Occurring in the mountains from middle eastern New Mexico west to central Arizona in an area to the north of that occupied by typical *M. viridiflora.*

A very well marked species readily recognized by its strap-shaped filaments and dorsally hairy anthers, and also by the villulose inner surface of its corolla-tube.

The typical form of the species has slender, very elongate corollas. Like many other plants of the Sierra Madre Occidental, true *M. viridiflora* has a range that extends north into the Chiricahua and Huachuca mountains, just north of the United States-Mexican boundary, but no further to the northward. Some collections from the Chiricahua and Huachuca mountains are indistinguishable from those of Mexican origin, but others have their flowers somewhat smaller. Even in these latter, however, the corollas are larger than those on plants referable to var. *Thurberi* which occur further northward in New Mexico and central Arizona. The differences in flower size are geographically correlated and sufficiently striking to merit nomenclatorial recognition.

2. **Macromeria notata,** sp. nov.

Planta perennis 4–5 dm. alta e radice valida purpureo-tincta erumpens; caulibus simplicibus foliosis erectis breviter hispidis basim versus ad 5 mm. crassis; foliis numerosis lanceolatis evidenter venosis acutis, eis medium versus caulis gestis majoribus 6–8 cm. longis 16–20 mm. latis, pilos rigidos adscendentis 0.2–1 mm. longos e basi bulboso vel discoideo minuto non rariter pallido erumpentibus proferentibus, facie inferiori pallidioribus venis prominulis ornatis; cyma scorpioidea solitaria caules simplicos terminanti; calyce 15–18 mm. longo, lobis inaequalibus 1–2.5 mm. latis, pedicellis sub anthesi 0–5 mm. longis maturitate 10–15 mm. longis; corolla flavescenti regulariter 50 mm. longa extus hispidula pilis 0.5–1 mm. longis plus minusve curvatis ornata, intus glabra et solum in appendiculis faucium glandulifera; tubo 2–2.5 mm. longo 1–1.5 mm. crasso; annulo anguste annulato; faucibus 1.5–2 cm. longis gradatim ampliatis apicem versus 5–6 mm. crassis; appendiculis faucium depressis elongatis a 2 mm. infra basim loborum corollae sursum fere ad 2 mm. infra apicem loborum corollae prolongatis cuneiformibus leviter invaginatis prominulis dense glanduliferis basi 1–1.5 mm. latis truncatis; lobis corollae triangularibus adscendentibus viridescentibus ca. 5 mm. longis et latis summum ad apicem rotundis secus medium appendiculi faucium glanduliferi decurrenti notatis alibi minute sparseque strigulosis; filamentis 6–9 mm. longis ca. 5–7 mm. infra basim sinuum limbi affixis; antheris 2–2.5 mm. longis rectis apice haud appendiculatis; pollinis ellipsoideis 28–30 $\times$ 23–25 μ, poris 8 secus equatorem dispositis; stigmatibus 2, terminalibus; nuculis 4 mm. longis laevibus albis ovoideis obscure asymmetricis obscure carinatis, late basaliter affixis, cicatrice convexo; gynobase subplano, pulvinis distinctis margine cartilagineis prominulis circumdatis.

MEXICO (Nuevo Leon): Ascent of Sierra Infernillo, ca. 15 miles south of Galeana, 9–10,000 ft., common over small areas just below peak, fl. yellow, June 16, 1934, *C. H. & M. T. Mueller 830* (TYPE, Gray Herb.); canyon below Las Canoas on Cerro Potosi, scattered in dense shade on arroyo bank, July 20, 1935, *C. H. Mueller 2238* (G).

The distinctive features of this species are the weakly invaginate elongate densely glanduliferous plaits which extend from the upper part of the throat out upon each of the corolla-lobes. These glanduliferous plaits are the closest approximation in the genus to the localized well-developed faucal appendages present in many species of *Lithospermum*. In *M. longiflora* and *M. Pringlei* there are small vague convex areas bearing glands at or below each lobe of the corolla, but in other congeners of *M. notata*, even this suggestion of faucal invagination is lacking. The present species is certainly a very distinct one. Its closest relations are possibly with *M. Pringlei* and *M. longiflora*.

3. **Macromeria longiflora** [Sessé & Moc.] D. Don, Edinb. New Philos. Jour. **13**: 239 (1832); Johnston, Contr. Gray Herb. **92**: 93 (1930). Type from Mexico, *Sessé & Mociño*.

Lithospermum longiflorum Sessé & Moc. ex D. Don, Edinb. New Philos. Jour. **13**: 239 (1932), in synonym.
Onosmodium longiflorum (Don) Macbr. Contr. Gray Herb. **49**: 21 (1917).
Lithospermum flavum Sessé & Moc. Fl. Mex. 32 (1893): Johnston, Jour. Arnold Arb. **30**: 109 (1949). Type from Michoacan, Mexico, *Sessé & Mociño*.
Macromeria discolor Benth. Pl. Hartw. 49 (1840). Type from Mexico.
Onosmodium discolor (Benth.) Macbr. Contr. Gray Herb. **49**: 20 (1917).

Cymes terminal on the stems and frequently also arising directly from the uppermost axils. Calyx 13–15 mm. long, lobes slender, 1–1.5 mm. broad, unequal. Corolla 45–55 mm. long, regular or very obscurely prolonged on the adaxial side, outside clothed with slender spreading or loosely appressed hairs up to 1 mm. long, inside bearing inconspicuous elliptic congregations of glands on obscurely convex areas below each corolla-lobe and sometimes glands also along the decurrent base of the filaments, annulus not developed. Corolla-lobes elongate, lance-oblong, acutish or the tips obtusish, 11–15 mm. long, 4–7 mm. broad, ascending, upper face without hairs or glands. Filaments 14–15 mm. long, affixed ca. 4 mm. below limb-sinus, anthers 2–4 mm. long, affixed at or near the middle, erect, apex minutely appendaged. Pollen elongate, $25–28 \times 16–18\ \mu$, constricted below the middle, broadest and bearing the row of pores about $8\ \mu$ above the base. Stigmas 2, usually subterminal. Nutlets ovoid, erect, symmetric, 4 mm. tall, 3 mm. thick.

Mountains of western Mexico from Colima to Oaxaca.

A species probably most closely allied to *M. Pringlei*, from which it differs in its more herbaceous stems and its larger leaves devoid of evident hairs on the upper surface. Although at first glance the upper leaf face appears to be smooth and glabrous, close examination under the microscope shows it to be actually dotted with minute mineralized warts or conic muriculations. When the minute roughenings are pointed, the surface may be perceptibly scabrellous. The minute mineralized roughenings on the leaf of *M. longiflora* are evidently homologous with the very much coarser bulbose or discoid hair bases present on the upper leaf face of *M. Pringlei.* The lower face of the leaves in *M. longiflora* is strigose with an abundance of short, stiff, closely appressed hairs. It is usually cinereous and contrasts very strongly with the upper surface, which in most herbarium specimens dries a chocolate brown.

4. **Macromeria Pringlei** Greenm. Proc. Am. Acad. **34**: 570 (1899). Type, Sierra de Pachuca, Hidalgo, *Pringle 11044.*

Onosmodium Pringlei (Greenm.) Macbr. Contr. Gray Herb. **49**: 20 (1917).
Macromeria guatemalense Johnston, Jour. Arnold Arb. **29**: 232 (1948). Type, Volcán Tajumulco, dept. of San Marcos, Guatemala, *Steyermark 35898.*

Cymes terminal on the stems and frequently also terminating short axillary branches arising from the uppermost axils. Calyx 12–15 mm. long, lobes slender, 0.5–1.2 mm. wide. Corolla pale yellow-green, 35–53 mm. long, regular, straight, outer surface bearing slender ascending hairs ca. 1 mm. long, inside glabrous bearing very scattered glands, or these only in very vague slightly swollen areas at or below the base of the corolla-lobes. Corolla-lobes triangular, acute, erect or ascending, 9–10 mm. long, 5.5–7.5 mm. broad, apex obtusish, upper face usually without hairs or glands. Filaments 9–12 mm. long, equal, affixed in the throat 3–4 mm. below the base of the corolla sinus. Anthers 2–3.5 mm. long, medio-affixed, apex minutely appendaged. Pollen ellipsoidal, sides rounded or nearly parallel, $25–26 \times 15–18\ \mu$. Stigmas 2, subterminal. Nutlets erect, symmetric, pointed, ca. 4 mm. tall, 3–3.5 mm. thick, without a ventral keel.

Mountains of Mexico in the states of Hidalgo, Guerrero, and Oaxaca.

Closely related to *M. longiflora* but a less vigorous plant with more slender fruticulose stems and smaller, usually more elongate leaves bearing evident appressed hairs on the upper surface. *Macromeria guatemalense* of northern Guatemala appears to differ from Mexican *M. Pringlei* only in its more elongate, more decidedly fruticose stems and smaller (to 35 mm. long) corollas. Possibly it may represent a southern variety of *M. Pringlei,* but hardly a species distinct from it.

5. **Macromeria leonotis** Johnston, Jour. Arnold Arb. 16: 188 (1935). Type, ascent into Taray, Sierra Madre ca. 15 mi. s.w. of Galeana, Nuevo Leon, *Mueller 754.*

Cymes terminal on the stem. Calyx 19–25 mm. long, lobes unequal, very slender, 1–1.5 mm. wide. Corolla yellow, 55–75 mm. long, slightly zygomorphic, straight or somewhat curved, outside hispidulose-villulose, densely clad with short curly hairs 0.3–0.7 mm. long, inside glanduliferous on the lower part of the lobes and over the upper half of the throat and most abundantly so in a band at the throat summit; annulus a very narrow interrupted ring bearing five groups of short, very inconspicuous hairs. Corolla-lobes triangular-oblong, 7–12 mm. long, 5–8 mm. wide, becoming reflexed, apex rounded, upper surface minutely strigulose or rarely glabrous, glanduliferous at the base. Filaments 14–20 mm. long, compressed, affixed 7–8 mm. below the corolla sinus, sometimes hairy below the middle and on the decurrent base. Anthers 2–3.5 mm. long, affixed just below the middle, apex minutely appendaged. Pollen broadly globose-ellipsoidal, sides angulate, 25–26 $\times$ 23 μ, pores 8, equatorial. Stigmas apparently subterminal. Nutlets not seen.

Mountains of northeastern Mexico in states of Nuevo Leon and Tamaulipas.

A species notable for its short soft indument and abundantly glanduliferous summit of the corolla-throat. The corolla appears to be slightly zygomorphic, being somewhat curved and perhaps also slightly prolonged on the adaxial side. The elongate lobes are strongly reflexed at the base and the opening into the throat is accordingly the most forward part of the corolla. The rounded lip surrounding this opening to the throat is densely glanduliferous. Some glands are present on the lower part of the corolla-lobes and also inside the throat down at least to the level of the stamen attachments, but only on the lip about the opening into the throat are they extremely abundant. No other species of the genus has corollas with glands so numerous. The species is a very distinct one, but seems to share more characters with *M. longiflora* and *M. Pringlei* than with other congeners.

6. **Macromeria barbigera** Johnston, Jour. Arnold Arb. **16**: 189 (1935). Type, slope of Sierra Tronconal, ca. 15 mi. s.w. of Galeana, Nuevo Leon, *Mueller 741*.

Cymes terminal on the stem and also arising from the uppermost leaf axils. Calyx 15–20 mm. long, lobes very slender, 1–1.5 mm. broad, unequal. Corolla ("cream-white" but when dry with a distinctly reddish throat and somewhat greenish lobes) 45–65 mm. long, regular, with a very slender tube 15–30 mm. long which abruptly expands into a cylindric throat that is 20–30 mm. long, 5–10 mm. thick, and sometimes perceptibly broadest below the middle, outer surface of corolla villose, the hairs slender, white, and 2–3 mm. long, inner surface glanduliferous above the level of the filament attachments and especially so on the upper face of the lobes, annulus an interrupted ring. Corolla-lobes deltoid, 4–5 mm. long, loosely but distinctly recurved especially beyond the middle. Filaments 12–15 mm. long, affixed 8–10 mm. below the base of the corolla sinus. Anthers 2–3 mm. long, medio-affixed, apex minutely appendaged. Pollen ellipsoidal, sides rounded or angled, 30–33 $\times$ 25–28 μ, pores 9, equatorial. Stigmas terminal. Nutlets ellipsoidal to ovoid, 3–3.5 mm. long.

Northeastern Mexico in the mountains of Nuevo Leon and Tamaulipas.

A very distinct species notable for its coarse habit, bristly indument, and broad leaves, as well as for the form of its large corollas. The corollas have a very slender tube, an abruptly expanded elongate throat, and loosely recurved deltoid lobes glanduliferous on the upper surface. The immediate relatives of the species are obscure.

7. **Macromeria hispida** Mart. & Gal. Bull. Acad. Brux. **11**: 339 (1844). Type, near Morelia, Michoacan, *Galeotti 1917*.

Macromeria longiflora var. *hispida* (M. & G.) A. DC. Prodr. **10**: 68 (1846).
Onosmodium longiflorum var. *hispidum* (M. & G.) Macbr. Contr. Gray Herb. **49**: 21 (1917).
Macromeria longiflora sensu DC. Prodr. **10**: 68 (1846).

Cymes terminal and commonly also arising directly from a number of the uppermost axils to form an elongate thyrse. Calyx with very unequal lobes, the abaxial one largest and becoming 18–22 mm. long and 1.5–2.5 mm. broad. Corolla yellow, 50–55 mm. long, zygomorphic, usually somewhat curved and the throat prolonged on the adaxial side, in the bud thickly clavate with the outer half swollen and evidently more rounded on the adaxial side, outer surface of corolla bearing numerous ascending or loosely appressed hairs 0.5–1 mm. long, inside bearing scattered inconspicuous slender gland-tipped hairs in the throat above the stamen attachments and also on the upper face of the lobes; annulus not developed. Corolla-lobes equal, elongate, ovate-elliptic, 8–10 mm. long, 6–7 mm. broad below the middle, becoming reflexed, apex rounded, margins revolute. Filaments equal, 10–15 mm. long, affixed at slightly unequal heights above the corolla base, the medial adaxial filament ca. 2 mm. higher than the abaxial pair and ca. 1 mm. above the adaxial pair, all attached 4–5 mm. below the oblique summit of the throat. Anthers 2–3 mm. long, affixed slightly below the middle, erect, apex frequently bearing a slender minute appendage. Pollen globose-ovoid, 38–41 $\times$ 33–37 μ, upper and lower halves of the grain slightly unequal, pores eight in a row and borne slightly below the middle. Stigma terminal. Nutlets not seen.

A Mexican plant known only from the state of Michoacan, especially near Morelia and Patzcuaro.

In floral organization this species most resembles *M. exserta*, but in general habit it is more suggestive of *M. Pringlei* and *M. longiflora*.

8. **Macromeria exserta** D. Don, Edinb. New Philos. Jour. 13: 239 (1832); Lindley, Bot. Reg. **33**: t. 26 (1847). Type from Mexico, *Sessé & Mociño*.

Echium longiflorum Sessé & Moc. Pl. N. Hisp. 20 (1888); Johnston, Jour. Arnold Arb. **30**: 109 (1949).
Macromeria exserta var. *imparata* Macbr. Contr. Gray Herb. **49**: 22 (1917). Type from Oaxaca, 1842, *Ghiesbreght*.

Cymes terminal and commonly also arising from the uppermost axils to form a loose thyrse. Calyx 20–30 mm. long, lobes very unequal, 1–7 mm. broad. Corolla very large, 60–90 mm. long, yellow, zygomorphic, with the tube curved and the throat prolonged on the adaxial side, in the bud with its thickened distal half conspicuously distended on the adaxial side, outside of corolla bearing abundant spreading hairs usually ca. 0.5 mm. long, inner surface of throat and lobes bearing scattered, usually inconspicuous slender gland-tipped hairs; annulus not developed. Corolla-lobes elongate, equal, 15–28 mm. long, 5–8 mm. broad, becoming reflexed, apex rounded or obtusish, margins revolute. Filaments very slender, elongate and long-exserted, 55–70 mm. long, usually curved, affixed in the corolla-throat 4–5 mm. below its oblique summit at three superimposed levels, the odd medial stamen 5–8 mm. higher above the corolla base than the abaxial pair and 3–4 mm. above the adaxial pair. Anthers 3–4 mm. long, frequently curved, affixed below the middle, becoming versatile, apex usually bearing a minute appendage. Pollen ovoid-ellipsoidal, 38–41 $\times$ 25–28 μ, upper and lower halves of grain slightly dissimilar, pores 8, slightly inframedial. Stigmas terminal. Nutlets 4–5.5 mm. long, 2.5–4.5 mm. thick, weakly keeled.

Mountains of western Mexico from Nayarit to Oaxaca.

A very distinct species notable for its very coarse habit and extremely large zygomorphic corollas with excessively long-exserted stamens. Because of the curved adaxially swollen buds and the eventually long-exserted curved stamens the corolla has a form and appearance more suggestive of some of the Verbenaceae, e.g., *Clerodendron*, than of other members of the Boraginaceae. In size the corolla of *M. exserta* surpasses that of all other species in the whole of the Boraginaceae.

2. **Onosmodium** Michx. Fl. Bor. Am. **1**: 132, t. 15 (1803). Based upon *O. hispidum* Michx. [= *O. virginicum* L.] and *O. molle* Michx.

Osmodium Raf. Med. Repos. N. Y. **5**: 353 (1808); Merrill, Index Raf. 203 (1949). A substitute name for *Onosmodium* Michx.

Purshia Spreng. Anleit. ed. 2, **2**: 450 (1817); Lehm., Asperif. **2**: 382 (1818). A substitute name for *Onosmodium* Michx.

Osmidium Walp. Ann. **3**: 134 (1853). Apparently a printers' mistake for *Onosmodium* Michx.

Plants perennial, with few to many frequently coarse, erect stems, strigose or more commonly hispid, glanduliferous in one species only, simple or bearing ascending leafy fertile branches above the middle. Leaves mostly cauline, numerous, bearing several pairs of strong assurgent veins; lowest leaves usually larger and more elongate than the middle and upper ones, usually shed before the time of flowering, persisting in only a few species. Cymes scorpioid, single or paired, borne terminal on the main stem and its branches, usually many-flowered, at first dense and coiled and later in the fruiting condition becoming straight, greatly elongate, and loosely flowered. Bracts numerous, one adjacent to each flower, lanceolate to ovate, becoming large and conspicuous in age, foliaceous. Calyx 5-fid; lobes attenuate or broadly linear or slightly spathulate, acute to obtuse or rounded at the apex, usually evidently unequal, after maturity of the fruit usually disarticulating at the base. Pedicels short to elongate. Corolla opening (and its style exserted and its anthers mature) while incompletely developed. Mature completely developed corolla white to cream or yellow, usually with the lobes more or less green or greenish, subtubular, two to three times as long as broad, regular, straight; outside hairy, usually strigose or with appressed hairs; inside glabrous (or a few hairs near the tip of the lobes in one species), without any glands or true faucal appendages; annulus evident, consisting of a narrow flange or ten lobules, glabrous; throat usually about twice the thickness of the corolla-base, broadest (and in lateral silhouette somewhat angulate) a short distance below its summit, bearing ten externally protrudent gibbose convexities, five below the base of the corolla-sinus and five lesser ones below the corolla-lobes. Corolla-lobes nearly one half to nearly one fifth (but most commonly about one third) the total length of the corolla, erect, more or less elongate, very narrowly imbricate in the bud, cuneate or triangular or ovate-triangular with the apex acute or acute with an attenuate tip; sinus between the lobes narrow, acute, thickened and inflexed at the very base. Stamens borne at equal heights in the thickest part of the throat, affixed at or distinctly above the middle of the corolla; filaments short, usually somewhat unguiculate, one third the length of the anthers or less; anthers oblong-lanceolate, with their tips reaching up to or slightly beyond the base of the corolla-sinus, affixed between the base and the middle usually at about one third of its total length above its base; apex of anther bearing a minute appendage (appendage semicircular or quadrate or three-lobed or sometimes attenuate, composed of prolongations of the thecae and the narrow connective, with the portion prolonged from the connective frequently darkened and perhaps glandular); base of anther emarginate or lobed, reaching downward in the corolla-throat to or distinctly below the point of attachment of the filaments; connective narrow, glabrous; thecae below the anther attachment distinct and usually spreading, their basal tips very obscurely if at all thickened. Pollen small, 16–24 $\times$ 13–22 μ, ovoid to globose-ovoid, lower half rounded more broadly and evenly than the upper half, always longer than broad, though at times only slightly so; pores inframedial, six or seven in a single row, usually obscure; grains in polar profile circular or rarely somewhat polygonal. Style filiform, precociously long-exserted, emerging from the incompletely developed corolla when the latter has not yet attained half of its eventual size; stigmas two, minute, terminal on the style. Ovules four but usually only one maturing and very rarely more than two. Nutlets ovoid or ellipsoidal, white or tawny, lustrous, smooth or pitted, gradually narrowed to the base or sometimes with a suprabasal constriction, nearly circular in transverse section, lacking a prominent ventral keel or any evidence of a ventral suture; attachment-scar flat, basal, nearly as broad as long, towards ventral edge bearing the slightly prominent broken end of the bony tubular funicular canal and towards the dorsal edge a small, attenuate, obliquely ascending prominence representing a thickening of scar tissue about the base of a vascular strand leading to the dorsum of the nutlet body. Gynobase depressed, nearly flat, attachment surface plane, distinct, lacking strongly thickened upturned margins.

A genus confined to middle and eastern sections of the United States and to northeastern Mexico. Most authors have recognized seven species within the United States, cf. Mackenzie, Bull. Torr. Bot. Cl. **32**: 495–506 (1905); Johnston, Contr. Gray Herb. **70**: 17–18 (1924); and Fernald, Manual Bot. 1200–1201 (1951). Two additional species are endemic to northeastern Mexico. Of the total only four are sharply definable and always positively recognizable, viz., *O. unicum* Macbr. and *O. dodrantale* Johnston of Mexico, *O. Helleri* Small of Texas, and *O. virginianum* (L.) DC. of the eastern border of the United States. The other five "species" intergrade and are incapable of sharp definition. There is *O. hispidissimum* Mack., ranging in the Ohio Valley and the Middle Atlantic States, *O. occidentale* Mack., widespread in the region between the Mississippi River and the Rocky Mountains, and *O. bejariense* DC., confined to Texas. These three are habitally similar and obviously related, and over the larger portion of the area in which they are found they seem relatively constant in their characters. Another group of related plants is practically confined to Tennessee, Kentucky, Arkansas and Missouri. These have slender stems and an indument usually closely appressed and frequently scanty. Representative of them are *O. molle* Michx. and *O. subsetosum* Mack. Embarrassing transitional forms between these two groups, as well as between their members, appear to be frequent in Missouri, Iowa, and Illinois, where the ranges of the various species converge or even overlap. Analysis will probably reveal evidence of much hybridization and intragression affecting *O. hispidissimum*, *O. occidentale*, and *O. molle* in that area.

The genus has general relations with *Macromeria* and *Lasiarrhenum* but is more closely related to the American and particularly to the Mexican species of *Lithospermum* and, along with the two genera mentioned, is probably derived from them. It is a sharply defined and thoroughly natural group readily recognizable by a number of strong characters. Particularly noteworthy are its precociously sexual flowers. In these the anthers mature and the style becomes long exserted in corollas that have opened before they have attained half their eventual size. The subtubular corolla is also distinctive in having very narrowly imbricate, erect, sharply acute or acuminate corolla-lobes and sinuses between the lobes which are distinctively thickened and inflexed at the very base. The corolla-throat may have five to ten gibbose swellings outside, but inside is devoid not only of faucal appendages but also of any hairs or glands. The included glabrous anthers are attached between base and middle to very abbreviated filaments and are appendiculate at the apex and lobulate at the base.

Most of the species commonly referred to *Onosmodium* are obviously congeneric. To be excluded, however, are *O. revolutum* (Robins.) Macbr., Contr. Gray Herb. **49**: 21 (1917), the type of the genus *Psilolaemus*, and *Onosmodium strigosum* (HBK.) Don, the type of the genus *Lasiarrhenum*. Gray, Synop. Fl. Am. 2 [1]: 205 (1878), and later Macbride, Contr. Gray

Herb. 49: 19 (1917), have suggested that all species of *Macromeria* except *M. exserta* should be accommodated in an enlarged *Onosmodium*. Justification for this apparently rests solely on general vegetative similarities and in the fact that corolla-lobes of *Macromeria* may be acute. In size, form, and behavior of the corolla and in structures inside the corolla the species of *Onosmodium* are extremely different from those of *Macromeria*. Indeed, the two genera differ more from each other than they do individually from *Lithospermum*. If generic values are not to be lowered, *Onosmodium* and *Macromeria* must be kept distinct.

In the Mexican *O. dodrantale*, the plant not only has very short stems, 1–3 dm. long, but also has the leaves smallest at the base of the stem and gradually increasing in size upward along it. In the other species of the genus, all of them with much longer stems (usually 5–12 dm.), the leaves at the base of the stem are larger and more elongate than those on its middle sections. The indications are that the stems elongate from the center of a winter rosette of leaves and not directly from a bud on the caudex, as in *O. dodrantale* and in most species of *Lithospermum*. The large lowermost leaves have usually fallen away in herbarium specimens of most species. Indeed, only in those of *O. bejariense* and *O. Helleri* are they commonly found dried up and still persisting in some numbers crowded at the base of the stem. In most species the foliage has reached full size and has become firm before anthesis. This is not the case, however, in *O. Helleri*. In that species the plant flowers while it is still growing vigorously and before it has attained full stature and the upper leaves have attained their maximum size and mature firmness. Plants of *O. Helleri* at anthesis and those maturing fruit have a very different appearance. In fruiting plants of this species the bracts become unusually large and conspicuous.

The cymes in *O. dodrantale* are weakly developed and hardly more than three- to six-flowered bracteate glomerules terminating the short stems. In the other species of the genus, however, they are distinctly scorpioid and abundantly flowered and eventually become straight, extremely elongate, and very loose at extreme maturity. The flowers maturing their corollas are borne crowded on the arched summit of the cyme, those with completely grown corollas just above the point where the rachis begins to straighten. Since the pedicels are strict, the corollas incline backwards towards the summit of the cyme, and those near its summit become nearly horizontal. After the corolla is shed the rachis straightens, its internodes elongate, and the abundant bracts, previously inconspicuous, increase in size and become very conspicuous.

The indument on the herbage may be either strigose or bristly. *Onosmodium subsetosum* is unusual in having the stems glabrous or nearly so. A very distinctive feature of the Mexican *O. unicum* is the presence of very slender multicellular, gland-tipped hairs intermixed among the stiff ascending hairs on the leaves, stems and rachis of the cyme and even on the calyx. I know of no other American herbaceous borage having generally distributed hairs of this type.

The flowers of *Onosmodium* are precociously sexual. The corolla opens and its anthers are matured and its style is exserted long before the corolla has attained full size, commonly when it is less than half its eventual size or even sufficiently elongate to surpass the calyx. In this behavior of the corolla the genus differs from all other American Boraginaceae, and among the Lithospermeae, at least, has a parallel only in the monotypic *Halacsya* of Albania and Montenegro, cf. Jour. Arnold Arb. **34**: 276 (1953). On the densely flowered arched summit of the scorpioid cyme in *Onosmodium*, as in *Halacsya*, the styles are to be seen projecting not merely from the fully developed conspicuous corollas but also above the latter from a series of gradually less well developed corollas on younger and higher parts of the cyme. The style may first emerge when the corolla is so small as to be overtopped by its calyx lobes. When the corolla is sufficiently large to equal or slightly surpass the calyx, the style is long exserted, the corolla-lobes have unfolded completely, and the anthers have attained nearly full size and in herbarium specimens are dehiscent. At this stage, above the level of the filament attachments the corolla is approaching mature form and has attained about seventy-five per cent of its eventual size. Below the level of the filament attachments, however, growth has lagged, for the tube is still very short and scarcely developed. It is after the corolla opens and the anthers and style are exposed and functioning that the tube elongates and increases in diameter and the corolla achieves full size and mature proportions. The early emergent, eventually long exserted style evidently makes self-pollination in this genus practically impossible. How the corolla may function in pollination during the period in which it doubles its size after opening and maturing its anthers is a subject deserving investigation.

The fully developed corolla in this genus may be 8–12 mm. long, as in *O. virginianum* and *O. hispidissimum*, or as much as 12–18 mm., as in *O. occidentale*. From a base 1.5–2.5 mm. thick they gradually expand upwards to just below the summit of the tube where they are broadest, ca. 4 mm. in *O. virginianum* and 6–7 mm. in most other species. The lobes are a third to a fifth (usually about a third) the total length of the corolla. They are cuneate to triangular or ovate-triangular, and from the base or just above it contract with straight convergent sides to the sharp apex, which is acute or sometimes (in *O. unicum*) acute with an attenuate tip. The lobes, except near the very margin (i.e., on all surfaces exposed while folded in the bud), have their outer face hairy, as elsewhere on the outside of the corolla. The inner face of the lobes is usually completely glabrous. Indeed, the only exception is in the corolla of *O. dodrantale*, which is unique in having the inner surface of its lobes always inconspicuously hairy just below their tip. In the bud the lobes are imbricate very narrowly and only sufficiently to produce a very narrow glabrous margin, narrowing upward, on the dorsum of each lobe. It is this very narrow imbrication of the lobes, becoming negligible towards the tip of the bud, that facilitates the early egress of the precociously elongating style that has pushed upwards inside the very immature flower bud.

The base of the acute sinus between the erect corolla-lobes is distinctly plicate, inflexed, and thickened. A somewhat similar condition occurs in the flowers of some species of *Heliotropium*, but among the Lithospermeae in no other genus save *Onosmodium* is it present or at least so well developed. In most species the corolla is locally distended outwardly by convex gibbose swellings, one directly below the plicate base of each sinus. These gibbosities make the corolla more or less five-angled just below the summit of the throat where it is broadest. Gibbosities of a similar sort may also be present below the base of each corolla-lobe and alternate with those below the sinus, but are usually less conspicuous than the latter. Inside the corolla-throat, except for the inflexed bases of the sinus, there are no intrusive appendages or invaginations. Faucal appendages and stipitate glands, common features in the corolla-throat of other Lithospermeae, are completely absent. Pubescence of any sort is also absent inside the corolla, even on the annulus. The annulus is clearly developed, either as a narrow thickish continuous flange or as ten lobes.

The anthers, 2.5–3.5 mm. long, are attached to a very short filament at about a third of their length above their base, and hence very definitely below their middle. The filaments, a third the length of the anther or less, are attached in the corolla commonly about 2 mm. below the summit of the throat. The anthers, accordingly, usually reach up to about the base of the sinus above them or at most have their tips only a millimeter beyond. The base of the anther projects downward to the same level as the attachment of the filament on the walls of the throat or slightly below it. In the lower quarter of the anther the thecae are not united. They may remain parallel and the base of the anther appear emarginate, but usually, particularly in age, they tend to spread, making the anther lobulate at the base. The thecae are only slightly narrowed above the middle. The anther is always minutely appendiculate at the apex. The very diminutive appendages appear to be formed not merely by a prolongation of the narrow connective but also by apical prolongations of each theca. These parts may be confluent or distinct. The appendage is variable in form within the species, and even according to the age of the anther bearing it. It may be three-pronged, it may be quadrate with either truncate or toothed summit, or occasionally, in *O. dodrantale* and *O. unicum*, subulate or lanceolate. In *O. virginianum* the anther summit may be even broadly emarginate and the thecae each tipped by a minute appendage and distinct from the third small appendage arising from the depth of the sinus between them.

The pollen of the various species of *Onosmodium* differs slightly in size but very little in shape. It is ovoid, or at times, even in the same species, very broadly so and even globose-ovoid in form. The grains are always perceptibly longer than broad with the upper and lower half differing to some degree in outline. In lateral profile the pores are at most very weakly protrudent. Usually they are very obscure. They are borne in a single row perceptibly below the middle of the grain and are usually six but not infrequently seven in number. In polar profile the grains are almost invariably circular in outline. The size of the grain seems to be roughly correlated with corolla-size. Species with large flowers usually have grains larger than those in species with small flowers. Small-flowered *O. virginianum* produces the smallest pollen, 15–18 × 13–16 μ. In *O. subsetosum*, *O. molle*, *O. hispidissimum*, and *O. Helleri* the grains measure 16–18 × 15–16 μ, in *O. unicum*, 16–22 × 15–18 μ, in *O. occidentale*, 18–22 × 16–20 μ, in *O. bejariense*, 20–22 × 16–20 μ, and in *O. dodrantale*, 22–24 × 20–27 μ.

As in the case of all genera of the Lithospermeae previously examined, pollen production in *Onosmodium* was found to be prevailingly normal and abundant, with imperfect pollen very scanty and infertile anthers rare. Worthy of note, therefore, is the fact that the reverse condition seems prevalent in *O. occidentale* over the northern parts of its range, in the northern Plains and adjacent Rockies. The species deserves cytological examination.

The nutlets of the genus are generally similar to those of *Lithospermum*. Unlike those of *Macromeria* their ventral suture is always closed and completely obliterated. There is no appreciable ventral keel. Although the ovary is four-ovulate, flowers of the genus seldom mature more than a single nutlet. Only in *O. occidentale* are the exceptional fruits, frequently present in limited numbers, found to be maturing two nutlets. In that species fruit with three nutlets may be encountered very rarely, but none with four nutlets have been found. Accordingly I have not seen a symmetrically developed gynobase. In those maturing one to three nutlets, the attachment faces are nearly horizontal and plane or nearly so. The faces are not concave, nor do they have strongly thickened upturned margins as in *Macromeria*. The attachment scar on the nutlet is flat, not convex as in *Macromeria*, but, like the scar in that genus, it does bear a projecting end of the broken tubular funicular canal, and also another more dorsal projection in the form of an obliquely ascending protuberance.

3. **Nomosa**, gen. nov. Lithospermeae.

Planta perennis herbacea strigosa. Caules hornotini erecti simplices foliosi ut videtur e caudice ex caulibus vetustis 3–4 mm. crassis procumbentibus laxe ramosis composito orientes. Folia breviter strigosa cinerea vel plus minusve argentacea supra basim triplinervia. Folia basalia oblanceolata in fasciculos steriles aggregata. Folia caulina numerosa sessilia a basi caulis sursum gradatim majora, superiora anguste oblonga vel lanceolato-oblonga apice acuta vel plus minusve obtusa. Cymae terminales geminatae laxe scorpioideae pauciflorae tandem rectae racemosae. Bracteae numerosae foliaceae haud conspicuae calycem haud superantes. Flores sub anthesi in parte curvato supremo symae gesti erecti vel horizontales vel declinati. Calyx 5-fidus; lobis evidenter inaequalibus firmis costatis elongatis linearibus vel cuneatis. Pedicelli crassiusculi stricti modice elongati. Corolla ut videtur alba regularis crasse tubularis, calyce subduplo longior, a basi sursum lente gradatimque ampliata (haud faucibus distinctis donata) in tertia parte superiore crassissima, triplo longior quam lata, extus dense breviterque strigosa, intus inter basis decurrentis filamentorum pilis gracilibus glanduliferis praedita alibi glabra; faucibus nec appendiculas nec glandulas stipitatas proferentibus; lobis imbricatis parvis quam longitudine corollae 10-plo brevioribus erectis late ovatis infra medium latissimis basi aliquantum contractis tam longis quam latis vel paullo latioribus quam longis; annulo nullo. Filamenta angusta elongata sursum gradatim attenuata crassiuscula, in quarta parte inferiore corollae affixa, supra medium teretia et glabra, infra medium plus minusve compressa et pilis gracilibus glanduliferis abundanter donata, basi breviter decurrentia incrassata pilis glanduliferis vestita. Antherae elongatae lanceolatae, supra basim affixae, filamentis duplo breviores, in parte suprema tubi corollae gestae, basim versus latissimae deinde sursum gradatim angustatae, appendiculis sterilibus pallidis gradatim attenuatis e tubo corollae exsertis sed lobos corollae haud superantibus terminatae, dorso connectivum pallidum laeve latum (latitudine quam antheram triplo angustius) pilis paucis (1–4) rigidis valde adpressis praeditum proferentes; thecis basim versus distinctis sed parallelis infra medium apicem versus angustatis, basi imo acutiusculis apiculo inconspicuo incrassato donatis sed nullo modo appendiculatis. Granulae pollinis late ovoideae 25–28 $\times$ 21–23 μ infra medium latissimae et ibi 7 vel 8 poris obscuris instructae, a latere visae late ovatae ca. 8 mm. supra basim semicircularem latiores deinde sursum per margines rectos convergentes in apicem latum abrupte rotundum contractae. Stylus gracilis glaber tandem evidenter exsertus; stigmatibus 2 distinctis terminalibus. Nuculae ignotae. — Nomen a *Onosma* litteris interversis desumptum.

Nomosa Rosei, sp. nov.

Planta 25–30 cm. alta; caulibus erectis basim versus ad 3 mm. crassis pilis rectis antrorsis laxe adpressis ad 1 mm. longis vestitis, internodiis brevibus ca. 5 mm. longis; foliis strigosis (pilis valde adpressis rectis 0.2–0.6 mm. longis), margine inconspicue ciliolatis (pilis strictis vel adscendentibus 0.5–1 mm. longis), costa 10–20 mm. supra basim nervos 2 assurgentes validos conspicuos perelongatos proferenti donatis; foliis basalibus 40–60 mm. longis supra medium 8–12 mm. latis; foliis caulinis superioribus 40–55 mm. longis medium versus 8–10 mm. latis; cymis ca. 10-floris maturitate rectis ad 8 cm. longis; lobis calycis strigosis margine hispido-ciliatis, sub anthesi 8–11 mm. longis tandem 10–15 mm. longis, lobo majore 1–3 mm. lato quam lobis minoribus 3–5 mm. longiore; pedicello sub anthesi 3–5 mm. longo tandem ad 8 mm. longo recto; corolla 20 mm. longa a basi 2–3 mm. crasso sursum gradatim expansa, 5 mm. infra basim loborum 7 mm. crassa, apice (basi ima loborum) ca. 6.5 mm. crassa; lobis corollae 2 mm. longis medium versus 2–2.5 mm. latis, basi ima 2 mm. latis; filamentis 9.5–10 mm. longis, 5 mm. supra basim corollae orientibus, basim versus 1 mm. latis, apicem versus ad 0.5 mm. latis, infra medium pilos 0.5 mm. longos proferentibus; basi decurrente filamenti incrassato 2–3 mm. longo ca. 0.8 mm. lato pilis glanduliferis vestito; antheris 5 mm. longis ca. 1.4 mm. supra basim affixis, thecis 3.5 mm.

longis basi 3–3.5 mm. infra basim loborum corollae gestis; appendiculo terminali antherae 1.5 mm. longo imam ad basim ca. 0.5 mm. lato; stylo 23–25 mm. longo.

MEXICO: in Sierra Madre near the southern border of the state of Durango, Aug 16, 1897, *J. N. Rose 2360* (TYPE, Gray Herb.).

This remarkable plant is known only from a collection made over a half-century ago by J. N. Rose during his first expedition to Mexico. In general appearance it mimics *Onosma* to a remarkable degree. The original collection was distributed with locality data given merely as "Durango." Accepted as a member of the large and diverse Old World genus *Onosma*, and believed to have been introduced into Mexico, presumably at Durango City, the plant attracted no careful study, particularly since no plant similar to it was subsequently found in America. Only recently, when it was dissected and carefully compared during a study of *Onosma* and related genera, were the very many distinctive features of this neglected Mexican plant fully recognized. Upon investigation it was found that the specimens were made not at Durango City, but rather in the Sierra Madre, ca. lat. 22° 15′ N., at the extreme southern end of the state of Durango, in a wild and infrequented area. It was discovered by Rose when on horseback and with pack-animals he journeyed through Nayarit across the southern tip of Durango and on eastward into Zacatecas, crossing the Sierra Madre in a section not subsequently visited by a botanist. Our plant is apparently endemic in the mountains of this particular region.

Although extremely suggestive of *Onosma* in external features, *Nomosa* is actually a very close ally of the Mexican *Lasiarrhenum*. Its affinities are with such American genera as *Lasiarrhenum*, *Macromeria*, and *Onosmodium*, which appear to be derivatives of American *Lithospermum* rather than of the strictly Old World *Onosma*. Along with *Lasiarrhenum*, *Nomosa* is distinguished from *Onosma* by its 7–8-porate pollen, unequal calyx-lobes, triple-nerved leaves, and free anthers with hairy connectives. From *Lasiarrhenum* it differs in having very elongate gradually narrowed filaments which are attached very low in the corolla and, below the middle, are densely clothed with an abundance of slender elongate multicellular gland-tipped hairs. The anthers, only half as long as the filaments, are carried higher in the corolla and have their elongate terminal appendage exserted from the mouth of the corolla. Unlike the anthers of *Lasiarrhenum*, which are abundantly and conspicuously hairy on the back, those of *Nomosa* bear only a very few closely appressed, much shorter inconspicuous hairs on the connective. The corolla of *Nomosa*, coarsely tubular, does not swell into a campanulate throat as in *Lasiarrhenum*. Its lobes are ovate rather than deltoid, and the inner surface of the throat bears no hairs nor stiped glands. The annulus, very well developed in *Lasiarrhenum*, in *Nomosa* is absent or obscure.

The plant is not bristly. The foliage is closely strigose with the minute hairs abundant but not extremely crowded nor overlapping. The thin indument is tidy and smooth and gray or somewhat silvery. The leaves usually have only two strong elongate veins. These arise from the midrib 1–2 cm. above the leaf-base. They are assurgent and nearly as strong as the midrib and are frequently prolonged almost to the leaf-tip. Occasionally less well developed veins may also be present, but these are never as conspicuous as the major veins. The corolla, if not perfectly regular, departs from that condition only by having its two adaxial lobes perhaps very slightly larger than the other three. The lobes are involutely curved, and the upper half of the tube directly below each of them is somewhat swollen. The upper half of the corolla, accordingly, has five weakly inflated ribs. The filaments are attached unusually low in the corolla. The position of their thickened short decurrent base is marked on the outside of the corolla by five oblong-elliptic glabrous areas extending 2.5–5 mm. above the corolla-base. The slender, elongate, gradually narrowed filaments are glabrous above the middle, but below the middle and on their thickened decurrent base they bear multicellular gland-tipped hairs in great abundance. This shaggy indument on the filaments is a distinctive feature of *Nomosa.* Some of the multicellular gland-tipped hairs occur also on the walls of the corolla immediately adjacent to the stamen bases. Elsewhere the inner surface of the corolla bears no hairs or stipitate glands. The anthers are carried high enough in the corolla-tube to have their terminal appendage exserted from the corolla-mouth. From below the middle the anthers narrow towards an attenuate tip. The terminal 1.5 mm. of the anther, its appendage, consists of a sterile prolongation of the connective. This is narrowed to a slender point and is frequently curved to one side. It is the only part of the anther exserted from the corolla-tube. Although exserted, it does not become conspicuous, since it remains hidden behind the erect corolla-lobes which overtop it. The back of the anther has a broad, smooth, weakly convex connective which bears a very few stout closely appressed hairs. These hairs, unlike those on the anther in *Lasiarrhenum,* are few and inconspicuous and must be looked for under the microscope. At the base of the anther the thecae, though distinct for 0.6 mm. above the base, are not spreading but parallel. The lower end of each theca is acutish. Its tip never becomes appendaged or distinctly thickened as in *Onosma.* The style emerges from the fully developed corolla as its lobes unfold and soon bears its two stigmas 5–6 mm. beyond the tips of the erect corolla-lobes. Fruit of the plant is unknown. I am confident, however, that the nutlets will prove to be very similar to those of *Lasiarrhenum.*

4. **Lasiarrhenum** Johnston, Contr. Gray Herb. **70**: 15 (1924). Type species *Onosma strigosum* HBK.

Plant perennial, prevailingly strigose, with spreading hairs only on the stem and veins of the leaf. Stems coarse, erect, several or more, simple or bearing ascending leafy floriferous branches above the middle. Leaves all cauline, numerous and usually crowded, elongate, triple-ribbed, narrowly lanceolate or the lower ones oblanceolate, those near the middle of the stem usually largest, those near the base of the stem small and even imperfectly developed. Cymes scorpioid, always terminal, geminate on the main stem but usually single on the branches, in age straightening and elongating but remaining moderately crowded. Bracts numerous, linear to lanceolate, ascending, not very conspicuous even in fruiting inflorescences, scarcely if at all overtopping the adjacent fruiting calyx. Calyx 5-fid; lobes unequal with the abaxial one largest, acute, usually slightly more than half the length of the corolla, moderately accrescent in fruit; pedicel slender, straight, strictly ascending, half as long to as long as the calyx. Corolla white, regular, below the middle coarsely tubular and above the middle swelling to form a somewhat campanulate throat, the outer surface strigose; lobes erect, relatively small, more or less deltoid with the apex frequently rounded, as broad or broader than long, imbricate; throat on inner surface bearing scattered stipitate glands, frequently inconspicuously strigose along lines below the corolla-lobes, without faucal appendages; the annulus well developed, glabrous, a thick ridge or narrow collar, obscurely lobed. Filaments affixed at the base of the throat, nearly as long as the anther, thickish and somewhat fleshy, broad, dorsiventrally compressed, narrowly obovate to oblanceolate, usually bearing some stiped glands especially below the middle, but otherwise glabrous, below the attachment narrowly decurrent and forming thickened ridges on the walls of the corolla-tube. Anthers lanceolate, deeply included in the corolla-throat, attached distinctly below the middle, appendaged at the apex; terminal appendage evident, narrow, attenuate, compressed, base as broad as the connective of which it is an attenuate prolongation, with a length not exceeding and usually less than the maximum width of the dehiscent anther; base of anther lobed; thecae narrowing towards their apex, free for a short distance above the base, parallel or somewhat spreading at the lower end, the basal end usually acutish with a thickened tip; venter of anther glabrous, bearing the thecae closely juxtaposed, with the connective exposed only at the apex; dorsum of the anther with a broad connective, conspicuously hispid-villose both on the connective and on the back of the thecae, the hairs slender, white, loosely and antrorsely appressed. Pollen broadly but distinctly ovoid, $20–23 \times 16–20\ \mu$, broadest and bearing the pores about $8\ \mu$ above the broadly rounded base; lateral profile ovate, above the pores with the converging sides nearly straight and the apex abruptly rounded; polar profile circular; pores 7 or 8, usually obscure. Style emerging from the well-developed corolla-bud as the lobes unfold, shortly but distinctly surpassing the erect corolla-lobes; stigmas evidently two, diverging from the summit of the style. Nutlets smooth, white, lustrous, ovoid, narrowed at the base, all four frequently developing, divergent, on the venter bearing a low, rounded, weakly developed keel but no evidences of a ventral suture, dorsum convex; attachment scar basal, horizontal, nearly as broad as long. Gynobase broadly pyramidal, surmounted by the thickened persisting 4-angulate base of the style; attachment faces sloping, distinct, with thickened margins.

A very well marked genus with a single species, endemic to south central Mexico (Michoacan to Puebla and adjacent Jalisco to Oaxaca).

Lasiarrhenum strigosum (HBK.) Johnston, Contr. Gray Herb. **70**: 15 (1924).

Onosma strigosum HBK. Nov. Gen. et Sp. **3**: 93 (1818).
Onosmodium strigosum (HBK.) Don, Gen. Syst. **4**: 317 (1837).
Onosma trinervium Lehm. Asperif. **2**: 378 (1818) and Icones **1**: 11, t. 9 (1821).
Lithospermum longifolium Willd. in R. & S. Syst. **4**: 742 (1819).

Plant 5–10 dm. tall; stems abundantly short hispid with hairs 1–2 (–3) mm. long. Leaves at middle of stem 5–10 cm. long, 6–22 (usually 8–15) mm. broad, paler beneath, triple-ribbed, the strong midrib producing (about 10 mm. above its base) two evident strong, greatly prolonged assurgent veins, the veins nearly as strong as the midrib and extending almost to the leaf tip, evident on both sides of the leaf, hairs on the upper surface of the leaf provided with minute discoid bases but these seldom conspicuous. Corolla 15–23 mm. long, below the middle 3–4.5 mm. thick and subcylindric or slightly ampliate, at or slightly below the middle expanding into a campanulate throat 6–12 mm. broad at the top; corolla-lobes 3.5–5 mm. broad at the base, 2–3 mm. long. Filaments 3–5 mm. long, from the narrow attachment gradually expanding to become 1.3–1.5 mm. broad between the middle and the acute apex, arising 5–10 mm. above the corolla-base. Anthers 4–5.5 mm. long, 1–1.3 mm. broad below the middle, affixed 1.2–1.5 mm. above the base, reaching up to 1–3 (usually 2) mm. below the base of the corolla-sinus; terminal appendage 0.4–1 mm. long and 0.2–0.3 mm. wide at the base; base of anther held 1.5–3 mm. above the base of the filament; thecae free 0.5–1 mm. above the anther-base; dorsum of anther bearing hairs 0.6–1.3 mm. long, connective one third of the width of the anther. Style 16–23 mm. long, surpassing the corolla-lobes 1–5 mm. Nutlets ovoid, usually ca. 3 mm. long and 2.5 mm. thick, in transverse section with the ventral side broadly obtuse but elsewhere nearly circular in outline.

This monotype is particularly notable for its broad, fleshy, usually oblanceolate filaments and for its large lanceolate appendaged anthers which are coarsely and abundantly white-hairy on the back. In gross habit the plant is very suggestive of *Onosmodium*, a genus with which it was long confused. In floral structure, however, it is extremely different. The closest relations of *Lasiarrhenum* are with *Nomosa*. Details concerning this relationship are treated in the discussion of the latter genus.

The anthers of *Lasiarrhenum* have a somewhat less well developed terminal appendage than those of *Nomosa*, but otherwise are very similar as to form and size. Unlike the anthers of Nomosa, which bear only a few inconspicuous hairs on the connective, the whole of the dorsal surface of the anthers in *Lasiarrhenum* bears slender ascending white hairs in conspicuous abundance. The presence of hairs on the back of the anther is no common feature. Among American Lithospermeae they occur only in *Lasiarrhenum*, *Nomosa*, and one species of *Macromeria*, *M. viridiflora* DC.

The terminal appendage on the anther of *Lasiarrhenum* (and *Nomosa*) is very suggestive of that in *Onosma*, and because of this the possibility has been recognized that our plant might have close affinity with that genus of the Old World. In structures other than the anthers, however, *Lasiarrhenum* and *Nomosa* have much more in common with *Onosmodium* and *Macromeria* The indications are that all these four genera are American derivatives of either *Lithospermum* or *Lithospermum*-like ancestors and so probably have no direct affinity with *Onosma*. The well-developed anther-appendages of *Lasiarrhenum* and *Nomosa* appear to be simply the extreme expression of the same tendency towards prolongation of the connective that is to be observed less well expressed in *Onosmodium* and *Macromeria*. In *Onosmodium* the connective is narrow, and the maximum prolongation of it, as in *O. unicum* Macbr. and *O. dodrantale* Johnston, is slender, weak, and at most 0.5 mm. long. The connective is also narrow in most species of *Macromeria*. In the one species of that genus, *M. viridiflora* DC., in which the connective approaches in width that of *Lasiarrhenum* and *Nomosa*, its prolongation is very short and stout. In *Macromeria* the thecae are equally broad from base to tip, and the anthers, accordingly, are more or less distinctly oblong in outline and have a broad summit. In *Onosmodium* the thecae are slightly narrowed above the middle and usually have an apiculate tip. The anther tends to have a lanceolate outline. In *Lasiarrhenum* and *Nomosa* the thecae are gradually narrowed to the apex. The anther as a whole is narrowed to the width of the broad connective at the level of the anther-tips, and the attenuate prolongation of the connective provides the pointed tip and thus completes the lanceolate outline of the whole anther.

5. **Perittostema,** gen. nov.

Herba parva perennis. Caules graciles erecti simplices strigosi foliosissimi. Folia gracilia lineari-subulata medio-costata sed enervata margine valde revoluta. Cymae scorpioideae solitariae glomeratae terminales. Bracteae lineares calyce breviores inconspicuae. Calyx 5-fidus; lobis ut videtur paullo inaequalibus cuneatis corolla plus quam duplo longioribus. Corolla lutea extus strigosa; tubo infra medium cylindraceo, supra medium in fauces subinflatos differentiato summum ad apicem (i.e., infra basim loborum corollae) paullo constricto; lobis tubi (faucibus inclusis) 5-plo brevioribus stricte adscendentibus paullo longioribus quam latis rotundis, in alabastro late imbricatis; faucibus quam parte inferiore cylindrico tubi subduplo crassioribus aequilongis, intus medium versus appendiculas invaginatas arcuatas glandulis stipitatis obsitas gerentibus; annulo vix elevato adpresse villuloso. Stamina in faucibus profunde inclusa. Filamenta basi faucium affixa, valde compressa, medio-costata, a basi angusta sursum valde gradatimque expansa, apicem versus latissima deinde abruptissime contracta, obovata vel deltoidea, subduplo longiora quam lata. Antherae oblongo-ellipticae filamento subduplo longiores paullo infra medium affixae apiculo attenuato recurvato terminatae basi bilobatae; thecis atro-marginatis quartem partem inferiorem distinctis et ibi sinu acuto separatis; connectivo late glabro laevi. Granulae pollinis ellipsoideae 24–25 $\times$ 20 μ, a latere visae ellipticae lateris angulatae, desuper visae circulares; poris aequatorialibus 6–8 sed saepissime 7. Stylus gracilis lobos stricte adscendents corollae superans; stigmate terminali parvo obscure bilobo. Fructu ignoto. — Nomen derivatur a περιττος, insolitus, et στημα, stamen, quia filamenta formam anomalem habent.

Perittostema pinetorum (Johnston), comb. nov.

Lasiarrhenum pinetorum Johnston, Jour. Arnold Arb. **16:** 187 (1935).

Stems 10–15 cm. long, 2.5 mm. thick towards the base, internodes very short; leaves very numerous, 1–2 mm. broad above the base and very gradually narrowed towards the apex, linear-subulate, 10–30 mm. long, becoming gradually smaller upwards along the stem, bearing appressed stiff pallid hairs 0.3–0.5 mm. long, on lower surface all but the midrib hidden by the inrolling of the strongly revolute leaf-margins; cymes 3–7-flowered; calyx 4–4.5 mm. long, lobes ca. 0.7 mm. wide at the base, gradually narrowed; pedicel about 1 mm. long; corolla ca. 10 mm. long; tubular portion of corolla ca. 8 mm. long, below the middle cylindric and 2–2.5 mm. thick, above the middle expanding to form a swollen throat which becomes 3–4 mm. broad near its middle and then contracts to become 2–3 mm. thick at the summit; veins in the cylindric tube rather prominent; corolla-lobes ca. 2 mm. long and 1.8 mm. broad, rounded; faucal appendages arcuate, ca. 1 mm. broad, prominent, thickened and weakly invaginate, bearing some stipitate glands, included, borne 1.5 mm. below the constricted summit of the throat; anthers ca. 2 mm. long and 1 mm. broad, obtusish summit bearing a strongly compressed narrowly ligulate and strongly recurving terminal appendage which is 0.2 mm. long and nearly 0.1 mm. broad at the base; thecae free for 0.4–0.5 mm. above their base, in age somewhat spreading to form an open acute sinus at the base of the anther; base of anther held ca. 0.3 mm. above the base of the filament; apex of anther held 0.6–0.9 mm. below the summit of the corolla-throat, surpassing the faucal appendages 0.6–0.8 mm.; style 17–18 mm. long, surpassing the strict corolla-lobes ca. 2 mm.

A plant known only from the type collection now preserved in the herbarium at Paris. The specimen was collected by Ghiesbreght, no. 311, in September [? 1841] in temperate montane pine forests somewhere in Mexico. No geographical data were provided by the collector. Until the plant has been rediscovered, its home must remain subject to conjecture. I suspect that it is in the mountains of Oaxaca.

Although originally described as a species of *Lasiarrhenum*, the plant has no close relationship with that genus. Its closest affinities are with *Lithospermum*, and particularly with its Mexican species. It differs from the latter chiefly in its unusual filaments and in the form of the anther. From *Lasiarrhenum* it differs not only in habit and very narrow veinless leaves, but also in its rounded corolla-lobes, its faucal appendages, its ellipsoid pollen, and its glabrous anthers with dark-margined thecae and recurved terminal appendage.

Since the type collection is not a generous one and has only a relatively few flowers, only two corollas have been available for dissection and close examination. Changes in the maturing corolla have not been studied, and the possibility that the corolla may be slightly zygomorphic has not been eliminated. The corolla-bud just before opening is ellipsoidal and at the base is prolonged downward into a short cylindric tube. At this early stage the swollen throat near its middle has a diameter about twice that at the summit of the throat (i.e., at the base of the broadly overlapping corolla-lobes), and more than twice that of the tube below the throat. The form of this corolla-bud is unusual in the Lithospermeae, indeed is approximated only in *Onosma* and *Maharanga*. The mature corollas retain their swollen throat, but this appears to be less constricted above the middle than previously. In the dissections available I find some indication that the mature corolla may possibly be somewhat prolonged on one side and may possibly have two of its lobes slightly larger than the other three. Inside the throat there are evident arcuate faucal appendages. These are formed partially by invagination and partly by thickening of tissue. They are dark in color and bear numerous but not crowded stipitate glands. It is to be noted that the appendages are borne not at the mouth of the corolla, at the summit of the throat, as in *Lithospermum*, but rather distinctly below the corolla-mouth, slightly above the middle of the throat, and hence are not exposed but are distinctly included in the throat.

The filaments of *Perittostema* are unique. They are firm in texture, dark in color, and very strongly dorsiventrally compressed. They gradually broaden upward from the narrow attachment and are broadest just below their truncate or broadly obtuse summit. In shape they are triangular or obovate-triangular. They measure usually about 1 mm. long and about 0.6 mm. broad across their summit. On the ventral side they have a small ridge down their middle. They are attached to the anthers by a small tip arising from the middle of their broad upper edge. These filaments of *Perittostema* are extremely different from those of *Lithospermum*, for in the latter genus the filaments are never laterally expanded and never other than linear, subulate, or unguiculate. The only member of the Lithospermeae with filaments even suggestive of those of *Perittostema* is the genus *Lasiarrhenum*. In the latter genus the filaments are compressed and are broadened upward, but are much larger and more elongate, being oblanceolate rather than triangular.

The anthers in *Perittostema* are relatively large for the size of the corolla and are accommodated within it largely because the throat is somewhat inflated. Although the anthers project above the level of the faucal appendages, their tips still fail to closely approach the mouth of the corolla. They are completely included. The open thecae have a dark-colored margin, an unusual feature which I have encountered among the Lithospermeae only in the genus *Halacsya*. For the lower quarter of their length the thecae are not joined together, and in age these tend to diverge, opening a deep acute sinus at the base of the anther. The broad summit of the anther is appendaged by a small but definite prolongation of the connective, which is unusual in being not straight but strongly recurved. In no species of *Lithospermum* do the anthers evidently surpass the faucal appendages, nor do the anthers have a distinctly bilobed base. A few species of that genus have their anthers terminally appendaged, but when present the appendage is always straight and erect.

The pollen is ellipsoid, having the upper and lower half equal and the usually obscure pores, commonly seven in number, equally spaced about the equator. It is very similar to the pollen produced by species of *Lithospermum*, *Macromeria*, and *Psilolaemus*. That of *Lasiarrhenum* differs in its ovoid form.

The style is early elongate and before the corolla-bud opens is pressed upward and decurved against the still tightly imbricate corolla-lobes. It is promptly exserted and surpasses the corolla-lobes as soon as the latter unfold. In *Lithospermum* this behavior is duplicated in only a few species, all Mexican.

In addition to its floral structures *Perittostema* is also notable as a small plant with slender stems. Indeed, in these regards, among the Lithospermeae it is surpassed only by members of *Buglossoides* § *Rhytispermum*. Among American members of the tribe its slender stems and very slender leaves are approximated only by the Mexican *Lithospermum strictum*. The habit of *Macromeria*, *Onosmodium*, *Lasiarrhenum*, and most species of *Lithospermum* is very coarse and vigorous when compared with that of *Perittostema*. The leaves of our plant are extremely narrow and, *Lavendula*-like, have strongly revolute margins that roll back and cover all but the midrib on their lower surface.

6. **Psilolaemus,** gen. nov.

Planta perennis strigosa scabrella. Caules foliosi fruticulosi simplices vel laxe ramosi decumbentes vel adscendentes adpresse hispiduli e radice valida palari lignosa purpureo-tincta erumpentes. Folia omnino caulina sessilia firma valde costata enervata vel obscurissime paucissimeque nervata margine angusto-revoluta, facie superiore lucentia pilis rigidis brevibus saepe valde adpressis e discis pallidis erumpentibus instructa, facie inferiora breviter hispidula pilulis non rariter retrorsis donata, inferioribus oblanceolatis, superioribus lanceolatis. Cymae scorpioideae multiflorae solitariae caulibus ramisque foliatis terminatae maturitate rectae valde elongatae. Bracteae foliatae abundantes foliis supremis gradatim minores lanceolatae vel lanceolato-ovatae acutae pleraque calyce breviores. Calyx 5-fidus; lobis inaequalibus linearibus vel lanceolato-linearibus erectis, eo exteriore maximo. Corolla lutea ("armeniacea") tubulosa 3-plo longiore quam lata in parti tertiaria superiore gradatim ampliata alibi cylindracea, extus pilis minutis sparsis pleraque retrorsis donata, intus glaberrima nec appendiculis faucialis nec glandulis stipitatis praedita; lobis ovatis stricte adscendentibus supra basim latissimis quam longitudine corollae 6-plo brevioribus; sinibus limbi clausis basi nec incrassatis nec plicatis; faucibus angulatis lobis aequilongis, extus apice infra bases sinuum limbi gibbosis et infra bases gibbarum areolas depressas verticaliter elongatas apice maxime invaginatas gerentibus, inter areolas 5 depressas venis 3 prominulis donatis; annulo obscuro glabro. Filamenta attenuata apicem versus faucium e plicis invaginatis faucium orientia supra medium exserta basi anguste breviterque decurrentia. Antherae oblongae 3–4-plo longiores quam latae utroque emarginatae nullo modo appendiculatae paulo infra medium affixae filamentis duplo longiores solum tertiam vel quartam partem inferiorem in faucibus inclusae, parte majore exsertae. Granulae pollinis ellipsoideae vel globoso-ellipsoideae $23–26 \times 16–22\mu$, desuper visae circulares vel obscurissime polygonales, a latere visae ellipticae margine saepissime convexae poris obscurissime aequatorialibus (7 –) 8 donatae. Stylus gracilis evidenter exsertus, stigmatibus 2 distinctis terminalibus. Nuculae erectae parvae ellipsoideae albo-griseae laeves vel perinconspicue tuberculatae carinam ventralem versus utrinque profunde punctatae vel interrupte profundeque sulcatae, dorso convexae, ventre obtuse angulatae carinam latam vix prominentem proferentes, sutura obscura vel non rariter praesertim supra medium carinae inconspicue lineato-sulcata donatae. Gynobasis pyramidalis facies 4 planas adscendentes angulis prominentibus pyramidis separatas gerens basi incrasso styli terminata. — Nomen derivatur ab ψιλος, calva, et λαιμος, fauces, propterea quod fauces corollae glaberrimae et nec glandulis stipitatis nec appendiculis faucialis ornatae sunt.

Psilolaemus revolutus (Robins.) comb. nov.

Lithospermum revolutum Robins. Proc. Amer. Acad. **27**: 182 (1892).
Onosmodium revolutum (Robins.) Macbr. Contr. Gray Herb. **49**: 21 (1917).

Plant at first simple and erect but becoming branched and spreading in age; stems pale, 1–3 mm. thick, slightly fruticulose; leaves all cauline, with a strong conspicuous midrib which is sulcate above and prominent below; lower leaves largest, 3–7 cm. long, 6–15 mm. broad; cymes elongating, becoming 10–25 cm. long in age; calyx at anthesis 7–10 mm. long, weakly accrescent; pedicels ca. 1 mm. long at anthesis, becoming 2–4 mm. long in age; corolla 9–15 mm. long; tubular portion of corolla 7–12 mm. long, lower 9–10 mm. cylindric and 2–2.5 mm. thick, upper 2.5–3 mm. expanding to form a short throat 3–5 mm. thick at the summit; sinus between lobes closed above the base by the overlapping margins of adjoining corolla-lobes, neither thickened nor plicate at the base; corolla-throat outside with rather prominent veins and bearing five swellings and five depressions and hence somewhat angulate, bearing a small swelling directly below the base of each sinus of the corolla and bearing a small elongate depression (the complement of an inflexed plait inside the corolla) located directly under each swelling; stamens borne 0.4–0.5 mm. below the summit of the throat, arising from a small plait-like invagination of the corolla-wall; filaments 0.5–1.1 mm. long, exserted from the throat 0.1–0.5 mm.; anthers 1.4–2 mm. long, 0.4–0.6 mm. broad, oblong or slightly broader above the middle, emarginate at both ends, exserted from the throat 0.7–1.5 mm. but overtopped by the strictly ascending imbricate corolla-lobes and hence not conspicuous; style surpassing the corolla 1–2 mm., frequently emerging from corollas which have not yet attained maximum size; nutlets 2 mm. long and 1.5 mm. thick.

A plant known only from the gypseous saline marshes in southeastern San Luis Potosi, Mexico. As has been suggested by Macbride, Contr. Gray Herb. **49**: 21 (1917), it shares characters with both *Lithospermum* and *Onosmodium*. Its closest relations, however, are with *Lithospermum*, with its Mexican species in particular.

Psilolaemus is distinguished from *Lithospermum* by the form of the corolla and the form and behavior of its stamens. The corolla-throat is angulate as in *Onosmodium* and as in that genus bears localized external swellings between the filament-attachments and the base of the corolla-sinus above. The stamens arise from small invaginations which are complementary to small elongate depressions on the outside of the corolla-throat directly below the subsinal swellings. In *Lithospermum* the corolla-throat bears invaginate appendages or stipitate glands or both, and the corolla-tube, sometimes hairy inside, always bears a basal annulus moderately to well developed. In *Psilolaemus* the annulus is very obscure and the inside of the corolla is completely glabrous and devoid not only of faucal appendages but also of all stipitate glands. The exserted style and the nearly erect corolla-lobes of the present genus are features duplicated in only a few of the many species of *Lithospermum*.

The plant has flowers resembling those of *Onosmodium* in being glabrous inside and devoid of stipitate glands and faucal appendages, as well as by having erect corolla-lobes, an exserted style, and an angulate throat with swellings below each corolla-sinus. It differs from *Onosmodium* in having elliptic pollen, oblong non-apiculate strongly exserted anthers, longer filaments, broadly and persistently imbricate ovate corolla-lobes, and closed corolla-sinus not thickened or plicate at the base. The leaves of *Onosmodium* are strongly veined. Those of *Psilolaemus*, as in most species of *Lithospermum*, are veinless or practically so. The style may be early exserted, but the flowers of *Psilolaemus* are not precociously sexual as in *Onosmodium*.

7. **Ancistrocarya** Maxim. Bull. Acad. St. Petersb. **17**: 443 (1872) and Mel. Biol. **8**: 543 (1872). Type species *A. japonica* Maxim.

Plant perennial, minutely strigose, stems fistulose, erect, simple. Leaves alternate, oblanceolate, evidently veined, all cauline; on lower half of stem small and imperfectly developed, deciduous at flowering time; on upper half of stem becoming very large and ample. Cymes scorpioid, 3–5, loosely disposed at the top of the stem, lowest one axillary, the others extra-axillary or terminal, simple, pedunculate, bracteate only towards the base, at maturity becoming stiff, straight elongate and loosely racemose. Calyx 5-parted, usually evidently pedicellate at least at maturity; lobes linear or sometimes oblanceolate, acute, erect, weakly costate, subequal or the abaxial one longest, about half as long as the corolla tube. Corolla lavender (becoming orange in drying), minutely strigose outside; tube subcylindric, length greater than the diameter of the limb, abruptly constricted at the base, upper portion not differentiated into a distinct throat, bearing no faucal appendages or glands, inside abundantly and antrorsely villose-strigose above the middle; annulus represented by 10 tufts of hairs just above the base of the tube; lobes ascending, rounded, elongate, elliptic, imbricate in the bud; stamens included; filaments unguiculate, affixed at equal heights near the middle of the corolla tube, a third to a half the length of the anthers; anthers linear-oblong, affixed between the base and the middle, borne in the hairy upper middle third of the corolla tube, ends emarginate. Pollen small (20 $\times$ 12–13 μ long), elongate with rounded ends, constricted at the middle, encircled by a single row of 6 (– 8) inconspicuous pores about the broadest part of the broader lower half of the grain, polar profile circular or sometimes very obscurely polygonal. Style reaching up to the middle of the corolla-tube; stigmas 2, terminal, erect and ellipsoidal, juxtaposed and usually connate on the back below their middle. Ovary at anthesis 4-lobed, the lobes ellipsoidal. Nutlets smooth, lustrous, gray, elongate, obliquely lanceolate and conspicuously rostrate with the tip hamate, only one or two maturing, broadest just above the base and then very gradually attenuate into a very conspicuous slender laterally flattened strongly out-curving subulate beak with a hooked tip; venter of seminiferous lower half of nutlet distinctly convex, weakly or not at all keeled, lacking an evident suture; dorsum obtusish; attachment scar basal, large, slightly broader than long, flabelliform, bearing a conspicuous pit formed by the open funicular canal and (paralleling the dorsal edge) an arc of about 6 minor vascular strands. Seeds asymmetric, the lower end appearing obliquely truncate. Gynobase pyramidal when maturing more than a single nutlet, nearly as high as broad, with cartilaginous thickenings between the attachment faces and at the apex.

A very distinct monotypic genus of Japan especially notable for its very ample veined cauline leaves, its nearly bractless cymes, its corollas with the tube densely villous-strigose inside, and its elongate nutlets which are gradually attenuate into an elongate out-curved beak hooked at the apex. It appears to be most closely related to *Lithospermum*, which it resembles in pollen and in having broadly basifixed nutlets with a lustrous smooth pericarp.

Ancistrocarya japonica Maxim. Bull. Acad. St. Petersb. **17**: 444 (1872) and **20**: 471 (1875); Mel. Biol. **8**: 544 (1872).

Ancistrocarya japonica var. *albiflora* Honda, Bot. Mag. Tokyo **49**: 790 (1935).

Endemic to middle and southern Japan. The stems, branched only in the apical inflorescence, are 3–10 dm. tall. The underground parts are unusual and merit description from fresh material. They apparently consist of a congested sympodial rhizome that forms a crowded cluster of short, ascending, thickened, bulbose branches, each producing an aerial stem. No radical leaf-clusters are developed. The stems arise directly from the rhizome. The leaves are imperfectly developed at the base of the stem but rapidly increase in size as they are produced higher up along it and above the middle of the stem become unusually large and ample for an herbaceous borage, as much as 20 cm. long and 7 cm. broad. The leaves of *Ancistrocarya* not only differ from other Lithospermeae in their large size but also in being conspicuously and loosely veined with the veins anastomosing.

Among the Lithospermeae the genus is also aberrant in its nearly bractless cymes. The lowermost flowers in the scorpioid cyme may be opposed by a small foliar bract 10–20 mm. long, and the second flower in the cyme may be subtended by a bract 1–3 mm. long, but the numerous later flowers are borne on a completely bractless rhachis. The cymes themselves have differing relations to stem-leaves. When more than two cymes are produced by the stem, the lowermost one is distinctly axillary and the others either distinctly supra-axillary or not at all intimately associated with a leaf. The two terminal cymes are usually about equal in development and may appear to be geminate. However, since no flower is borne in the fork at their base, they are simple cymes and not formed by the basal forking of a terminal cyme.

Superficially the corollas of *Ancistrocarya* much resemble those of the American species of *Lithospermum*, particularly so when seen in the herbarium. When dried they even assume an orange tonality similar to that presented by the orange or yellow corollas of the American plants in the same state. Unlike the American plants, however, *Ancistrocarya* has corollas that are lilac or bluish (or rarely white) when fresh. The radially symmetric corolla (11–14 mm. long in total length) has a well-developed tube 7–10 mm. long and 2.5–3.5 mm. thick, which is abruptly constricted to 1–2 mm. thick at the very base. At the summit it abruptly expands into the ascending corolla-limb. There are no markings nor constrictions of the tube to delimit the throat. The lower half of the tube is glabrous inside except for the ten tufts of hairs representing the undeveloped suprabasal annulus. The inner wall of the upper half of the corolla tube is clothed with abundant, antrorsely appressed, slender white hairs 0.5–1 mm. long. The filaments (0.8 mm. long), all equal and all affixed at the same altitude on the corolla, arise from amongst the hairs near the base of the villose-strigose upper portion of the corolla-tube. The anthers (1.5–2 mm. long) are accordingly mattressed dorsally by the dense indument on the corolla-walls; a condition paralleled among the Boraginoideae only in *Echiochilon*, *Sericostoma,* and one species of *Lithodora*. Another feature distinguishing the corolla from that of most species of *Lithospermum* is the complete absence of faucal appendages and stipitate glands.

In form, the nutlets of *Ancistrocarya* are unique, and furthermore the most bizarre in the family. They have a broad basal attachment and are broadest (ca. 2.5 mm.) about 1 mm. above their base. Above their broadest part they become gradually attenuate and prolonged into a strongly out-curving, laterally compressed subulate beak bearing a hook at the tip. Of their total length (7–9 mm.), only the lower half is seminiferous. Although the ovary is 4-lobed, only one or two of the lobes mature into nutlets, either a solitary abaxial one or an abaxial one and its adjacent axial companion. When two are developed they are somewhat divergent, for they are basifixed on adjacent faces of a pyramidal gynobase. The slender hooked beak is strongly curved outward (away from the center of the flower), but the lower lanceolate seminiferous body of the nutlet is only very slightly so. The ventral side of the nutlet body is more rounded and swollen than the dorsal side. It develops no longitudinal ventral keel and furthermore bears no trace of a suture. The elongate, curved, subulate beak is a sterile apical prolongation of the pericarp, completely without parallel elsewhere in the Boraginaceae. Hooked at the tip it may function as an adaptation useful in animal dissemination.

8. **Buglossoides** Moench, Meth. 418 (1794). Type species *B. ramosissima* Moench. (= *Lithospermum tenuiflorum* L.)

Aegonychon S. F. Gray, Nat. Arrang. Brit. Pl. 2: 354 (1821). Based upon two species, *Lithospermum purpureo-caeruleum* L. and *L. arvense* L.

Rhytispermum Link, Handb. 1: 579 (1829). Based upon eight species, of which the first and third (*Lithospermum arvense* L. and *L. purpureo-caeruleum* L.) represent the present genus. The other six species mentioned belong to *Neatostema* (1 sp.), *Lithodora* (2 spp.), *Alkanna* (2 spp.), and *Rochelia* (1 sp.).

Margarospermum Opiz in Berchtold & Opiz, Oekon.-techn. Fl. Böhmens 2^2: 73 (1839). Although Opiz cites *Lithospermum* § *Margarospermum* Reichenb. (1831) as a synonym, the description of his genus is based solely upon *Lithospermum purpureo-caeruleum* L.

Plant annual or perennial, herbaceous or fruticulose. Leaves veinless or nearly so. Cymes unilateral, simple or geminate or ternate, usually elongate, conspicuously bracted, usually racemose at maturity. Calyx 5-parted or 5-lobed, lobes narrow, at times united at the base to form a short cupulate tube, equal or unequal. Corolla blue, bluish, or white, funnelform or hypercrateromorph, outside usually bearing some appressed hairs, inside from the base of the corolla-lobes downward to between the tips of the anthers bearing five distinct longitudinal bands of hairs and/or glands or five hairy and/or glanduliferous inflexed plaits, below the insertion of the filaments naked or with five congregations of glands and sometimes with invaginate swellings, lobes spreading or ascending, imbricate; annulus near the base of the tube consisting of a narrow collar or ten scale-like lobes, frequently weakly developed and sometimes apparently absent; stamens borne at or below the middle of the corolla, included; filaments equal, affixed at equal heights on the corolla, shorter than the anther (usually about half as long); anthers lance-oblong or oblong, affixed at or slightly below the middle, base cordate, apex appendaged by a short prolongation of the connective; pollen small (15–25 μ long, 12–16 μ in diameter), cylindric or somewhat ovoid or rarely slightly elliptic, bearing the inconspicuous pores in a single row on or distinctly below the equator, in lateral profile with the sides usually straight or nearly so and either parallel or somewhat convergent towards the upper end; style not much if at all surpassing the anthers, usually much shorter than the calyx; stigmas two, rounded, borne laterally at the summit of the simple style or at the base on opposing sides of a short bilobed sterile apex of the style, usually evidently subterminal; nutlets 1–4, erect to strongly divergent, smooth or rough, rounded or angulate, attachment basal or obliquely basal, ventral suture fused, obscure, sometimes prominent; gynobase flat or depressed pyramidal.

This genus is closely related to *Lithospermum* and is distinguished only by the structure of the corolla. In *Lithospermum* the corolla-throat may bear hairy and glanduliferous, invaginate, gibbose appendages or be variously glanduliferous or glabrous. The distinctive feature of the corolla of *Buglossoides* is the well-developed guides for insect visitors in the form of five distinct vertical bands of glands and stout hairs or five hairy and glanduliferous inflexed plaits. These guide-lines may be traced from the base of the corolla-lobes downward along a vein to between the anther tips or slightly above them. The gibbose invaginate faucal appendages present in many species of *Lithospermum* are also a feature of the flowers in many other genera of the Boraginaceae. The elongate inflexed plaits or the well-developed vertical bands of hairs and glands occur only in *Buglossoides*. Several other developments in the genus distinguish its species from most members of *Lithospermum*. These are the prevalence of blue as a corolla color, the apiculate anthers, the lobed sterile tip of the style, and the small size of the usually cylindric or ovoid-cylindric pollen grains. Singly, these latter features may occur here and there in species of *Lithospermum*, but never together nor in any species possibly a close relative of any species of *Buglossoides*. Floral dimorphy, in the form of heterostyly or cleistogamy, well developed in *Lithospermum*, does not occur in the present genus. Since the group gives every evidence of being a natural one, and since it can be readily distinguished from *Lithospermum* by well-marked, very unusual features of its corolla, it seems to merit generic recognition.

The stamens of *Buglossoides* are deeply included in the tubular portion of the corolla in all species except *B. purpureo-caeruleum*. In *Lithospermum*, stamens are borne at or below the middle of the tube only in species with a very abbreviated tube or in corollas of long-styled flowers of some heterostyled species.

The anthers are oblong or narrowly oblong and several times longer than broad and are borne on filaments half to a third of the anther length, in all species except *B. Gastoni*. In the latter the anthers are broadly oblong and only about twice as long as broad, and are borne on filaments nearly as long as the anther body. The largest anthers are those of *B. purpureo-caeruleum* and *B. Zollingeri*. These are 1–1.5 mm. long, twice the length of the anthers in other species. In all species the connective is prolonged to form a minute but definite tip on the anther. This tip may be subulate, cuneate, deltoid, or quadrate. It becomes as much as 0.2 mm. long in *B. purpureo-caeruleum*, but in other congeners it is usually only 0.1 mm. or less in length. It is least developed in *B. Gastoni*, in that species being stout, quadrate or deltoid, and scarcely projecting beyond the summits of the thecae. This tip on the anthers in species of *Buglossoides* is a character that separates the genus from practically all species of *Lithospermum*. The connective is prolonged apically in only a very few species of *Lithospermum*, noticeably only in *L. tschimganicum* Fedtsch. of Central Asia and *L. papillosum* Thunb. and *L. cinereum* DC. of South Africa. Some of the Mexican species of *Lithospermum* have the anthers obscurely thickened at the apex but never to the degree found in *Buglossoides*. In most species of *Lithospermum* there is not even a vague suggestion of a terminal appendage.

The style is short. At anthesis it never reaches upward beyond the tips of the anthers. Rarely it may bear its stigmas between the anthers, but more commonly they are held below the level of the anther bases. In fruit the style is never more than half the length of the mature nutlets. In *Lithospermum* such short styles occur only in cleistogamic flowers or in the short-styled flowers of some heterostylic species.

The two stigmas are separated by the sterile tip of the style and are accordingly lateral and borne at or more commonly obviously below the style apex. The sterile tip of the style is commonly prolonged above the stigmas and is usually evidently bilobed. This condition is extremely well developed in *B. purpureo-caeruleum* and *B. Zollingeri*. In these two species the style tip projects beyond the stigma for a distance equal to or surpassing the diameter of the latter, and consists of two attenuate lobes. In *B. calabrum* and *B. Gastoni* the lobes of the style tip are shorter, stouter, and obtusish, but even so, they evidently project above the stigma. In the four species named, all members of the section *Margarospermum*, the stigmas are clearly subapical and well separated. Frequently the two stigmas are not equally well developed, and not uncommonly one may be borne slightly lower on the style than its companion.

Among the species of the section *Eubuglossoides* the style tips show greater variation. The two stigmas tend to be less sharply defined than in the section *Margarospermum*. In typical *B. arvense* the terminal lobes of the style may be cylindric or narrowly conic and always evidently surpass the stigmas. In *B. incrassatum* the lobes are evident, but usually less well developed than in *B. arvense* and its allied forms (e.g., *Lithospermum Sibthorpianum* Gris.) in the eastern Mediterranean area. In *B. tenuiflorum,* in most allies of *B. arvense* in northern Africa, as well as in plants referable to *L. minimum* Morris, the sterile tip of the style extends up between the stigmas but projects weakly if at all above them. The sterile tip of the style in these plants has either an unlobed truncate apex or an apex that is only obscurely lobed or merely notched.

The prolonged lobed sterile tip of the style in this genus needs investigation. Superficially the stigmas and the tip of the style, taken together, are very suggestive of the stigmatic head of the Heliotropioideae. It remains to be determined if the course of the vascularization is similar, cf. Hanf. Beiheft Bot. Centralbl. **54** A: 126 (1935). Among the Lithospermeae lobed style-tips are best developed in the present genus. In almost all species of *Lithospermum* the stigmas are terminal on the style, or if there is a prolongation of the style-tip between the stigmas it is only moderate and does not surpass the stigmas. Only in a few Mexican species (*L. Nelsoni, L. Berlandieri, L. mediale, L. oblongifolium, L. calci-*

cola, L. sordidum, and *L. distichum*) does the somewhat lobed style-tip ever project above the stigmas. However, in most of these species the style-tip is actually short and becomes prominent only because the oblong stigmas are widely spreading.

The pollen of *Buglossoides* is small and shows little variation in size from species to species. Though sometimes ellipsoidal or ovoid, its usual form is subcylindric or barrel-shaped, being circular in polar outline and commonly straight-sided or nearly so in lateral profile. Its pores, always in a single row, are extremely small and obscure, so much so that I have been unable to determine their number. In the section *Eubuglossoides* the pores are distributed around the grain exactly half-way between the poles, i.e., on the equator. The upper and lower halves of the grains are always similar in size and outline. In lateral profile the sides are usually straight and parallel and only occasionally somewhat convex. With proper lighting the grains may show a vague but definite narrow band about the equator. This equatorial band in which the pores are located has not been detected in any pollen of the other section of the genus. In the section *Margarospermum* the pores are borne perceptibly below the middle of the grain. The shorter lower portion of the grain (that below the line of pores) is usually perceptibly broader than the upper portion. In lateral outline the grains vary from oblong to more or less ovate, even within a single species. In profile they may have their straight sides practically parallel or very slightly convergent towards the upper end. Sometimes the sides are evidently convergent and the grain obviously somewhat ovoid. Frequently the grains show a very localized contraction just above the pores, with the result that they tend to develop short sloping shoulders which, though very much less well developed, are still recognizable as similar to the shoulders developed on the asymmetric pollen of *Lithospermum*, cf. Jour. Arnold Arb. **33**: 310 (1953). Such grains, narrowed very slightly in a zone above the pores (to form the shoulders), usually have their upper half with straight paralleling sides, but this portion is discernibly narrower than the shorter rounded basal portion. Accentuation of these tendencies would produce the strongly asymmetric grains of the footprint and hour-glass type known in *Lithospermum.* In the genus *Buglossoides*, however, this tendency to develop shoulders on the grains is only very weakly expressed and frequently must be looked for before it is detected.

The distinctive corollas of *Buglossoides* have been illustrated and compared by Spengler, Oesterr. Bot. Zeitschr. **68**: 110 and 116, ff. 1, 2, 23–26 (1919). Synonymy for most of the species has been compiled by Stroh, Beih. Bot. Centralbl. **58** B: 203–4 and 206 (1938).

Section **Eubuglossoides.**

Lithospermum § *Rhytispermum* (Link) Reichenb. Fl. Germ. Excur. 336 (1831).

Plant annual or biennial, herbaceous; corolla small, 4–9 mm. long, white to blue, regular, inside bearing 5 vertical bands of glands or hairs but no strongly inflexed plaits, lacking congregations of glands or invaginations directly below the stamen attachments; pollen symmetric, bearing the pores about the equator; style with or without a prolonged bilobed sterile tip; nutlets rough, usually all four developing, ventral keel prominent.

The corollas of species belonging to this section are more simply organized than those of the section *Margarospermum*. In the present section the walls of the corolla are only very slightly swollen beneath the five vertical bands of hairs and glands on its inner surface. Complementing these bands on the outside of the corolla are merely five shallow lineate grooves. Only an incipient tendency for invagination along the hairy vertical bands is accordingly present. In the section *Margarospermum* the invagination is very pronounced, and the hairs and glands clothe well-developed inflexed plaits that form the five intruding ridges on the inside of the corolla.

To be included in the section *Eubuglossoides* is *Lithospermum tenuiflorum* L., as well as *L. arvense* L. and the undetermined number of critical species all closely related to it.

Buglossoides tenuiflorum (L. f.) comb. nov.

Lithospermum tenuiflorum Linn. f. Suppl. 130 (1781).

A well-marked species which ranges from Greece east to Irak. The nutlets are distinctive. They have a very fragile pericarp. They are erect or slightly incurving and when *in situ* have their tips proximate and their ventral keels parallel. These nutlets are also smaller than those of *B. arvense* and its allies and are further differentiated by being distinctly constricted just above their smaller attachment surface. The cymes are short (even in maturity seldom more than 8 cm. long) and obviously geminate or ternate at the ends of the branches. The flowers (with a very small blue corolla) are always crowded and evidently biseriate on the cyme. The calyx does not develop a cupulate tube nor does it become enlarged abaxially as may be the case in *B. arvense* and its allies.

Buglossoides arvense (L.) comb. nov.

Lithospermum arvense L. Sp. Pl. 1: 132 (1753).

This species is either exceptionally variable or is a complex of minor species awaiting analysis by a monographer. The typical form is that with the largest flowers. Its white corollas are decidedly funnelform and evidently longer than the calyx. It is the form prevalent in middle and northern Europe and thence extends across Asia. In southern Europe and north Africa there are a number of distinguishable closely related plants, some of which are certainly geographically correlated and deserve specific recognition. Among these only *B. incrassatum* can be mentioned in the present paper. Others seem to merit recognition. Useful in distinguishing them from true *B. arvense* are differences not merely in habit but also in size, form, and color of corolla, size and form of the calyx lobes, degree of development of the sterile style tip, and the presence or absence of a band of scattered short ascending hairs on the inner surface of the corolla just below the attachment of the stamens.

The fruit of *B. arvense* and its allies presents a number of very interesting features. The bony, hard, rough nutlets are straight and have a broad basal attachment which tends to become oblique. In the Boraginaceae nutlets with oblique attachments ordinarily have the attachment surface sloping upward towards the center of the flower and hence transgressing on the ventral side of the nutlet body. In *B. arvense* and its allies the reverse condition is true. If the nutlets are held in a vertical position, it is to be seen that the scar slopes upward, not towards the ventral but towards the dorsal side, and that as a consequence the nutlets are shorter on the dorsal side than on the ventral. Nutlets with an oblique attachment surface of this sort, when affixed to a low-pyramidal or nearly flat gynobase, are not erect with paralleling ventral keels, but are necessarily strongly divergent. This strong divergence of the nutlets of *B. arvense* and its allies is a development late in ontogeny. When they are young the nutlets are erect and parallel. They become noticeably divergent only as they approach full maturity.

Buglossoides incrassatum (Guss.) comb. nov.

Lithospermum incrassatum Guss. Ind. Sem. Hort. Boccad. 6 (1826); Fl. Siculae Prodr. 1: 217 (1827); Fl. Siculae Synop. 1: 217 (1842).

A close ally of *B. arvense* notable chiefly because of its remarkable calyx. After the fall of the corolla, the calyx, as it increases in size and the ensheathed nutlets mature, gradually becomes greatly modified in form as a result of excessive abaxial prolongation. At first the calyx is very similar to that of *B. arvense* at the same stage of development. It is affixed centrally on its symmetric base to the pedicel. At this early stage the central axis of the flower (or for all practical purposes, the style) points away from the leaf axil and is hence divergent from the stem. In later development, because of excessive growth on the abaxial side of the calyx-base, the axis of the flower is gradually shifted in an arc as great as 90° and finally points, not away from, but actually towards the adjacent stem. In other words the calyx is shifted from a central basal attachment to one that is distinctly lateral. The central line up the pedicel, if projected outward, no longer passes up the style but rather across the low gynobase, where it meets the style at an angle of as much as 90°. The mature nutlets are accordingly borne on a low gynobase which is now adaxial and which actually faces the adjacent stem. Because of the dislocation, the distorted calyx-base faces outward and so becomes the most conspicuous part of the fruiting calyx. The condition is unusual but not unique among the Boraginaceae. A very similar development is found in the genus *Pectocarya*, cf. Jour. Arnold Arb. 20: 400 (1939).

Various authors have dismissed the remarkable fruiting calyces of this species as teretological. With this I cannot agree. In *B. arvense* and other near relatives of *B. incrassatum*, there is also a tendency for some enlargement of the fruiting calyx on the abaxial side and also a slight but definite tendency for the transverse axis of the gynobase to slope downwards towards the adjacent stem. In the present species these tendencies, merely incipient in its relatives, are developed excessively. The wide distribution of *B. incrassatum* about the Mediterranean area, where in many localities it appears to be the only representative of its group, is evidence that it is not a casual freak.

Section **Margarospermum** (Reichenb.) comb. nov.

Lithospermum § *Margarospermum* Reichenb. Fl. Germ. Excur. 337 (1831). Founded to include four species of which the first listed was *Lithospermum purpureo-caeruleum* L.; the other three are representatives of the genera *Lithodora* and *Moltkia*.

Plant perennial, herbaceous or fruticulose; corolla larger, 15–19 mm. long, blue or purple, the limb slightly oblique with the three abaxial lobes more spreading than the posterior two, inside bearing 5 vertical glanduliferous and/or hairy inflexed plaits and below each filament attachment bearing a congregation of glands and sometimes an invaginate swelling; pollen slightly asymmetric, the pores borne below the equator; style always with a bilobed sterile tip; nutlets smooth and lustrous or rugose, not strongly keeled, usually only one maturing.

This section includes only the four extremely well marked species enumerated below.

Buglossoides purpureo-caeruleum (L.) comb. nov.

Lithospermum purpureo-caeruleum L. Sp. Pl. 1: 132 (1753).

Ranging from western Europe to Iran. Leaves usually broadest below the middle. Flowering stems clustered, arising from a densely branched rhizome, terminated by a pair of leafy racemose cymes. Corolla bearing faucal plaits 2–3 mm. long which originate 6–9 mm. above the base of the tube; also bearing distinct invaginate swellings 2 mm. long below each stamen; plaits glanduliferous but not hairy. Filaments attached 5–8 mm. above the base of the corolla; anthers ca. 1.5 mm. long, elongate, apiculate, twice as long as the filament. Style 8–9 mm. long, the sterile tips attenuate. Nutlets ellipsoidal, smooth, white, 3.5–4 mm. long, 3–3.5 mm. thick, back convex, venter obtuse.

The nutlets of this species are usually slightly larger but otherwise very similar to those of *B. Zollingeri* and *B. calabrum*. In being smooth, white, and porcelain-like, they much resemble the type of nutlet prevalent in *Lithospermum*. Unlike the nutlets of the other species of *Buglossoides* those of the present species have a relatively small basal attachment-surface which is located not at the center of the nutlet-base but rather on its ventral half. For notes on the habit of growth of this species see White, Jour. Bot. 22: 74–76 (1884).

Buglossoides Zollingeri (A. DC.) comb. nov.

Lithospermum Zollingeri A. DC. Prodr. **10:** 586 (1846).

A plant of Japan, China, and Korea. Leaves usually broadest above the middle. Flowering stems arising from procumbent stems persisting from the previous season, terminated by a simple unilateral cyme. Corolla on inner surface bearing glanduliferous, short-hairy inflexed plaits 4–5 mm. long which originate 5–6 mm. above the base of the tube, and also provided with short glanduliferous invaginate plaits below the attachment of each stamen. Filaments attached 3–4 mm. above the corolla base; anthers 1.5 mm. long, elongate, apiculate, several times as long as the filaments. Style 2–4 mm. long, the sterile tips attenuate. Nutlets ellipsoidal, 3–3.5 mm. long, smooth, white, back convex, venter obtuse or weakly keeled.

Collectors appear to have been aware of this plant only in its flowering state. Nearly a hundred collections of the species in American and European herbaria have been examined, but in this large suite only five collections show the plant in the fruiting state, and none of them bear nutlets that are completely mature.

Buglossoides calabrum (Tenori) comb. nov.

Lithospermum calabrum Tenori, Fl. Nap. **3:** 174 (1824–29).

Endemic in southern Italy. Leaves broadest at the middle. Flowering stems arising from slender procumbent stems persisting from the previous season, terminated by a simple racemose cyme. Corolla with a tube evidently much surpassing the calyx, inside bearing hairy, sparingly glanduliferous plaits 7–8 mm. long which arise 4–6 mm. above the base of the tube, below the filament attachments obscurely if at all invaginate. Filaments attached 2 mm. above the base of the tube; anthers almost 1.5 mm. long, elongate, apiculate, twice as long as the filaments. Style 1–2 mm. long, the sterile tips stout and obtuse. Nutlets ellipsoidal, smooth, white, 3.5 mm. long, 2.5 mm. thick, back convex, venter obtuse.

Buglossoides Gastoni (Benth.) comb. nov.

Lithospermum Gastoni Benth. ex DC. Prodr. **10:** 83 (1846); Bot. Mag. **47:** t. 5926 (1871).

Known only from the French slopes of the western Pyrenees. Leaves broadest below the middle, lanceolate. Flowering stems clustered, arising from a densely branched rhizome, terminated by a crowded densely flowered forked cyme. Corolla with hairy and glanduliferous inflexed plaits 3–4 mm. long which arise 2.5–3 mm. above the base of the tube, bearing no invaginations below the filament attachments. Filaments borne 1–1.5 mm. above the base of the corolla; anthers oblong, less than 1 mm. long, weakly apiculate, about as long as the filaments. Style 0.5–1 mm. long, the sterile tips stout. Nutlets yellowish, punctate and abundantly rugulose, very stout and plump, 4.5 mm. long and nearly as thick, keeled only about the sharp apex, attachment broad and basal.

A very distinct species differing from the other members of its section in having small anthers, very congested forked cymes, and very large, very plump, short-beaked, yellowish rugulose nutlets.

9. **Stenosolenium** Turcz. Bull. Soc. Nat. Moscou **13**: 253 (1840); DC. Prodr. **10**: 103 (1846). Type species *Anchusa saxatilis* Pallas.

Plant a hispid annual herb with one to many erect or decumbent stems. Leaves costate but veinless, lower oblanceolate, the upper ones becoming lanceolate. Inflorescence scorpioid, elongate, bracted throughout (lower bracts foliaceous), distinctly racemose in age. Calyx short-pedicellate, 5-fid, hispid; lobes slenderly lanceolate, attenuate, slightly unequal with the abaxial one usually the longest. Corolla violet or purple, salverform, outer surface with minute, short, usually spreading hairs, inner surface with a villulose annulus but otherwise glabrous, bearing no stipitate glands; limb spreading, breadth less than the length of the tube, rounded lobes slightly broader than long, imbricate in the bud; tube elongate, about twice as long as the calyx, subcylindric, upper third to half broadest and forming an ill-defined throat, above the base bearing a short thickish collar-like villulose annulus; throat unappendaged. Stamens borne at unequal heights in the throat, included, the uppermost one usually abaxial; filaments slender, a half to a third as long as the anther; anthers elongate, laterally compressed, affixed near the middle. Pollen elongate with rounded ends, symmetric, constricted at the middle, 38–41 $\times$ 22–25 μ (16–20 μ thick at the middle), bearing two rows of 8 or 9 inconspicuous pores one at each end of the grain, polar profile circular. Style shorter than the calyx, forked below the apex; stigmas two, distinct, compressed, obovate-spathulate. Gynobase flat or concave, with four triangular attachment faces, usually maturing four nutlets. Nutlets tuberculate, usually brownish, ascending, supported on a stout, laterally affixed inframedial vertical stipe; axial edge angulate, vertical, nearly straight, above the middle formed by the short ventral keel on the nutlet-body and below the middle by the ventral side of the stipe; seminiferous body of the nutlet ovoid, inclined at an angle of 40–45°, its pointed apex held above the nutlet-attachment and its rounded base abaxial to it; stipe stout, usually partially hollow, expanding abruptly at the base, sides minutely verrucose; funicular canal ascending vertically inside the stipe and entering the oblique nutlet-body near the middle of its ventral side; ventral keel short, supramedial, formed of a usually completely fused ventral suture. Seed straight, funicular attachment slightly above the middle.

A monotypic genus of eastern Asia. In most characters it shows close similarities with the Asiatic species of the genus *Arnebia* and is probably most closely related to them. Its fruit, however, is very different, not only from *Arnebia* but from all other members of the Lithospermeae.

Stenosolenium saxatile (Pallas) Turcz. Bull. Soc. Nat. Moscou **13**: 253 (1840).

Anchusa saxatilis Pallas, Reise 2[3]: 718, t. "F", f. 1 (1773).

Onosma saxatile (Pallas) Lehm. Asperif. **2:** 371 (1818).
Arnebia saxatilis (Pallas) B. & H. ex Forbes & Hemsl. Jour. Linn. Soc. **26:** 155 (1890).

Ranging from the mountains near Pekin and northwestward across eastern Mongolia towards the Baical region.

The corolla is 12–19 mm. long in total length and has a spreading limb 7–10 mm. broad. The tube is 8–12 mm. long and its lower half or two thirds averages ca. 1 mm. thick. The upper half or third of the tube, however, is perceptibly thicker (ca. 1.5 mm.) and so forms an ill-defined cylindric throat. This elongate throat bears no hair nor glands on its inner surface and no appendages.

The stamens vary as to their distribution in the throat. In some plants they are affixed all at evidently different altitudes in the throat along most of its length, while in others they tend to be grouped below the middle of the throat, most of them with very slight differences in height of attachment and only one obviously higher than the others. When the stamens are loosely distributed, the uppermost stamen may be affixed 2–3 mm. above the lowermost one, but when crowded towards the base of the throat, the maximum difference in height of attachment may be reduced to 0.5–1 mm. The distribution of the stamens seems best described as spiral. Except that the uppermost one always appears to be on the abaxial side of the tube, the relative heights of the stamens seem to have no relation to any possible plane of symmetry in the corolla. The behavior of the androecium is suggestive of that in forms of *Arnebia decumbens*, cf. Jour. Arnold Arb. **33**: 322 (1952). In that species the stamens may have a loose spiral arrangement in the corolla-throat or be grouped near the summit of the tube, sometimes with only one stamen attached obviously lower than the others. This grouping, when present, is at the top of the throat rather than at the bottom as in *Stenosolenium*, but the extreme range of variation in stamen attachment is otherwise very similar.

Although there are differences among plants as to the distribution of the stamens in the throat, the variation seems to be independent of any differences in style length. The forked style is always short, 3–5 mm. long, and reaches up into only the narrow lower half of the corolla-tube. The two compressed, somewhat spathulate stigmas are borne, accordingly, always well below the level of the lowest stamen. There is no evidence that either heterostyly or cleistogamy are ever present.

The pollen of *Stenosolenium* is elongate, constricted at the middle, with the upper and lower halves similar in size, form, and other details. At both ends, where broadest, it is encircled by a set of eight or nine equally spaced very conspicuous pores. These elongate, medially constricted, symmetric grains with biseriate pores closely resemble those of the species of *Arnebia*. Indeed, the only striking difference appears to be in the number of pores in each encircling row, eight or nine in *Stenosolenium* and four or five in *Arnebia*.

The nutlets of *Stenosolenium* are very distinctive. Viewed laterally, their seminiferous body (2 mm. long) is inclined about 45° and is supported ventrally by a stout downwardly directed vertical stipe. This stipe is affixed obliquely below the middle of the sloping (ventral) under side of the nutlet-body and is short-columnar with the base ampliate and flaring. In lateral profile the nutlet has a vertical, nearly straight ventral edge (2 mm. high) which is formed above the middle by the short vertical ventral keel and below the middle by the ventral side of the stipe. Because of this the stipe appears to be a downward projection from the base of the short supramedial ventral keel. This keel, formed of a prominent fused ventral suture, ends abruptly. There is no suggestion of a downward prolongation onto the stipe below it. The stipe is minutely verrucose on all sides. Although distinct from the nutlet-body for most of its length, it remains close to the latter and its lower attachment end is in the same horizontal plane as the lower end of the body. Superficially, at first glance, the nutlet seems to have a strongly excentric but still basal attachment. A study of the course of the funicle, however, proves this is not the case. The funicle in its tubular canal is conducted upward from the gynobase inside the partially hollow stipe and then through the pericarp near the middle of the sloping ventral side of the nutlet-body. The important fact here is that the funicle enters the nutlet-body not at the base but below its middle on the side. In the strict morphological sense, the nutlets of *Stenosolenium* are laterally attached! Were the stipe on these nutlets suppressed and the attachment scar sessile, the latter would have a position almost half-way up on the venter of the nutlet. *Stenosolenium*, accordingly, has a character of the Eritrichieae.

The position of the attachment on the nutlet-body usually has phylogenetic significance and is the most important single character used in assigning genera to the tribes of the subfamily Boraginoideae. As an indicator of natural relationships it is prevailingly satisfactory, but as with all single characters, there can be expected to be instances in which its indications are not acceptable. Such seems to be the case as regards *Stenosolenium*. Only in the position of its nutlet attachment does that genus suggest the Eritrichieae. Other indicative structures all point to the Lithospermeae, and even more precisely to a close relationship with *Arnebia*. More significant than the nutlets in determining the affinities of *Stenosolenium* are its forked style with two stigmas, its unequally affixed stamens, its elongate corolla with well-developed basal nectary but unappendaged non-glanduliferous throat, and its elongate symmetric medially constricted pollen with two rows of pores. Only in *Stenosolenium* and *Arnebia* are these characters found associated. These and many other minor similarities seem to be unmistakable evidence of close affinity. *Stenosolenium* appears to be a member of the Lithospermeae, aberrant only in nutlet structure.

Among the Boraginaceae distinctly stipitate nutlets are developed in only a relatively few genera, in *Stenosolenium* and *Alkanna* of the Lithospermeae, in *Caryolopha* of the Anchuseae, and in *Plagiobothrys* § *Echidiocarya* of the Eritrichieae. Because it is partially hollow and has a dilated base, the stipe on the nutlets of *Stenosolenium* obviously differs in structure and appearance from those of the other genera mentioned. Surprisingly, the closest approximation is found in the obconic obliquely affixed attachment on the fossilized nutlets of the extinct *Prolithospermum Johnstonii* Elias, Special Paper Geol. Soc. Amer. **41**: 105, t. 15, f. 10 (1942) and Am. Midland Nat. **36**: 374–77, f. 3 (1946). These remarkably preserved nutlets, all that is known of the species, are found in middle Pliocene deposits of Kansas and Nebraska in middle United States. Thanks to Prof. Maxim K. Elias of the Nebraska Geological Survey, I have had a series of them for close study and comparison. They have a smooth, nearly erect, ovoid, slightly asymmetric body 2–2.5 mm. long, and on their convex side below the middle and above the rounded base bear a short, hollow, downward directed, basally expanding appendage with the attachment-surface on its horizontal base. This appendage is structurally similar to the stipe on the nutlets of *Stenosolenium*. Indeed, it differs only in originating less high on the side of the nutlet, in being shorter, and in being laterally adnate to the nutlet-body rather than free and slightly divergent from it. If the appendage on the nutlet of *Prolithospermum* were free rather than completely adnate laterally, it would be shorter, but would otherwise closely resemble the stipe in *Stenosolenium*. The homologies are so very clear that I am content to believe that the fossil plant belonged in a group ancestral to *Stenosolenium* and possibly even congeneric with it.

The nutlets of the extinct *Prolithospermum* give us an early stage in the evolution of the medio-lateral stiped attachment of the nutlets of *Stenosolenium*, and furthermore are suggestive of the manner by which it could have been originally evolved from a truly basal attachment on a *Lithospermum*-like nutlet. The attachment in our plants was probably evolved from a broad, horizontal, exactly basal attachment by shifting its center first to the ventral side of the nutlet-base and subsequently to a buttressed projection on the ventral side of the latter. As the attachment-surface, still large and still in relatively the same horizontal plane, became more and more to one side of the nutlet-base, the latter would cease to be truncate and would become more and more convex. The laterally dislocated attachment-surface could remain in the same relative plane only by buttressing its support higher on the ventral side of the nutlet-body. The combined results would place the attachment at the base of an obliquely affixed outgrowth to one side of the rounded base of the nutlet-body, precisely as is to be seen in the nutlets of *Prolithospermum*. A still further horizontal shift of the attachment would produce a still higher buttress on the nutlet venter and eventually even a "flying buttress" (i.e., the stipe) on the nutlets of *Stenosolenium*.

The peculiar feature of this support of the attachment in *Stenosolenium* and *Prolithospermum* is that it is more or less hollow. It is a tube-like or somewhat funnel-like organ which conducts the funicular canal from the flat gynobase upward to the point where it enters the nutlet-body. Accordingly it appears to be appendicular on the pericarp and not formed by constriction of the pericarp above the attachment or by localized gibbose prolongations of its walls, as in other stipitate nutlets. In various species of *Lithospermum* and its relatives the attachment scar is surrounded by a projecting rim of pericarp. The nutlets of *Lithospermum incisum* provide one of the best examples of this. In that species the abscission is about the edge of the collar-like rim surrounding the centrally depressed scar. By modification of such a rim attachment the obliquely affixed suprabasal attachment support in *Prolithospermum* and the tubular support in *Stenosolenium* might have been evolved. If the ancestors of these two genera had such a rimmed attachment, the attachment, as it was shifted to a position off the nutlet base, could remain in the same horizontal plane by increasing the height of the rim, particularly so on the off side. Certainly the laterally adnate, more or less funnelform support of the attachment in *Prolithospermum* is very suggestive of some such origin. If such is the case, then the tubular support of the attachment in *Stenosolenium* is only a more advanced modification by which a rim about an attachment scar has become transformed into a hollow stipe.

The gynobase of *Stenosolenium* is flat and horizontal, or its four attachment pads slope slightly towards its center. On this gynobase a basifixed nutlet would be erect. A nutlet with a sessile lateral attachment would be oblique or horizontal. The peculiarities of the nutlets of *Stenosolenium* and *Prolithospermum* appear to be those modifications necessary if the large attachment on an originally basifixed *Lithospermum*-like nutlet was shifted from the base to a more and more lateral position while at the same time the body of the nutlets maintained an erect or nearly erect orientation and the flat gynobase continued unaltered. As the attachment shifted, the funicular canal within it would also be displaced and would enter the nutlet no longer at the base, but laterally. An increasing development of tubular stipe would be required for conducting the funicular canal upward from the flat gynobase, for the greater the horizontal shift of the actual attachment, the higher up on the venter of the nutlet body would become the point at which the funicular canal pierced the pericarp.

Change in position of attachment from basal to lateral, and even apical, is a progressive evolutionary trend responsible for much of the diversity of the fruit in the Boraginaceae. The various stages represent increasing degrees of specialization and in general are associated with the phylogeny of the groups in which they are illustrated. The tribe Eritrichieae has nutlets usually with lateral attachments. The fact that it has a higher evolutionary position than the Lithospermeae is suggested also by its more specialized corollas and other floral structures. In the Eritrichieae the development of lateral nutlet-attachment has been concomitant with the development of a pyramidal, spire-like or columnar gynobase. *Stenosolenium* and *Prolithospermum* have a funicle that enters the nutlet-body laterally, and hence, certainly in a morphological sense, have a lateral attachment. This character, however, appears to have had an origin independent of that in Eritrichieae, most likely as an aberrant development in the genus *Lithospermum*. It is an example of parallel evolution and not an indicator of relationships in the Eritrichieae. Unlike the condition in that tribe, the lateral attachment of *Stenosolenium* was developed unaccompanied by compensating alterations of the gynobase, which has continued primitively flat as in *Lithospermum*.

10. **Arnebia** Forsk. Fl. Aegypt.-Arab. 62 (1775). Type species *A. tetrastigma* Forsk.

Dioclea Spreng. Syst. **1**: 502 and 556 (1825), not HBK. (1823). Type species *Arnebia hispidissima* (Lehm.) DC.

Strobila G. Don, Gen. Syst. **4**: 327 (1837). A renaming of *Dioclea* Spreng., not HBK.

Meneghinia Endl. Gen. 648 (1839). A renaming of *Dioclea* Spreng., not HBK.

Macrotomia DC. in Meisner, Gen. **1**: 281 and **2**: 190 (1840); DC. Prodr. **10**: 26 (1846). Type species *M. Benthami* (Wall.) DC.

Munbya Boiss. Diag. ser. 1, **11**: 114 (1849). Based on five species, the first two being forms of *Arnebia euchroma* (Royle) Johnston and the last three forms of *Arnebia densiflora* Ledeb.

Toxostigma A. Rich. Tent. Fl. Abyss. 2: 86, t. 77 (1851). Based on *T. luteum* A. Rich. and *T. purpurascens* A. Rich., both forms of *Arnebia hispidissima* (Lehm.) DC.

Leptanthe Klotzsch, Ergebn. Reise Prinz Waldemar 95, t. 63 (1862). Type species *L. macrostachya* Klotz., a synonym of *Arnebia Benthami* (Wall.) Johnston.

Arnebiola Chiov. Fl. Somala 227, t. 24, f. 1 (1929). Type species *Arnebiola migiurtina* Chiov., a form of *Arnebia hispidissima* (Lehm.) DC.

Plants annual or perennial, herbaceous. Stems simple or loosely branched, arising from a taproot. Leaves all cauline or some in a basal cluster, numerous, veinless or in a few species with a few well-developed, greatly prolonged assurgent veins that parallel the midrib. Cymes scorpioid, simple or forked, terminal on the main stem and leafy branches and frequently also arising directly from the upper leaf-axils along the main stem, few to many, loosely to densely disposed, at times aggregated in dense corymbose or cylindric thyrsoid clusters terminating the main stems, in age remaining densely flowered or becoming loosely flowered. Bracts numerous, only rarely surpassing the adjacent calyx. Flowers heterostylic or monomorphic. Calyx lobed nearly to the base or 5-parted, weakly to strongly accrescent, in age sometimes developing a short swollen tube enclosing the ripening fruit, persistent or deciduous when the enclosed fruit is matured, usually shorter than the corolla-tube; calyx-lobes slender to coarse, linear, ligulate, subulate or lanceolate, in age sometimes prominently and coarsely veined and crested or papillate towards the base. Pedicels short, erect. Corolla regular or nearly so, yellow, cream, blue or purple, sometimes yellow with the limb conspicuously spotted with blue or black, salverform or rarely tubular, outer surface hairy or at least so on the outer surface of the limb; tube elongate, gradually ampliate or enlarging above the middle to form a cylindric throat; limb usually well developed, flat or broadly funnelform, narrow to broad; lobes strongly imbricate in the bud, usually rounded and about as broad as long, usually spreading or widely ascending, entire or sometimes with the margins lacerate, erose or crisped; throat inside without hairs or faucal appendages and usually without any stipitate glands (stipitate glands when present very scattered and few, occurring about the mouth of the corolla, present only in some heterostylic species and usually only in the short-styled flowers); corolla-tube glabrous within or strigulose or villulose in two species only; annulus a papery collar, a thickened ring or completely absent, usually hairy. Filaments linear or unguiculate, usually very much shorter than the anther but in the short-styled flower of one heterostylic species nearly as long as the anther, affixed in the corolla-throat all at the same level or in one species at different levels. Anthers oblong to narrowly oblong, affixed at or slightly below the middle, in short-styled flowers and some monomorphic flowers borne high in the throat and frequently with their tips exserted, in long-styled flowers usually borne low in the throat and deeply included, apex emarginate or rounded or rarely acute, base rounded or rarely with the thecae somewhat pointed at the lower end, thecae usually joined down to the very base, connective narrow to relatively broad, not sulcate. Pollen elongate, 25–75 $\times$ 14–43 μ, in lateral outline oblong with rounded ends, the sides straight or more or less strongly incurving and the grains medially constricted, encircled by a row of pores at both the upper and the lower end of the grain, upper and lower half of the grain equal in size and configuration, polar outline circular, pores four or five in each row, obscure; in all heterostylic species the grains of long-styled flowers conspicuously smaller and more constricted medially than those of the short-styled flowers. Style slender, simple or simply forked or bis-bifid, included or shortly exserted; stigmas two or sometimes four, capitate, oblong or flabellate or rarely cylindric, simple or somewhat bilobed, juxtaposed and either strict or divergent at the apex of the simple style, or solitary and terminating the individual branches of the style. Nutlets one to four developing, erect, gray, brown, fulvous, greenish or rubiginous, never white nor porcelain-like, rough, never perfectly smooth, usually evidently tuberculate, verrucose, rugose or rugulose, surface usually dull, frequently minutely verruculose, papillate or muriculate; body of nutlet usually narrowing and more or less rostrate above the middle, sometimes conic-ovoid, conic-lanceolate or lance-ovoid and usually broadest below the middle and longer than broad, or sometimes more or less dorsiventrally compressed, much broadened below the middle and as broad or nearly as broad as long and ovate, triangular-ovate, or even cordate in dorsal outline; venter usually decidedly angulate, keel well developed or more or less obscure or well developed only above the middle of the nutlet; suture usually absent, when present usually obscure; dorsum frequently carinate above the middle, below the middle convex or medially depressed (in one species the dorsum plane or slightly concave and the venter convex); attachment basal, large, usually flabellate or ovate, rarely lobed, horizontal or somewhat oblique, occasionally prolonged upward for a short distance on the venter of the nutlet body, plane on the truncate base of the nutlet or sometimes margined by the downwardly prolonged pericarpial walls, rarely convex and protrudent and visible even when the nutlet is viewed laterally. Gynobase flat or broadly pyramidal; attachment surfaces separated by lineate grooves, not margined by prominent cartilaginous tissue, plane or somewhat concave and sometimes very strongly upcurved ventrally to form a side of a frustum-like prominence at the center of the gynobase.

Arnebia as here defined includes the first fifteen species keyed and described in my recent study of *Lithospermum*, Jour. Arnold Arb. **33**: 315–316 (1952), as well as four others discussed in a supplementary paper, op. cit. **34**: 10–15 (1953). The well-known garden plant *Arnebia Echioides* (L.) DC. is excluded and assigned to the monotypic genus *Echioides*. As here accepted, therefore, the genus includes most of the species that have been traditionally assigned to *Arnebia* or its segregate *Macrotomia*. A few species of *Arnebia* extend into the drier portions of northern Africa, but most of the species in the genus are confined to Asia.

Over a year ago *Arnebia* was considered only in relation to *Lithospermum*, and after an evalution of its characters it was merged with that genus. Returning to *Arnebia* and *Lithospermum* after having critically examined all the other genera of the Lithospermeae, I find myself judging the two genera not merely by the number and decisiveness of characters useful in distinguishing them, but also according to the degree of phyletic divergence they represent as compared with that given generic recognition elsewhere in the Lithospermeae. It is now apparent that the amplified *Lithospermum* includes greater morphological extremes and is accordingly a relatively more comprehensive unit than other genera recognized within the tribe. Since I believe that genera within a natural circle of relationship should be roughly equivalent in value, it now seems best to abandon my broad concept of *Lithospermum* and reclassify its species under three smaller, more homogeneous genera (*Lithospermum*, s. str., *Arnebia*, and *Echioides*) that represent units of evolutionary divergence comparable with those given generic recognition elsewhere within the tribe.

Arnebia and *Lithospermum* are very closely related but evidently represent diverging phyletic lines. The characters they share are more numerous than their differences. The intimacy of their relationship is evidenced by unusual morphological features present in precisely the same form in both genera. Especially notable is the heterostyly in many of their species. This heterostyly, occurring in diverse species-groups in both genera, is of the most advanced sort, involving not merely dimorphy in corolla-form, stamen-attachment, anther-size, style-length, and pollen-size, but also pollen-form. The latter feature is unknown in other heterostylic plants and may be unique. This unusual development as an indicator of affinity becomes especially significant when it is recalled that heterostyly is uncommon in the Boraginoideae and that elsewhere in the Lithospermeae it is developed in only one other genus, in a very simple form in *Lithodora*. A minor feature, also rare in this family and among the Lithospermeae, developed only in *Arnebia* and *Lithospermum*, is the lobulate, lacerate, or strongly crisped margins of the corolla-lobes. A few very dissimilar species in both genera share this character.

The difficulties in separating *Arnebia* from *Lithospermum* have been discussed at length, Jour. Arnold Arb. 33: 310–315 (1952). As has been noted, the only decisive character useful in distinguishing them involves pollen morphology. Other possible differences have occasional exceptions or are difficult to express. The fruit has evolved differently in the two genera, but the differences cannot be concisely stated. The corolla-throat in *Arnebia* is never decorated with faucal appendages as is frequently the case in *Lithospermum*, and seldom, and then only very sparingly, does it bear stipitate glands comparable to those always present, usually in abundance, on the corolla-throat of *Lithospermum*. Some developments present in only some species of a genus are also indicative. The annulus inside the corolla, extremely well developed in some species of *Arnebia*, is completely lacking in others. In *Lithospermum* the annulus, weak to moderately well developed, is always present. The forked style, frequently present in *Arnebia*, is unrepresented in *Lithospermum*. The subterminal stigmas, frequent in *Lithospermum*, do not occur in *Arnebia*. The evanescent dark-colored spot on the corolla limb, developed by various yellow-flowered species of *Arnebia*, occurs also in *Echioides* but not in *Lithospermum*. With only one exception, all species of *Lithospermum* have corollas that are yellow, orange, or white. In *Arnebia* the corolla has a greater range of colors, including not only yellow and orange, but also blue, pink, and brown. Seven of the eighteen species of *Arnebia* are very definitely herbaceous annuals. Of the forty-four species of *Lithospermum* only two are plants of short duration, and these may be biennials or very short-lived perennials.

Since I discovered that *Arnebia* has very different pollen from that of *Lithospermum*, cf. Jour. Arnold Arb. 33: 308–311, f. 1–32 (1952), I have examined the pollen in all the other genera of the Lithospermeae. I am now of the opinion that the differences in pollen are much more important than previously realized. Pollen of a type similar to that of *Arnebia* has been encountered only in *Stenosolenium*. It differs from that in all other genera of the Lithospermeae in bearing two rows of pores, one at each end of the grain. The grains are always elongate and are symmetrical with the upper and lower half similar in size and configuration. In all other genera of the tribe, including *Lithospermum*, the pores are in a single row and the grains vary from symmetrical to very asymmetrical. The lower half of the grain is frequently much larger and more rounded than the upper half and hence different in configuration. No evidences of transition between the two types have been detected. The pollen in *Arnebia* (and *Stenosolenium*) has unusual and distinctive features and is the most extreme type in the Lithospermeae.

During my study of the Lithospermeae I have become increasingly impressed by the prevailing constancy as to type that is exhibited by the pollen within the various genera of the tribe. Within a given genus pollen may be very uniform in all species or it may present a limited number of variations which are all modifications of a single basic type. Closely related genera usually show close similarities in pollen. Other than in the amplified *Lithospermum* (including *Arnebia*), now abandoned, I found a single type of pollen or modifications of a single type in all genera except *Moltkia*. In that genus § *Echianthus* has globose-ellipsoidal grains with six to eight equatorial pores. In § *Eumoltkia*, however, the globose grains appear to have about twenty pores, these not lined up about the equator but arranged, rather, in a strongly undulate line that crosses the equator diagonally at four places. The precise description of the pollen of § *Eumoltkia* is impossible with my technique, but in any case I am sure that the pollen in this section differs more from that in § *Echianthus* than is customary within the genera of the Lithospermeae. Even so, the differences are less fundamental than those between the pollen of *Arnebia* and that of *Lithospermum*. It is therefore not inconsistent to emphasize the pollen differences separating *Arnebia* and *Lithospermum* and to use them in bolstering the less decisive macroscopic differences in justifying my present recognition of both these genera.

The eighteen species of Arnebia have been described and discussed, their synonymy listed, and keys provided for their identification, in two previous papers of this series, Jour. Arnold Arb. 33: 315–334 (1952) and **34**: 7–16 (1953). In the reports mentioned the species were treated as members of the genus *Lithospermum*. Their correct names as members of *Arnebia* are given below.

Section **Euarnebia.**

Corolla subtubular; lobes erect, triangular, acute, longer than broad. Stigmas four, elongate, cylindrical. Nutlets plano-convex with a cordate base, dorsum plane or very slightly concave, venter broadly convex, lacking a ventral keel; attachment surface three-lobed, the scar of the dorsal vascular traces located in the sinus of the cordate nutlet-base much more conspicuous than that of the funicular canal. Plants annual. Corolla without annulus.

1. **Arnebia tetrastigma** Forsk. Fl. Aegypt.-Arab. 63 (1775); Johnston op. cit. 321 (1952).

Section **Strobilia** (G. Don), comb. nov.

Corolla with a well-developed spreading limb, lobes rounded, spreading, about as long as broad. Stigmas usually two, capitate or oblong or flabellate. Nutlets with a rounded back, an angulate keeled venter, and a broad base, attachment surface not lobed, the scar of the dorsal vascular traces less conspicuous than that of the funicular canal.

* *PLANTS ANNUAL; COROLLA WITH ANNULUS.*

2. **Arnebia decumbens** (Vent.) Coss. & Kralik, Bull. Soc. Bot. France **4**: 402 (1857); Johnston, op. cit. 322 (1952).

3. **Arnebia hispidissima** (Lehm.) DC. Prodr. **10**: 94 (1846); Johnston, op. cit. 325 (1952).

4. **Arnebia Griffithii** Boiss. Diag. ser. 2, 3: 135 (1856); Johnston, op. cit. 326 (1952).

5. **Arnebia fimbriopetala** Stocks in Hook. Jour. Bot. & Kew Miscl. 3: 180, t. 6 (1851); Johnston, op. cit. 7 (1953).

6. **Arnebia minima** Wettst. in Stapf, Denkschr. Acad. Wiss. Wien **50**: 30 (1885); Johnston, op. cit. 327 (1952).

7. **Arnebia linearifolia** DC. Prodr. **10**: 95 (1846); Johnston, op. cit. 328 (1952).

*** PLANTS PERENNIAL.*

× *COROLLA WITH ANNULUS.*

8. **Arnebia fimbriata** Maxim. Bull. Acad. St. Petersb. ser. 3, **27**: 507 (1881); Johnston, op. cit. 328 (1952).

9. **Arnebia obovata** Bunge, Mem. savants étrang. St. Petersb. **7**: 407 (1851); Johnston, op. cit. 329 (1952).

10. **Arnebia Szechenyi** Kanitz, Pl. Exped. Szecheny 42, t. 5 (1891); Johnston, op. cit. 329 (1952) and 8 (1953).

11. **Arnebia guttata** Bunge, Ind. Sem. Hort. Dorpat. p. vii (1840); Johnston, op. cit. 330 (1952).

12. **Arnebia Lindbergiana** (Rech. f.), comb. nov.

Macrotomia Lindbergiana Rech. f. Ann. Naturhist. Mus. Wien **58**: 58 (1951); Johnston, op. cit. 10 (1953).

×× *COROLLA WITHOUT ANNULUS.*

13. **Arnebia densiflora** Ledeb. ex Nordmann, Bull. Acad. St. Petersb. 2: 312 (1837); Johnston, op. cit. 331 (1952).

14. **Arnebia inconspicua** Hemsl. & Lace, Jour. Linn. Soc. **28**: 326 (1891); Johnston, op. cit. 12 (1953).

15. **Arnebia euchroma** (Royle) Johnston, Contr. Gray Herb. **73**: 49 (1924); Johnston, op. cit. 333 (1952).

16. **Arnebia Benthami** (Well. ex G. Don), comb. nov.

Eichium Benthami Wall. Numerical List no. 931 (1829), nomen; G. Don, Gen. Syst. **4**: 333 (1838); Johnston, op. cit. 333 (1952).

17. **Arnebia speciosa** Aitch. & Hemsl. Proc. Linn. Soc. **18**: 81 (1880); Johnston, op. cit. 13 (1953).

18. **Arnebia nobilis** Rech. f., Ann. Naturhist. Mus. Wien **58**: 58 (1951); Johnston, op. cit. 14 (1953).

11. **Echioides** Ortega, Tabulae Botanicae 7 (1773); Johnston, Jour. Arnold Arb. **33**: 314 (1952). Type species, *Arnebia Echioides* (L.) DC.

Aipyanthus Stevens, Bull. Soc. Nat. Moscou **24**: 599 (1851). Type species *Arnebia Echioides* (L.) DC.

Plant perennial. Stems several, erect, simple below the inflorescence. Leaves borne along the stem and in basal clusters, uppermost ones with rounded or subcordate sessile bases, basal ones oblanceolate; midrib prominent but veins usually evident only on the basal leaves. Cymes scorpioid, simple or forked, terminal on the stems, in age elongating, becoming straight and racemose. Bracts numerous and conspicuous, foliaceous, usually evidently surpassing the adjacent calyx, lanceolate, asymmetric with the base rounded or subcordate. Calyx lobed almost to the base; lobes moderately unequal, cuneate-linear to narrowly lanceolate, shorter than the corolla-tube, accrescent; pedicels short, stout, erect. Flowers strongly heterostylic. Corolla yellow, villulose outside, with an elongate cylindric or weakly ampliate tube which towards its summit abruptly expands into the short open throat and the spreading limb; limb with a diameter about equaling the length of the tube, bearing five evanescent brown or blackish spots, one at the base of each sinus; lobes widely spreading, rounded, about as broad as long; throat open, shallow, glabrous, without stipitate glands or faucal appendages; tube villulose inside, without glands; annulus absent. Stamens borne in the tube at several superimposed levels, in the long-styled flowers within a zone below the middle of the tube and in short-styled flowers in a zone just below the summit of the tube; filaments linear, very short, one fourth to one fifth the length of the anther; anther narrowly oblong, affixed at or just below the middle, emarginate at base and apex, dorsum with a relatively broad connective that is sulcate above the middle; thecae separate for a short distance above their bases but remaining parallel and juxtaposed. Pollen spherical or very slightly longer than broad, bearing nine obscure pores about the equator, 30–35 μ in diameter in short-styled flowers and 40–50 μ in long-styled flowers. Style slender, half as long or as long as the corolla-tube, somewhat thickened directly below the terminal stigma; stigma deeply bilobed, the lobes joined at the base and becoming divergent. Nutlets large, very plump, ovoid or elliptic-ovoid, prominently and narrowly keeled on the venter but elsewhere convex, tawny and finely mottled with purple, opaque, smooth or sparsely and broadly low-tuberculate, ventral suture absent; attachment scar basal, large, plane, usually margined by the weakly protrudent pericarpial walls. Gynobase broadly pyramidal, the attachment faces flabellate, plane, sloping, margins not upturned nor thickened, adjacent faces separated by a groove.

A monotypic genus native to Armenia, the Caucasus, and adjoining northern Iran.

Echioides longiflorum (C. Koch), comb. nov.

Arnebia longiflora C. Koch, Linnaea 20: 640 (1849).
Lycopsis Echioides L. Sp. Pl. ed. 2, 199 (1762).
Arnebia Echioides (L.) DC. Prodr. **10**: 96 (1846).
Aipyanthus Echioides (L.) Stevens, Bull. Soc. Nat. Moscou **24**: 600 (1851).
Arnebia cyrousiana Parsa, Kew Bull. 1948: 211 (1948) and Fl. l'Iran **4**[1]: 221 (1952).
Lithospermum cyrousianum (Parsa) Johnston, Jour. Arnold Arb. **34**: 7 (1953).
Lithospermum Tournefortii Johnston, Jour. Arnold Arb. **34**: 7 (1953).

The present plant has been traditionally classified as an *Arnebia*, this with considerable justification, for indeed it does have many similarities with that genus. Its pollen, however, differs extremely from that of *Arnebia*, being very similar in type to that characteristic of *Lithospermum*. In this regard the plant destroys the universality of the one set of characters that might be used in separating *Arnebia* and *Lithospermum* in a decisive manner. Because decisive characters could not be found, I recently merged *Arnebia* and *Lithospermum*, Jour. Arnold Arb. **33**: 311–315 (1952). The amplified *Lithospermum* produced I now recognize is more heterogeneous than other genera of the Lithospermeae. In order to reestablish *Arnebia* and have it separated from *Lithospermum* by at least one crucial character, and at the same time have both genera homogeneous, it has been necessary to exclude the present plant from both of the genera mentioned.

Although *Echioides* shares many characters with *Arnebia* and *Lithospermum* it differs from both in the attachment of the stamens in its strongly heterostylic flowers. The stamens within a flower are borne at several different altitudes above the corolla-base, being irregularly distributed within a broad zone inside the corolla-tube. This staminiferous zone is located below the middle of the corolla-tube in long-styled flowers and just below its summit in the short-styled ones. In *Arnebia* the stamens may be borne at unequal distances above the corolla-base in *A. decumbens*, but that is not a heterostylic species. In both *Arnebia* and *Lithospermum* the stamens in all heterostylic species are always whorled. In having the irregularly distributed stamens confined to a zone on the corolla that varies in position according to whether the individual is long- or short-styled, the present plant differs from all other members of the Boraginaceae and may even be unique among all heterostylic plants.

The corolla of *Echioides* as to general form is more suggestive of species of *Lithospermum* than of those of *Arnebia*. The corolla-tube, in having hairy inner surfaces, finds its closest parallel among American species of *Lithospermum*. In having a naked throat the corolla agrees with that of *Arnebia* and is very different from that of *Lithospermum*, for in the latter genus the throat is always decorated with faucal appendages or stipitate glands. The complete absence of the annulus is also suggestive of *Arnebia*. The annulus is suppressed in some species of *Arnebia* but is always present in some form in all species of *Lithospermum*. Most suggestive of *Arnebia*, however, are the five transitory dark spots decorating the yellow corolla-limb, a very attractive feature usually present, which *Echioides* shares with only four or five species of *Arnebia.*

The large plump nutlets suggest those of *Lithospermum* in form but differ from that genus in their tawny mottled opaque surface. Their surface features are more like those of nutlets in Arnebia. The pericarp is not dotted with pits, nor does it bear a row of pits and slots paralleling each side of the ventral keel. These are features regularly present on the nutlets of many species of *Lithospermum* but never developed in *Arnebia.* The attachment faces on the gynobase are flat and separated by a groove. They do not have thickened margins, nor are they separated by prominent cartilaginous ridges. The gynobase, accordingly, is of a type universal in *Arnebia* but relatively uncommon in *Lithospermum.* The pollen grains of *Echioides* are spheric and have nine pores arranged about the equator. They are, hence, extremely different both as to form and type from the elongate grains with biseriate pores which are universal in *Arnebia.* Although much larger than those of any species of *Lithospermum,* the grains of *Echioides* are the same as to type. In form and general organization they are duplicated by several species of *Lithospermum.*

12. **Lithospermum** L. Sp. Pl. 132 (1753) and Gen. Pl. 64 (1754). Type species *L. officinale* L.

Batschia Gmel. Syst. **2:** 315 (1791); Rehder, Kew Bull. **1935:** 396 (1935). Based on *Anonymos caroliniensis* Walter, Fl. Carol. 91 (1788), which represents *Lithospermum caroliniense* (Walt.) MacMill.

Cyphorima Raf. Am. Monthly Magazine **4:** 191 and 357 (Jan. and March, 1819) and Jour. de Phys. Chem. Hist. Nat. **89:** 98 (Aug. 1918); Merrill, Ind. Raf. 202 (1949). ". . . le type du genre est le *Lithospermum latifolium* de Linné [*L. latifolium* Michx.!]. Les *Batschia longiflora* et *decumbens* (Nuttall) doivent peut-être s'y rapporter?"

Pentalophus A. DC. Prodr. **10:** 86 (1846). Based on *L. longiflorum* Spreng. and *L. mandanense* Spreng., both forms of *L. incisum* Lehm.

Plants distinctly perennial and arising from a strong, frequently dye-stained taproot or rarely short-lived and springing from a slender biennial or perhaps even annual root. Stems herbaceous or rarely somewhat fruticulose, simple or more or less branched, hispid, villose or strigose, erect or spreading, short to elongate. Leaves usually numerous, sometimes pinnately veined but more commonly veinless, occasionally in a sterile basal cluster but usually all cauline. Cymes scorpioid, simple or geminate, few- to many-flowered, borne terminal on the stems and branches or sometimes also in the uppermost leaf-axils and becoming aggregated into a cylindrical thyrse, usually elongating, straightening and becoming racemose in fruit. Bracts usually numerous and surpassing the adjacent calyx, foliaceous. Calyx 5-fid, the lobes linear-cuneate or lanceolate, short to elongate, usually evidently shorter than the corolla-tube, the abaxial one usually appreciably the largest; pedicels very short to elongate, strict or ascending and rarely decurved. Flowers monomorphic or strongly heterostylic, rarely cleistogamic. Corolla regular, yellow, orange, or white (or pinkish or bluish to purple-red in one Chinese species), hairy on the outer surface, salverform, funnelform, or cylindric; tube straight, usually elongate, subcylindric or gradually ampliate or more commonly enlarging at or above the middle to form a differentiated throat; limb usually spreading or broadly ascending, small to large, its diameter less than, equal to, or surpassing the length of the corolla-tube; corolla-lobes equal, strongly imbricate in the bud, usually orbicular to ovate but sometimes semicircular or obovate, spreading or loosely ascending or rarely strictly ascending and nearly erect, margins entire or rarely lacerate, crisped or erose; corolla-throat frequently bearing small invaginate pubescent or glanduliferous appendages and always bearing some stipitate glands either generally distributed or localized in a band or in congregations; faucal appendages when present weak to well defined, trapeziform, lunate, gibbose, or merely convex; corolla-tube glabrous inside or sometimes distinctly hairy; annulus usually evident and usually hairy, a tumid band, a narrow ring, or represented by ten quadrate or gibbose lobes or rarely reduced to 5 to 10 tufts of hairs. Stamens arising at or usually well above the middle of the corolla-tube, borne below the middle of the tube only in long-styled flowers of some heterostylic species. Filaments unguiculate or linear, usually half the length of the anther or less, longer than the anther in one species only, all affixed at the same height above the corolla base, usually hidden behind the anther, never exserted, glabrous and glandless or sometimes bearing a few glands on the decurrent base. Anthers small, oblong to narrowly oblong, usually compressed laterally, included or rarely with the tips exposed in the corolla mouth, rounded at both ends or with the tip obscurely apiculate, affixed at or near the middle; connective on dorsum usually narrow; thecae united to the base or free for only a very short distance above the base, parallel and closely juxtaposed throughout. Pollen isodiametric or more commonly longer than broad, 13–42 μ long and 8–42 μ broad, spheric or barrel-shaped or ellipsoid with the upper and lower halves of the grain equal in size and configuration, or ovoid or medially constricted with the upper and lower halves very dissimilar in size and configuration, in heterostylic species grains of long- and short-styled flowers differing in size and frequently also in form; pores 6 to 9 but most commonly 8, borne in a single row about the equator or about the lower half of the grain where it is broadest. Nutlets erect, usually ovoid or ellipsoid and plump, broadest at or below the middle, gradually narrowed to the base or sometimes suprabasally constricted to form a stout neck just above the broad flaring base or sometimes with a thickish collar about the base; apex usually obtusish, dorsum convex (flattened below the middle in one species); venter convex or somewhat obtuse, its medial keel rarely sharp, usually low and rounded and sometimes obscure, the ventral suture lineate or obscure; surface of nutlet usually polished and porcelain-like, white or somewhat stained with brown, rarely verrucose or rugose or tumulose, usually completely smooth or smooth with few to numerous punctate depressions, the depressions sometimes shallow but usually deep and pit-like and frequently on the venter of the nutlet elongating to become slot-like, a well-defined row of slots or pits or both frequently present on both sides of the ventral keel and parallel to it; attachment of nutlet large, basal, plane, convex or in one species excavated, horizontal or somewhat oblique, the end of the broken funicular canal usually evident near the ventral angle, near the middle of the dorsal half of the attachment the ends of the dorsal vascular supply marked by a dot, a swelling, or by an erect or ascending subulate or peg-like process. Style slender, simple, included in the corolla-tube or sometimes exserted; stigmas 2, usually distinct, globose, hemispheric or ellipsoid, usually small, terminal and juxtaposed on the tip of the style or subterminal and separated by the short, somewhat bilobed sterile tip of the style. Gynobase flat to broadly pyramidal, sometimes surmounted by a thickened angulate persisting base of the style; attachment faces flat or slightly concave (or saucer-shaped or cupulate in one species), horizontal or ascending, plane or the margins somewhat thickened and prominent, separated by a groove or by the thickened protrudent angles of the gynobasic pyramid.

In the past the genus *Lithospermum* has been very broadly defined. As one of the relatively few original Linnean genera of the family it early became a catch-all for a great variety of plants subsequently recognized as generically separable. During the past century its history has been one of shrinking limits. As here defined the genus is further shrunk and I believe at last reduced to homogeneity. Various diverse elements still included in the genus by recent classifiers I have excluded and treated under such genera as *Buglossoides*, *Lithodora*, *Psilolaemus*, *Moltkia*, *Moltkiopsis*, *Mairetis*, and *Neatostema*. Also excluded are *Echioides* and *Arnebia*, recently included in the genus in my "Survey of the Genus Lithospermum," Jour. Arnold Arb. 33: 299–363 (1952). My reasons for now excluding these two latter will be found discussed under *Arnebia*.

Lithospermum, as here accepted, includes forty-three of the fifty-nine species treated in my recent paper on the genus. The first fifteen species in the "Survey" are now referred to *Arnebia*, and species no. 17 (*L. Tournefortii*) to *Echioides*. To be added to the forty-three species keyed and described in the "Survey" is one other species that was improperly excluded. This is *L. cinerascens* of Peru and Ecuador, which will be discussed presently. The genus *Lithospermum* as now defined contains, accordingly, a total of forty-four species.

The genus is especially notable for its floral dimorphism and its diversity of pollen forms. For a discussion of these and various other details the reader is referred to the above-mentioned "Survey."

Lithospermum, among all the genera of the Lithospermeae, is the only one with representatives on all continents. Of the forty-four species, four (*L. officinale, L. erythrorhizon, L. tschimganicum*, and *L. Hancockianum*) are native to Eurasia, one is confined to the highlands of tropical Africa (*L. afromontanum*), four occur in South Africa (*L. papillosum, L. diversifolium, L. cinereum*, and *L. scabrum*), and five are indigenous to the highlands of northwestern South America (*L. cinerascens, L. Macbridei, L. mediale, L. peruvianum*, and *L. Gayanum*). The remaining thirty species occur in the United States and Mexico, with the greatest concentration in the latter country. Among the species in the Old World the most distinct is *L. Hancockianum* of southwestern China. The other species of the Old World have not only the technical characters, but the facies of the species in America, and were they natives of the New World would be accepted in *Lithospermum* without question. The interrelation of the species of Europe, Africa, and America is very clear and strong, and the genus, despite its wide distribution, is a very satisfactory and natural assemblage

The genus is not only notable for its wide distribution and particularly for its occurrence in both Old World and New but also for the number of other genera with which it seems to be closely related. It is the only genus in the Lithospermeae which has close generic affinities in both America and the Old World. The genus has affinity with all the genera of the tribe native in America and is very closely related with *Macromeria*, *Perittostema*, and *Psilolaemus*. In the Old World its closest affinities are with *Arnebia*, *Echioides*, and *Buglossoides*, and perhaps also *Lithodora*. Its affinities with other Old World genera are only very generalized, certainly not immediate.

The wide distribution of the genus and the number and distribution of genera closely related to it suggests that perhaps *Lithospermum* may be a relatively generalized conservative old stock from which many of the modern Lithospermeae may have been differentiated. Such a conclusion, however, is difficult to reconcile with the fact that *Lithospermum* in many features shows specializations not to be expected in a primitive group. The modification of the corolla-throat is noteworthy in this regard. In other tribes of the Boraginoideae, all without doubt containing more highly evolved plants than the Lithospermeae, faucal appendages, usually invaginate and frequently very elaborate, are features of the corolla in practically all genera. It is interesting to note, therefore, that among the twenty-three genera of the Lithospermeae, well-developed faucal appendages are developed only in *Perittostema* and in various species of *Lithospermum*. Elongate plaits in the throat, possibly homologous with the faucal appendages of other genera, occur only in *Buglossoides* and *Macromeria*, both closely related to *Lithospermum*. Stipitate glands in the corolla-throat, localized and usually abundant, which appear to have some relation with the development of faucal appendages in the Lithospermeae, occur only in *Lithospermum* and its close relatives (*Macromeria*, *Lasiarrhenum*, *Perittostema*, *Arnebia*, and *Lithodora*). The corollas of most genera of the tribe have no faucal appendages and bear no stipitate glands in the throat. Among genera evidently related to *Lithospermum* this is also the case in many or all the species of *Macromeria*, *Onosmodium*, *Psilolaemus*, *Nomosa*, *Lithodora*, *Arnebia*, and *Echioides*. Modifications of the corolla-throat are features developed only in *Lithospermum* or to some degree only in genera evidently related to it. As a complex elaboration of the corolla, it seems to indicate that the genus is a highly specialized member of the Lithospermeae and not a generalized conservative one.

A high position in the evolution of the Lithospermeae is also indicated for *Lithospermum* by the elaborate development of heterostyly among various groups of its species. Heterostyly of a precisely similar sort is also present among certain groups of species in *Arnebia* and in a slightly more complicated state in *Echioides*. Elsewhere in the tribe it is developed only in *Lithodora*, and there in only a very simple form. The condition, accordingly, occurs in the Lithospermeae only in *Lithospermum* and in genera evidently related to it. Heterostyly, like the elaborations of the corolla, gives reason for believing that *Lithospermum* is an advanced member of its tribe.

The nutlets of *Lithospermum* are prevailingly plump, ovoid or ellipsoid, and usually obtusely pointed, and have a convex dorsum and a venter that is merely obtusely angled or obtusely angled with a low rounded medial keel. Nutlets with a narrow sharp ventral keel occur only in a few species, e.g., *L. strictum* and *L. Hancockianum*. Only in *L. strictum* is the dorsum of the nutlet distinctly flattened. The surface of the nutlet is prevailingly lustrous and porcelain-like, white or somewhat stained with brown. It is completely smooth or smooth with scattered pits usually most abundant on the ventral surface. Tumulose, rugose, or verrucose nutlets occur only in *L. papillosum* and *L. cinereum* of South Africa and in *L. Parksii* and *L. mirabile* of Texas and adjacent Mexico. The only species with smooth nutlets that are not lustrous is *L. indecorum*.

A distinctive minor feature of the nutlets of *Lithospermum*, evident to some degree in most species of the genus, is the two vertical lines of deep pits or deep slots in the pericarp which parallel the ventral keel. One of these lines of depressions is usually present along each side of the keel, close to its lateral base or only a short distance removed. Outside of *Lithospermum* the lines of pits or slots associated with the ventral keel have been observed only in *Psilolaemus* and in one species of *Onosmodium*, *O. virginianum*. Possibly they may also occur on the nutlets of *Nomosa* or *Perittostema*, but at present the fruit of these genera is unknown. In any case they do not occur in *Arnebia*, *Echioides*, *Macromeria*, and *Lasiarrhenum*. In *Buglossoides* they are not developed in § *Margarospermum*, though possibly comparable developments may be present in § *Eubuglossoides*. Interestingly, they are present in *L. Hancockianum*, that very distinct species of unusual habit native to eastern China, which, of all species of *Lithospermum*, is most suggestive of *Arnebia*.

The nutlets usually narrow gradually towards the broad base or towards a constriction just above the base. In some species the suprabasal constriction forms a stout neck just above the flaring base of the nutlet. In others the suprabasal constriction is weak, but below it the nutlet is modified and has a more or less collar-like base. The scar is usually broad, distinctly basal, and horizontal or somewhat oblique. Towards the ventral edge of the scar the broken end of the funicular canal is usually evident either as a pit or as a short section of protruding tube. The lower end of the vascular supply to the dorsum of the nutlet may be undifferentiated or be marked by a small convexity near the middle of the dorsal half of the scar. Commonly, however, the tissue about the ends of the dorsal traces protrudes to form a small process on the scar. It is usually ascending and subulate in form but sometimes is peg-like and erect. Although in various genera related to *Lithospermum* there is frequently a modest elevation of tissue about the dorsal traces, when present it is usually less extreme than that to be encountered on the base of the nutlets in many species of *Lithospermum*. Indeed, outside of *Lithospermum* well-developed processes were noted only on the nutlets of *Macromeria viridiflora*. The most extreme elevation of tissue about the dorsal traces occurs on the nutlet base of *L. incisum*. In that species the process is relatively coarse, peg-like, and vertical, and because the surface of the scar collapses it gains in apparent height and becomes conspicuous in the excavated lower end of the nutlet. A similar, less extreme development of the peg-like process also occurs on the nutlet of the related species *L. Parksii*. The feature is probably a compensatory development associated with the elaboration of the broad collar-like base distinctive of the nutlet in these species, although strangely in *L. mirabile*, the other close relative of *L. incisum*, the nutlet base is flat and the process is very weak and short. The well-developed peg on the nutlet attachment of *L. incisum* is associated with another unusual feature of that species. When the nutlet detaches, the withdrawal of its peg leaves a central depression on the attachment face of the gynobase. After the fall of the nutlet the attachment face shrinks and assumes a cupulate form that is unique in this genus. Although the peg on the nutlets of *L. Parksii* is almost as prominent as that in *L. incisum*, its fall leaves no central depression on the attachment faces of the gynobase. In *L. Parksii* the faces remain permanently plane and are similar to those of other species in the genus.

A species deserving of special comment is *Lithospermum cinerascens* (DC.) Johnston, Contr. Gray Herb. **75**: 40 (1925), originally described as *Macromeria cinerascens* DC. Prodr. **10**: 69 (1846). This plant, a native of the mountains of Ecuador and northern Peru, was excluded from *Lithospermum* in my recent study of that genus. I have subsequently had all the representation of the species preserved at Kew and the British Museum (collections of Mathews, Jameson, and Lobb) available for close study and comparison, and am now of the opinion that the species is closely related to *L. guatemalense* of northern Guatemala and adjacent Mexico, and congeneric with it. The South American plant is distinguishable from *L. guatemalense* and all other members of its genus by its elongate filaments, these being once and a half to twice as long as the anthers. The corolla appears to be rather variable as to size and form. It is 3–4.5 cm. long. The elongate tube is gradually expanded for most of its length or it swells and becomes somewhat cylindric above the middle. Just below its summit the tube abruptly expands and is there somewhat funnelform. From its edges arise the short (3.5–5 mm.) ovate or ovate-triangular corolla-lobes. The lobes are usually ascending, but in one collection of Lobb there is indication that they may sometimes be reflexed. The anthers are borne in the open funnelform mouth of the tube, their tips barely if at all protruded from it. The slender filaments, 3–5 mm. long, arise 4–6 mm. below the tube summit. The medio-affixed anthers, 2–3 mm. long, are oblong and bear a pair of minute tips on their rounded summits. The thecae are joined to the very base. The corolla-tube bears scattered stipitate glands in a band 2–4 mm. broad just below the tube summit. There are no faucal appendages. The annulus consists of ten quadrate glabrous lobes. The lustrous white nutlets are sparsely punctate and bear pits and slots in a line on both sides of the ventral keel. The stigmas are subterminal and are separated by the very short and stout bilobed sterile apex of the style. The pollen is broadly ellipsoid, 25–28 $\times$ 22–24 μ, and has eight obscure pores on the equator. In large-flowered plants the trumpet-shaped corolla of the species is suggestive in size and form of that of the genus *Macromeria*. Though the filaments are more elongate than in all other species of *Lithospermum*, they are definitely included within the corolla-throat, as is characteristic in that genus. They are not exserted from the corolla-throat, as are the filaments in all species of *Macromeria*. The anthers are also included, or at most have only their tips exserted. The well-developed annulus in the corolla is that of *Lithospermum* and not *Macromeria*. The nutlets also have features of *Lithospermum*. They are punctate and bear pits and slots in a row on either side of the ventral keel, which is never the case in *Macromeria* but is frequent in *Lithospermum*. The plant gives no evidence of being closely related with any particular species of *Macromeria*. It does, however, have an evident ally in *Lithospermum* in *L. guatemalense*. Between *Macromeria* and *Lithospermum*, the plant clearly belongs in the latter genus.

13. **Cerinthe** [Tournef.] L. Sp. Pl. 136 (1753) and Gen. Pl. 66 (1754). Type species *C. major* L.

Annual, biennial, or perennial herbs, glabrous or nearly so, sometimes glaucescent. Stems leafy, one to numerous, simple or branched, usually erect. Leaves all cauline or some in basal clusters, glabrous or at most with very scattered appressed hairs or a ciliolate margin, with inconspicuous pinnate veins, upper surface usually dotted with pallid groups of mineralized cells; lower cauline leaves more or less oblanceolate but usually broadened at the very base and usually with a somewhat amplexicaul attachment; middle cauline leaves oblong or ovate, sessile, with a broad cordate-auriculate amplexicaul base, apex usually obtuse or rounded. Inflorescence loosely scorpioid, elongating and unilaterally racemose in age; cymes single or geminate at the ends of the stems and branches; bracts very well developed, foliaceous, very conspicuous, sometimes purpurescent, usually hiding the calyx, base cordate-auriculate and amplexicaul. Calyx 5-fid; lobes very unequal, strongly imbricate, foliaceous or somewhat membranous, glabrous or with margin ciliolate, usually accrescent in age, outermost sepal broadest and usually somewhat cordate at base; pedicel slender, glabrous or short hispidulous, in age elongate, ascending or decurved. Corolla yellow or partially purple or violet, completely glabrous, coarsely tubular, several times longer than broad, broadest at or above the middle, straight and regular or most prolonged on the two-lobed adaxial side with the tube ventricose and the limb more or less distinctly oblique; throat without appendages, hairs or stipitate glands; annulus evident, a narrow thickish glabrous ring or collar; lobes broadly to narrowly triangular, very short or as much as two thirds the length of the tube, more or less recurved or sometimes erect or even connivent, acute or the tip somewhat rounded. Filaments affixed above the middle of the corolla-tube, glabrous, usually thickish and narrowed from a broad base, equal or within the corolla differing slightly in shape (odd medial stamen adaxial), less than a quarter the length of the anther to nearly as long. Anther elongate, affixed above the base, included in the throat or more than half exserted from it, free or joined only by entangling of the tails on the thecae, terminated by an evident gradually narrowed sterile appendage; terminal appendage usually with a narrow tip, frequently with a denticulate margin; thecae with minutely papillate-ciliolate edges, near the base remaining separate and tending to spread and thus form the more or less sagittate base of the anther; basal end of theca sometimes with only a short stout thickened tip but more commonly with the tip prolonged into a slender flexuous barbellate tail; back of anther pale or frequently black, more or less coarsely muricate or muricate-papillate, connective usually smooth and only moderately prominent. Pollen barrel-shaped or ellipsoid to nearly spheric, $18–37 \times 15–33\ \mu$, polar profile circular or somewhat polygonal; pores eight, borne in a well-developed equatorial groove, rarely prominent; colpi eight, fusiform or linear. Ovary four-lobed, four-ovulate. Nutlets one or two, each two-celled (one-celled or one-ovulate only by abortion), smooth, rarely lustrous, usually mottled with brown or purple, erect or weakly incurved, more or less broadly ovoid, back convex, apex notched and bicuspid, venter flattened and not keeled; suture linear-sulcate, evident on the venter of the nutlet and frequently also down the dorsum and rarely even across the attachment scar; attachment broad, basal, plane. Gynobase strongly depressed, when fully developed bearing two semicircular to near circular attachment faces which are horizontal or are slightly inclined away from the base of the style. Style slender, eventually exserted from the corolla, dorsiventrally compressed at the base; stigmas two, small, terminal, juxtaposed, distinct or more or less united.

A very distinct and readily recognizable genus with representatives occurring from middle Europe and northwest Africa east to the Caucasus and northern Iran. No detailed comprehensive treatment of its species has been published. The genus contains at least three or four major species and also a goodly number of well-marked geographic varieties that are accepted as species by many authors. *Cerinthe* has its greatest concentration of forms in the western and northern portions of the Mediterranean area.

Among the Boraginoideae *Cerinthe* is notable for its practically glabrous herbage, its usually broad leaves and bracts that are cordate-amplexicaul at the base, its very strongly unequal broadly imbricate calyx-lobes, and especially its bilocular two-seeded nutlets. The plant is obviously a member of the Lithospermeae, and though very highly specialized and distinct, probably has its closest affinities with *Onosma* and related genera.

In general structure and appearance the corolla and androecium are very similar to those of *Onosma* and *Podonosma*. The corolla-lobes may be short and recurving as prevalent in *Onosma* or elongate and erect as in *Podonosma*. Although the corolla is completely glabrous and thus different from many of the species in *Onosma*, corollas that are glabrous or very scantily pubescent are found in *Podonosma* and in some species of *Onosma*. The stamens of *Cerinthe* show a prevailing basic similarity with those of *Onosma* and its relatives. The elongate anthers are terminated by a similar terminal appendage. They are also roughened on the back, and their thecae are also free and more or less spreading at the base. The lower end of each theca may have a thickened point as in *Onosma* or, unlike in that genus or in any of its allies, may be prolonged into a slender flexuous barbellate tail. Unlike in the genera mentioned, the anthers are joined neither by coherence at the base of the thecae nor by coherence along the margin of the thecae. The anthers of *Cerinthe*, though regularly free in some species and varieties (as in *Onosma*), in most species are held together at the base — not by growing together, but only by the entangling of the flexuous tails on the thecae. The synandrium produced, though not achieved by adnation, functions exactly like that in those species of *Onosma* which have only the basal tips of their thecae coherent.

The corolla of *Cerinthe* may be perfectly regular or have a more or less clear bilateral symmetry. In *C. retorta* Sibth. & Sm., and to a less extent in some of the forms of *C. major* L. and its allies, the corolla may be more or less distinctly ventricose, not only above the base on the abaxial side, but also above the middle of the adaxial side. When this is relatively well developed, as in *C. retorta* and *C. gymnandra* var. *macrosiphonia* Murb., the unilateral swellings can so modify the form of the corolla that it becomes weakly curved in a sigmoid manner. In the two plants mentioned, the corolla is slightly prolonged on its two-lobed adaxial side, and the upper portion of the tube is somewhat outcurved and the limb is oblique. Associated with this zygomorphy of the corolla is also some differentiation among the filaments inside. In *C. gymnandra* var. *macrosiphonia*, furthermore, the exserted cone of connivent anthers is not central and vertical in the mouth of the corolla, but rather, emerging from the abaxial side of the mouth, is directed obliquely upward, with the tip over the opposite side of the corolla-limb. The flowers of *C. retorta* and *C. gymnandra* var. *macrosiphonia* have an evident bilateral symmetry that has involved not only the corolla but also the androecium. Among the many species of *Onosma* the only parallel to the conditions described in these species of *Cerinthe* is that in *O. multiramosum* H.-M. of China. In that species the matured corollas in the bud and the exserted synandrium in the open flowers are prolonged on the adaxial side and are strongly out-curved, i.e., bent away from the cyne axis in a manner suggestive of the subapical out-curving of the corolla observable in *Cerinthe*.

The fruit of *Cerinthe* differs from that of all other Boraginoideae in having bilocular two-seeded nutlets and these never more than two in number. The two carpels of the fruit, which in other Boraginoideae are each divided to form a pair of distinct one-celled one-seeded nutlets, are unlobed in *Cerinthe*. The nutlets are superficially similar to the two-seeded nutlets produced by some species of *Heliotropium* and are comparable also to the two-seeded pyrenes of the drupaceous fruits of some Ehretioideae. For the proper interpretation of the fruit of *Cerinthe* the evolutionary steps in the development of fruit within the Boraginaceae should be recalled. The fruit in this family has been elaborated from a two-carpellate, two-celled ovary bearing four ovules which become four-celled by the development of a partition within each carpel, and then, subsequently, become two-lobed and then four-lobed, and finally in the Boraginoideae become four-parted, with each lobe (the nutlet) unilocular and one-seeded and affixed independently about the base of the style. Since the two-seeded nutlet of *Cerinthe* represents a whole carpel, and the one-seeded nutlets of all other members of the Boraginoideae only half of a carpel, it is perhaps not surprising that the fruit of *Cerinthe* has been interpreted by some authors as being not only the most simply but also the most primitively organized within the subfamily, and even as more or less transitional to the less highly evolved fruits in the Heliotropioideae and Ehretioideae. With such a conclusion, however, I cannot agree. Along with most authors, I am of the opinion that the two-seeded nutlets of *Cerinthe* are simply single-seeded nutlets which somehow have failed to develop separately during ontogeny. *Cerinthe*, like other genera of the Lithospermeae, no doubt had immediate ancestors with a typical boraginoid fruit consisting of four discrete single-seeded nutlets. In the present genus, the union of the four nutlets into two double nutlets, although presenting a condition suggestive of a primitive one, is actually a late secondary development and accordingly a highly specialized one.

The ovary of *Cerinthe*, viewed shortly after anthesis, is distinctly four-lobed and is generally similar in appearance to that of most Lithospermeae at the same stage of development. The pair of lobes (those derived from one carpel) which will develop into a bilocular nutlet are at this stage united only below the middle, usually for no more than one third their total length. The depth of separation between the lobes within each pair is evidently less than that between the two pairs. Serial transverse sections through the base of the ovary will show the presence of only a basal zone in which the ovarial lobes are united in pairs. Only if in its subsequent development growth is largely confined to this basal zone can the ovary of *Cerinthe* produce bilocular united nutlets. Growth centered above this zone would produce single-seeded nutlets as in other Lithospermeae. In *Cerinthe* growth in the upper zones of the ovary is retarded. The free tips of the ovarial lobes are represented in the mature nutlets only by the bicuspid apex.

The nutlets of *Cerinthe*, when perfectly developed, are two-celled and two-ovulate. Single-seeded one-celled nutlets may be found, but these always show some evidence of being imperfectly developed. In some unilocular nutlets the undeveloped half may be reduced to a narrow longitudinal ridge, or in others represented only by a discolored spot (i.e., the attachment-scar of the suppressed half) at the base of the nutlet. The attachment scar of the two-seeded nutlet is symmetrical and evenly rounded, but in the one-seeded nutlet it is irregular and somewhat lobed on the side of the nutlet with the suppressed cell. There are other indications that the nutlets of *Cerinthe* are duplex. The tips of the united nutlets remain free when both are equally developed and form the characteristic bicuspid tip to the *Cerinthe* nutlet. The wall separating the two cells within the nutlet is dense and homogeneous. It bears no cavities nor any abscission layer, as frequent in comparable partitions in the nutlets of the Heliotropioideae and the Ehretioideae. The endocarp of the united nutlets is completely confluent. There are, however, lines of suture on the exocarp delimiting the boundaries of the component nutlets. A lineate groove is always present down the middle of the flattened venter, from between the two nutlet-tips down to the base. This groove may also continue more or less clearly down the middle of the convex dorsum and occasionally even be traced across the middle of the attachment scar. In the attachment other evidence of the duplex nature of the nutlet is evident, for the two halves of the nutlet share no vascular supply, both being directly affixed to the gynobase, and each supplied directly from it.

Cerinthe has pollen very different from that of *Onosma* and *Podonosma*, which is surprising, for the corollas and androecium of the three are very similar. The symmetric grains of *Cerinthe* have eight pores borne in a well-marked equatorial groove and associated with eight colpi. The strong equatorial groove distinguishes the pollen from that of all other Lithospermeae. Pollen of *Onosma* and its allies is uniformly three-porate. In number of pores, accordingly, *Cerinthe* is in very much closer agreement with the pollen of *Lithospermum* and its allies and, interestingly, with that of the American genera which most resemble *Onosma* in corolla and androecium. The three natural species-groups within *Cerinthe* have each a distinctive pollen.

The largest grains (33–37 $\times$ 30–33 μ) are associated with the well-marked species, *C. retorta*. These are ellipsoid-sphaeric, almost as broad as long, and possess a narrow equatorial groove and eight linear (not fusiform) colpi which extend well towards the polar areas. The pores are unusually large. In *C. major* L. and its obvious relatives, the pollen grains are barrel-shaped. They are distinctly longer than broad and have convex or nearly parallel sides and abruptly narrowed ends. They measure 24–26 $\times$ 16–18 μ. The grains have a broad equatorial groove and moderately elongate fusiform colpi. The pores are obscure, but apparently always eight in number. *C. minor* L. and *C. glabra* Mill. and their varieties all have similar ellipsoid grains, 18–22 $\times$ 15–18 μ, the smallest in the genus. In lateral profile the sides are convex or slightly angled. The eight pores are associated with an equatorial groove and short fusiform colpi.

14. **Podonosma** Boiss. Diag. ser. 1, **11**: 113 (1849) and Fl. Orient. **4**: 178 (1875). Type species *Onosma syriacum* Labill.

Plant perennial, herbaceous, or fruticulose at the base, hispid-villose or somewhat hispid with intermixed slender gland-tipped hairs. Stems numerous, simple or laxly branched, loosely spreading or decumbent. Leaves numerous, cauline, lanceolate, acute, with evident midrib, obscurely pinnate-veined or veinless. Cymes loosely scorpioid, borne solitary or geminate, terminal on the stems and leafy branches, in age elongating and becoming unilaterally racemose. Bracts lanceolate, numerous, becoming foliaceous and conspicuous in the fruiting inflorescence. Pedicels slender, elongating in age and usually becoming decurved in fruit. Calyx lobed almost to the base; lobes lanceolate, nearly as long as the corolla-tube, equal or nearly so, in fruit accrescent and becoming lance-cuneate with the tips connivent and the bases reduplicate. Corolla blue, glabrous, regular, inside without faucal appendages or stipitate glands; tube cylindric, abruptly narrowed at the base, without a differentiated throat; lobes narrowly triangular, soon reflexed, twice as long as broad, a quarter to a third the length of the tube, sides straight, apex acute; annulus well developed, villulose, distinctly ten-lobed. Filaments not half the length of the anther, affixed in the upper third of the corolla-tube, compressed, narrowing upward from the base. Anthers elongate, becoming half exserted from the corolla mouth, laterally coherent below the middle, affixed about one fourth of their total length above the base, upper half consisting of a somewhat firm stramineaceous appendage which is narrowed to an acute tip, base emarginate; thecae spreading only at the very base, their lower end with a thickened tip, not coherent; back of anther with a broad slightly prominent stramineaceous connective, not evidently papillate nor muricate. Pollen globose-ovoid, 18–22 × 16–20 μ, broader and more rounded at the lower end; pores three, associated with fusiform colpi, submedial, borne about the broadest part of the grain. Style filiform, tardily exserted from the anther-tube; stigmas united, minute, terminal. Nutlets triangular-ovoid, tuberculate, abruptly bent 90° below the middle, the small substipitate attachment basal on the erect lower third of the nutlet body; ventral keel thick and prominent. Gynobase strongly four-lobed; the lobes pale, cartilaginous, pulvinate, each bearing a small oblique concave attachment surface.

A well-marked genus containing two species, *P. syriacum* (Labill.) Boiss., a plant of cliffs, walls, and other rocky places from Syria to Palestine and east to Iran, and *P. galalense* Boiss., said to be a rhizomatous plant of eastern Egypt. No material of the latter has been seen.

In general habit, glanduliferous herbage, form of calyx, decurved fruiting pedicels, and most important of all, in appearance and structure of nutlets and gynobase, *Podonosma* is extremely similar to *Alkanna* § *Eualkanna*. The corolla and androecium of *Podonosma*, however, is extremely different from that of *Alkanna*. In these floral structures it shows detailed similarities with those of *Onosma*. The similarities with both *Alkanna* and *Onosma* combined in *Podonosma* are so striking and involve so many significant details that I am forced to the belief that *Podonosma* shares a close relationship not only with *Alkanna* but also with *Onosma*, one possible only through a shared common ancestry.

The corolla and stamens of *Podonosma* are of the type present in *Onosma*. The most obvious difference in the corolla is in the length of the lobes. In our present genus these are elongate (twice as long as broad) and reflexed, whereas in *Onosma* they are practically always short (about as long as broad) and erect or only loosely recurved. Indeed in only one species of *Onosma*, *O. longilobum* Bunge, are the lobes as elongate as in *Podonosma*. The anthers of *Podonosma*, as in many species of *Onosma*, are united into a tube, but unlike the anthers in the latter genus, those of *Podonosma* cohere only for a limited time and then only along the margin of the fertile lower half, and not at the base of the theca nor along the margin of the terminal appendage. The terminal appendage is conspicuously developed as in *Onosma*, but differs in texture, being pale, firm, straw-colored, and opaque. Unlike that in all species of *Onosma* except *O. longilobum* it narrows to a pointed tip. The back of the anther has a well-developed convex stramineous connective, which, unlike the well-developed connectives in *Onosma*, is not evidently papillate nor muricate.

The pollen is globose-ovoid, 18–22 $\times$ 16–20 μ, slightly but distinctly longer than broad and with the lower end more broadly rounded than the upper. The three pores, in furrows, are usually obscure. They are submedial and borne about the broadest part of the grain. This pollen is similar to that in species of *Onosma* which have the anthers united into a tube. It approaches the isodiametric pollen which prevails among the more easterly ranging species of that genus. The pollen of *Alkanna* also has three pores and furrows, but is more elongate and is conic-ovoid rather than globose-ovoid in form.

The nutlets of *Podonosma* are very different from those of *Onosma*, but agree to a remarkable degree with the very unusual nutlets of *Alkanna*, cf. Jour. Arnold Arb. **34**: 279 (1953). The nutlets are small, 1–1.5 mm. long, and below the middle are abruptly bent 90° adaxially. The small substipitate attachment scar appears to be superbasally lateral, but morphologically speaking is actually basal on the short section of the nutlet below the bend which remains erect. Dissection of the nutlet reveals that the seed has a transverse flexure across the cotyledons. In situ within the nutlet the tip of the cotyledons is adjacent and vertical to the portion of the pericarp bearing the attachment scar, the proper position in a basifixed nutlet. As in *Alkanna*, but very unlike that in *Onosma*, the gynobase of *Podonosma* bears four pale cartilaginous cushion-like lobes, each bearing a small concave attachment surface on its summit. The attachment surfaces are sloping and the nutlets when affixed to them are accordingly ascending with their tips connivent.

15. **Cystistemon** Balf. f., Proc. Roy. Soc. Edinb. **12**: 82 (1883) and Trans. Roy. Soc. Edinb. **31**: 186, t. 56 (1888). Type species *C. socotranus* Balf. f.

15a. **Vaupelia** Brand, Fedde's Repert. **13**: 82 (1914); Green, Kew Bull. **1935**: 528 (1935). Type species *V. barbata* (Vaupel) Brand.

Material adequate for a survey of *Cystistemon* and *Vaupelia* is not available. *Cystistemon* I know only from the original description and illustration. Of the eight species of *Vaupelia* I have only two represented by specimens suitable for analysis, *V. hispida* (Baker & Wright) Brand, from 40 mi. s.w. of Norok, Kenya, *A. G. Curtis 649*, and *V. barbata* (Vaupel) Brand, from betw. Menongue and R. Chimpompo, Angola, *M. A. Pocock 610*. For details concerning the other species of *Vaupelia* I have been forced to rely on original descriptions and upon Brand's synopsis of the genus, Fedde's Repert. **13**: 82–83 (1914).

Cystistemon has a single species endemic to Socotra and *Vaupelia* has eight described species, one in southern Arabia and the others in tropical Africa, where they range from Somaliland to Angola. The two genera are immediately and very closely related and probably should be united. Their affinity with *Onosma* is clear. There seems to be every reason for believing that they represent a southern derivative of that genus in which the corolla-tube has become abbreviated as the corolla-lobes increased greatly in relative size and importance. In all species of *Onosma*, with the single exception of *O. longilobum* Bunge, the tubular portion of the corolla is many times longer than the corolla-lobes. In the present genera the lobes, or at least the well-developed limb, are one to six times as long as the tube, and furthermore are not erect or slightly recurving but spreading. In *Onosma* the throat of the corolla is glabrous or at most only scantily and inconspicuously strigose. It is never villose as in some of the species in the present genera.

The anthers are very conspicuous features in the flowers of *Cystistemon* and *Vaupelia*. They are extremely well developed, much longer than the corolla-tube, and borne on short stout variously modified filaments affixed near the middle of the short corolla-tube, and are accordingly almost completely exserted. The terminal appendage is extremely elongate, and unlike that of *Onosma* usually greatly surpasses the fertile portion of the anther in length. Its tip is usually pointed.

As in some of the species of *Onosma*, the anthers of the present genera are united, but unlike those in *Onosma*, they cohere not at the base and along the sides of the theca but only along the edges of the sterile terminal appendages. The back of the anthers has a prominent broad connective and a papillate surface, as is common in *Onosma*. The base of the anther is more or less emarginate. The lower end of each theca, unlike in *Onosma*, is completely unappendaged or at most has only an inconspicuously thickened tip.

The filaments are of special interest. They are relatively short and stout and affixed to the anther only a short distance above its base. In *V. hispida* they are flattened and ovate-lanceolate in outline and ventrally on their thickened base bear a small triangular ciliate appendage. In *V. barbata* they are narrow but thick and above their base are nearly encircled by a shelf-like ridge ciliate on the margin. Other members of the two genera appear also to have comparable appendages associated with the base of the filaments. The filaments of *Cystistemon* are described as "obcordatis expansis inflatis basi annulo villoso cinctis." Brand in his diagnosis of *Vaupelia* describes the filaments as "brevia basi andropodio globoso piloso inserta." The hairy appendages associated with the filament in *V. hispida* and *V. barbata* are unparalleled in *Onosma*. If similar structures are associated with the filaments in other members of *Vaupelia*, they provide a character of generic importance. The precise morphological nature of these appendages is uncertain. Those in *V. hispida* and *V. barbata* I found very suggestive of the infrastaminal appendages in *Lobostemon*, cf. Jour. Arnold Arb. **34**: 297 (1953). It seems unlikely, however, that the appendages in *Vaupelia* and *Cystistemon* can be homologized with displaced lobes of the annulus as in *Lobostemon*. The annulus is apparently suppressed or absent in *V. barbata*, but in *V. hispida* it is represented at the base of the corolla-tube by ten very minute tufts of hairs. In some species of *Onosma* the lower portion of the filaments may be decidedly hairy, and the base may be decurrent and thickened. Possibly from an ancestral condition of this sort the hairy appendaged base associated with the filaments of modern *Vaupelia* could have been elaborated.

The pollen of *V. hispida* is sphaeric, or in polar profile, sometimes obscurely three-sided. The grains measure 24–26 μ in diameter. The three pores, in furrows, are equatorial. In *V. barbata* the grains are globose-ovoid, as broad as long (20–23 μ) or at most only very slightly longer than broad. In lateral profile the grain is semicircular below the middle, but above the middle it is lightly narrowed and tends to be somewhat flattened at the upper end. The furrows are deep and rather conspicuous. The three pores are slightly inframedial. The pollen, accordingly, is in general agreement with that of *Onosma* and particularly with that of its more eastern species, and especially those with united anthers.

16. **Onosma** L. Sp. Pl. ed. 2, 196 (1762) and Gen. Pl. ed. 6, 76 (1764). Type species *O. echioides* L.

Colsmannia Lehm. Mag. Ges. Naturf. Berlin **8**: 92, t. 4 (1818) and Asperif. **2**: 356 (1818). Type species *C. flava* Lehm. [= *Onosma sericeum* Willd.].

Perennial or biennial, herbaceous or sometimes fruticulose, coarsely hispid with the hairs either appressed or spreading or frequently strigose or sometimes more or less tomentose, stellate hair-clusters sometimes abundant. Stems erect or spreading, simple or with leafy branches, arising from a taproot or caudex. Leaves with a strong midrib but usually veinless, veins when evident pinnate and usually weak; basal leaves clustered, usually oblanceolate; cauline leaves usually decreasing in size upward along the stem, usually numerous. Inflorescence simple and consisting of single or paired scorpioid cymes terminal on the stem and leafy branches, or a thyrse composed of few to many cymes arising along the stem below the terminal cyme; cymes distinctly scorpioid or loose and the flowers not distinctly biseriate, usually not greatly elongate in fruit. Bracts numerous but conspicuous only in a few species, usually shorter than the adjacent calyx, sometimes very small and shorter even than the adjacent pedicel. Flowers at anthesis borne on strict pedicels on the curved highest portion of the cyme, held vertically, horizontally or even pendulous according to position on the curve of the cyme. Flowers regular and radially symmetric or in one species with the corolla-bud and the anther-tube strongly curved abaxially. Calyx usually accrescent, lobed to the base or in a few species with a short tube which becomes distended by the ripening fruit; lobes 5, equal or practically so, all distinct or rarely two partially united, very elongate, linear to lanceolate or oblanceolate or ligulate, separated by narrow closed sinus, erect and parallel or in fruit more or less connivent, not imbricate. Pedicels short and stout to slender and elongate, usually lengthening in age. Corolla yellow, blue, or rarely white or red, tubular or obconic-tubular or rarely ellipsoidal, usually gradually enlarging upward from the base or sometimes more strongly ampliate above the middle to form a more or less campanulate throat, usually broadest a short distance below the base of the lobes but sometimes almost cylindric or less commonly broadest at or near the middle, shorter to much longer than the calyx, commonly about twice as long, outer surface glabrous or more commonly evidently puberulent or strigose or hispidulous. Corolla-lobes small, as broad or broader than long (or cuneiform in one species), triangular, acute or with the tip rounded or short-attenuate, erect or with the tip and margins more or less recurved. Corolla-throat without faucal appendages, devoid of glands except those sometimes present about the base of the filaments, glabrous inside or rarely with some appressed hairs along the veins below each corolla-lobe or on and about the bases of the filaments. Annulus usually evident, a well-developed ring or collar, usually more or less lobed and more or less evidently villulose. Filaments affixed below or near or above the middle of the corolla, short to very elongate, shorter to longer than the anther, narrowly ligulate or gradually narrowed upward or sometimes abruptly narrowed above a broadened base, glabrous or rarely hairy or somewhat glanduliferous particularly near the base; base frequently decurrent, symmetric or practically so. Anthers elongate, terminated by a well-developed appendage, usually coherent at the base and frequently joined laterally (usually by interlocking of minute marginal trichomes) to form a tube, usually affixed distinctly below the middle, included in the throat or partially to completely exserted from the corolla; terminal appendage short to very elongate, always evident, strap-shaped or attenuate, hyaline and chartaceous or sometimes firm and somewhat rostrate, tip emarginate or sagittate or sometimes obtuse, but rarely acute; thecae distinct and usually spreading for a short distance above their appendaged base, or rarely joined and parallel throughout and their basal appendages broadly joined and making a subtruncate or emarginate base to the anther; basal appendage usually short and thick, sometimes hardly more than a distinctly thickened basal tip of the theca, those of adjacent anthers usually coherent but those on the same anther usually distinct. Pollen usually sphaeric to ovoid and as long or longer than broad, 16–25 $\times$ 16–23 μ, but in one species strongly oblate, transversely elliptic and measuring

13–14 × 16 μ; polar profile circular or more or less three-sided; pores three, associated with fusiform furrows, equatorial to suprabasal. Style filiform, glabrous or very rarely hairy, usually becoming exserted from the corolla and surpassing the anthers, commonly emerging from the corolla as the bud unfolds but sometimes emerging precociously from corolla-buds which have not yet attained maximum size and in species with united anthers sometimes very tardily emerging from the synandrium, usually persisting until the fruit is ripened; stigmas two, distinct or partially to completely united, usually juxtaposed and terminal on the style, rarely subterminal and separated by the very short obtusish sterile tip of the style. Nutlets erect, small to large, smooth or less commonly variously tumulose or verrucose or rugose, lustrous to opaque, gray to olivaceous brown or blackish, frequently mottled, never white, somewhat ovoid to broadly lanceolate, frequently somewhat rostrate and in one species with terminal and lateral cornute appendages; venter usually angled, rarely with a thickened ventral keel; dorsum convex or sometimes flattened below the middle; ventral suture fused and obscure; attachment scar basal, usually triangular, as broad as long, horizontal or somewhat oblique, sometimes green. Gynobase pyramidal or flat or even depressed at the center, the attachment faces usually distinct, frequently concave.

A large and variable genus with species occurring from northwest Africa and Middle Europe east to southern Siberia and to western China and Burma. Stroh, Beiheft Bot. Centralbl. **59B**: 430–454 (1939) in a recent purely bibliographic listing of the species, enumerates 123 species referable to the genus as here accepted. Subsequent to Stroh's census *O. sericeum* and its allies have been treated by Levin, Not. Syst. Leningrad 12: 228–41 (1950), and Popov has published a detailed discussion of the genus, Proalemy botaniki 1: 70–108 (1950) and also, Not. Syst. Leningrad 14: 287–304 (1951) a key in Latin as well as in Russian covering the thirty-four species accredited to the U.S.S.R. The twenty-nine Chinese and Indian species have been keyed and described by Johnston, Jour. Arnold Arb. 32: 201–356 (1951).

The genus has its closest relatives in *Maharanga*, *Vaupelia*, *Cystistemon*, and *Podonosma*. Other close relations within the Lithospermeae are with *Alkanna*, *Echium*, and *Cerinthe*. American genera, such as *Onosmodium* and *Lasiarrhenum*, sometimes suggested as relatives of *Onosma,* appear to be more closely related to *Lithospermum* and are mimics of *Onosma* rather than close relatives of it.

The corolla is almost always coarsely tubular, from the base moderately and gradually expanding for most of its length or becoming more abruptly expanded near the middle and differentiated into a stout tube and a more or less campanulate throat. Such corollas are broadest a short distance below the base of the small, commonly deltoid lobes. A noteworthy departure from such conventional forms occurs in a few species. In *O. pyramidale* Hook. of the Himalayas, the corolla has an abbreviated proper tube and a large inflated throat. It is ellipsoid in form and hence suggestive of the corollas of *Maharanga.* In *O. stenosiphon* Boiss. of Iran, the corolla is scarcely at all ampliate, being very elongate and slenderly cylindrical. The most aberrant corolla is that of *O. longilobum* Bunge, of northeastern Iran and adjacent U.S.S.R., the only member of the genus with the lobes conspicuously longer than broad. It has a gradually ampliate tube and throat, together ca. 4 mm. long, and is broadest a short distance below the base of the lobes. The erect lobes, cuneate with an attenuate tip, are 2 mm. wide at the base and about 6 mm. long, and hence longer than the tubular portion of the corolla. They are loosely folded longitudinally (conduplicate) and the throat below them is angulate. The tube has five elongate invaginations, one below each filament attachment. Inside, the corolla is orthodox except for the terminal appendage of the anthers, which gradually taper to a slender point. Because the corolla of *O. longiloba* is so aberrant, it is probably inevitable that sooner or later the species will be given generic recognition. I have refrained from doing so because the plant, in all details other than corolla-form and pollen, is remarkably similar to *O. stenosiphon* Boiss. and *O. limitaneum* Johnston and apparently closely related to them. To be sure, these two latter species are not conventional members of *Onosma*, for both have small, unusually slender and elongate corollas, and *O. limitaneum* has somewhat tailed anthers and usually rounded, rather than deltoid corolla-lobes. They are, however, readily accommodated in *Onosma*, and *O. longilobum*, because of its relations with them, even though its corolla is aberrant, can be accommodated in the genus also.

The species of *Onosma* usually have corollas with perfect radial symmetry. Indeed, the only notable departure from this condition is that previously reported in Jour. Arnold Arb. **32**: 223 (1951) in *O. multiramosum* Hand.-Mazz. of China. In that species the corolla-buds and the anther-tube are both conspicuously bent abaxially above the middle. Though other species with slender corolla-buds may have an occasional bud showing a slight subapical bend, in none of these is it so consistent and extreme as in *O. multiramosa*. In the closely related *Maharanga* the filament-bases within each corolla are clearly differentiated into three types, and in this respect the androecium has a manifest bilateral symmetry. This is not so in *Onosma*. In the vast majority of species in *Onosma* the stamens within the corolla are indistinguishable. If differentiation of the filaments does exist in *Onosma*, as perhaps very obscurely in *O. Waddellii* Duthie, *O. Wardii* Johnston, and *O. mertensioides* Johnston, the difference is very slight and difficult to detect.

Among the most distinctive features of *Onosma* are its elongate anthers. These are almost always coherent, at least at the base, and are always terminated by an evident sterile appendage. Descriptions of the organ by past authors seem to have been largely if not exclusively based upon its representation in the species of Europe and the Near East. Among the Chinese, Indian, and some of the species of the Middle East, the organ shows more variation than is generally recognized. In western species the anthers, if joined, are coherent only at the base, but in many of the more eastern species they unite laterally to form a tubular synandrium. Similarly, western species have a terminal appendage that is strap-shaped and papery hyaline, whereas among the more easterly ones the appendage on the anther is frequently much firmer in texture, dark in color, more attenuate, and frequently somewhat rostrate in nature. Among the western plants the anther averages very much larger than in the east. The connective on the back of the anther, conspicuously developed and usually broad and prominent in the west, becomes very narrow and inconspicuous in many of the eastern species. The back side of the anther usually has its surface papillate or muriculate. Among eastern species, however, it may be nearly smooth. In most all species the anther has its thecae distinct and more or less evidently spreading for a short distance above the base, and the lower end of each theca is thickened and more or less prolonged to form a short basal appendage. Only in *O. limitaneum* are the appendages notably elongate. In *O. multiramosum* and to a less extent among other Chinese species, the thecae remain joined and parallel for their total length, and their broadened and confluent basal appendages form a truncate or weakly emarginate base to the anther.

Pollen of forty-five species of *Onosma* has been examined. The grains have three pores which are frequently somewhat protrudent and are always associated with fusiform colpi. In polar profile the grains may be circular or more or less three-sided with the angles rounded or emarginate. The pollen varies from species to species in lateral profile. All the many intermediate forms between decidedly ovate and perfectly circular and even transversely elliptic are represented. The lateral outline, as in *O. echioides* L., *O. arenarium* W. & K., and *O. dichroanthum* Boiss., can be decidedly ovate with the length evidently much greater than the breadth (25 $\times$ 16–20 μ). In such grains the pores are borne where the grain is broadest, about a third of the length of the grain above its base. In other species the grains may still retain a modified ovate outline but show less difference between length and breadth. In *O. confertum* W. W. Sm., for example, the grains are equal or practically so in length and breadth (16 μ) but are noticeably more broadly rounded below the inframedial pores than above them. From grains such as these there are many transitions to grains with equatorial pores and equal hemispheres, in which the lateral profile is perfectly circular or even very slightly broader than long. In *O. pyramidale* Hook. the grains have a polar axis which is obviously shorter than the breadth at the equator (13–14 $\times$ 16 μ). In lateral profile these grains are distinctly transverse-elliptic. The pores are equatorial or at most only very slightly inframedial.

Most of the species of Europe and the Near and Middle East have pollen of the ovoid type, i.e., longer than broad, 20–25 $\times$ 16–20 μ, and bearing the pores well below the middle, usually ca. 8 μ above the base of the grain. Among the Sino-Indian species, only seven out of the twenty-nine species have pollen of this type, viz., *O. chitralicum* Johnston, *O. hispidum* Wall., *O. khyberianum* Johnston, *O. barbigerum* Johnston, *O. Griffithii* Vatke, *O. bracteatum* Wall., and *O. dichroanthum* Boiss. Species with grains isodiametric or nearly so (16–26 μ) are most abundant in the more eastern portions of the range of the genus. There are twenty-two of the twenty-nine Sino-Indian species with pollen of this type. Among the species of the middle East I have encountered the type only in species such as *O. stenosiphon* Boiss. and *O. rostellatum*, which appear to be more closely related to the Indian and Chinese congeners than to the conventional Onosmas of Europe and the Near East. Interestingly, similar pollen occurs in *Vaupelia*, a very close relative of *Onosma*, which has long-exserted united anthers, as do many of the eastern species of *Onosma*.

17. **Maharanga** A.DC. Prodr. **10**: 71 (1846). Type species *Onosma Emodi* Wall.

Plants herbaceous, perennial or biennial or perhaps sometimes annual. Stems one to several, erect to decumbent, hispid or hispid-villose, simple or with strict to ascending leafy floriferous branches, arising from a cluster of basal leaves or more commonly from among the remnants of a leaf cluster produced the previous season. Leaves very obscurely to evidently veined; veins strictly ascending, usually pinnate but frequently with the lowest pair most elongate and most prominent; basal leaves usually oblanceolate; cauline leaves numerous, the middle and upper ones usually larger than those near the base of the stem, oblanceolate to lanceolate, usually hispid or hispid-villose with the hairs frequently appressed, hairs scanty to abundant and those on the upper leaf-face frequently with discoid bases, stellate hair-clusters present in two species. Cymes usually geminate, not clearly scorpioid and forming somewhat glomerate clusters broader than long, terminal on the main stem and sometimes also on the leafy branches, in fruit loosening to become somewhat corymbose or rarely loosely racemose. Bracts small, narrow, not conspicuous, none except the lowermost surpassing the adjacent calyx. Calyx with a broad deeply saucer-shaped or shallowly cup-shaped tube and ascending lobes; lobes cuneate or narrowly triangular, gradually narrowed from a broad base, one and a half to three times as long as broad, separated by open angulate sinus, tip acute or somewhat attenuate; lobes in fruit becoming loosely incurved and the two abaxial ones sometimes slightly larger than the other three; pedicels elongating, in fruit usually slender and as long or longer than the calyx. Corolla blue, purplish, yellow or white, about twice the length of the calyx, outside strigulose or villose-hispidulous, ovoid-ellipsoid or obovoid, contracted at both ends, abruptly expanding from a short tube into a relatively large inflated throat and at or above the middle contracting to a small mouth, above the middle usually with persisting narrow inflexed vertical plaits and hence appearing sulcate below each sinus, below each lobe with an inflated rib that protrudes between the calyx-lobes and has an abruptly contracted lower end that rests chin-like in the broad angulate sinus between the calyx-lobes, outside below the middle and usually hidden by the calyx-lobes bearing five elliptical glabrous areoles which are usually slightly depressed and sometimes invaginate near their upper end; mouth of corolla very small; lobes very small, more or less deltoid, loosely recurved above the middle, as long as broad or somewhat longer than broad, apex acute or rounded; inside of corolla glabrous or more or less hairy about the bases of the filaments, devoid of glands or faucal appendages; annulus evident, collar-like, more or less villulose. Filaments affixed at base of the throat, abruptly narrowed from a broad base, slightly longer than the anthers or distinctly shorter, two filaments with a symmetric base, a medial vein and a transverse attachment on the corolla, the other three with an oblique or vertical attachment and an asymmetric base with an excentric vein. Anthers lanceolate, always included, coherent at the base, affixed below the middle, terminated by a usually well developed, firm, gradually attenuate sterile appendage which is usually armed with some stout ascending hairs or cuneiform teeth on the margin and by a cluster of cuneiform teeth at the apex, base of anther with the thecae distinct and somewhat spreading; back of anther very obscurely papillate, the connective narrow and neither prominent nor conspicuous. Pollen cylindric or in one species ellipsoidal, pores three, equatorial, associated with fusiform colpi; polar profile circular or three-sided with notches at the corners. Style filiform, glabrous, included or short exserted, rarely persisting with the fruit; stigmas two, juxtaposed and terminal on the style, small, distinct or more or less united. Nutlets slightly incurved, brown or olivaceous, dull, tumulose and coarsely rugose with the surface very abundantly and densely muriculate or papillate, somewhat ovoid, with the venter angulate and provided with a coarse prominent ventral keel; ventral suture absent; attachment scar basal, about as broad as long. Gynobase broadly pyramidal, the sloping attachment surfaces separated by low cartilaginous ridges.

A group of nine species occurring in the mountains from the middle Himalaya east into southwestern China. The genus is obviously related to *Onosma* but is readily distinguishable by its calyx and pollen, as well as by the form and structure of its corolla.

The corolla of *Maharanga* has a very short proper tube and a relatively large, well-developed, much inflated throat, usually broadest near the middle. The mouth of the corolla and the base of the tube usually have about the same diameter. In *Onosma* the corolla form of *Maharanga* is closely simulated only by the inflated ellipsoid corolla of *O. pyramidale* Hook. This lacks, however, the characteristic outward features of the corolla of *Maharanga*, such as the narrow, tightly inflexed plaits below each sinus and, below each corolla-lobe, the distinctly puffed-out ribs which have an abruptly contracted lower end that rests chin-like in the angle of the open sinus between the calyx-lobes. Also lacking in *Onosma pyramidale* is the glabrous elliptical areole on the outside of the corolla which is associated with the very different attachment of the filaments in *Maharanga*.

The filaments are abruptly narrowed and become more or less linear above their broad base. They are affixed directly on the corolla-walls or arise from the shoulders of gibbose invaginations. The five stamens within the corolla differ in the shape of the filament, in the course of the vein within them, and in the orientation of their attachment on the corolla-walls. Two filaments have an arcuate attachment oriented transversely, and their vein is medial. Two other filaments are obliquely affixed, and their asymmetric base has an excentric vein. The fifth stamen (apparently the medial adaxial one) is vertically affixed and has a strongly excentric vein and a more prolonged and asymmetric decurrent base. Although no evidence of it has been detected elsewhere in the corolla, bilateral rather than radial symmetry is manifest in the filaments of *Maharanga*. In *Onosma* the stamens are all similar, or if there is any differentiation among them within the corolla it is very obscure.

The anthers of *Maharanga* in size and general form are similar to those in some species of *Onosma* (e.g., *O. pyramidale* Hook. and *O. cingulatum* W. W. Sm.) but differ from those of most species of that genus in their smaller size, narrow smoother connective, and firmer dark, beak-like terminal appendage. Occasionally in *Onosma* as in the species just mentioned, the terminal appendage of the anther may be obscurely papillate on the margin and so appear very minutely denticulate. In all species of *Maharanga*, except *M. bicolor* DC., the lateral margins of the appendage bear some short, stout, ascending hairs or subulate teeth. The tip of the appendage in *Onosma* may be attenuate, truncate, emarginate, or bidentate. In *Maharanga* the very tip appears to be somewhat thickened and commonly bears a number of cuneiform teeth, sometimes in a more or less crown-like arrangement.

The pollen of *Maharanga* is 3-porate and 3-colpate as in *Onosma* but is very different from that of *Onosma* in form. The grains (20–23 $\times$ 10–16 μ) are elongate and in most species are cylindric. In lateral profile they have abruptly rounded ends and sides that are nearly straight and parallel except for a weak constriction at the equator. The pores are equatorial. In polar profile the grains are circular or somewhat three-sided with the broad corners somewhat emarginate. The only departure from the cylindric form described occurs in *M. bicolor*. In that species, aberrant in a number of other minor details (included style, relatively large united stigmas, and very elongate laterally unarmed anther appendages), the pollen grains are distinctly ellipsoid. In lateral profile the sides are rounded or slightly angled at the equator where they are broadest and bear the pores.

The nutlets of *Maharanga* are similar in size and form to those of many of the Chinese species of *Onosma*, and like many of the latter they have a rough, tumulose, and rugose epicarp. The distinctive feature of the *Maharanga* nutlet is the surface of the epidermis, which is very abundantly and very densely beset with crowded minute papillae or muriculations. Only in a very few Chinese and Indian species of *Onosma* are the nutlets provided with comparable minute epidermal roughenings, and even in these they are never so well developed and so very abundant as on the nutlets of *Maharanga*.

The units of the inflorescence are not of the extreme scorpioid type prevalent among the species of *Onosma*. In *Maharanga* the rhachis of the cyme remains relatively slender and is not greatly elongate. The flowers, neither extremely numerous nor evidently biseriate, become slenderly pedicellate. Cymes resembling those of *Maharanga*, however, are developed in some Chinese species of *Onosma* such as *O. album* W. W. Sm., *O. confertum* W. W. Sm., *O. cingulatum* W. W. Sm., *O. exsertum* Hemsl., *O. fistulosum* Johnston, and *O. paniculatum* Bur. & Franch., as well as in such congeners from the Middle East as *O. stenosiphon* Boiss., *O. longilobum* Bunge, and *O. polyphyllum* Ledeb.

The species of *Maharanga* have been described and distinguished, as members of the genus *Onosma*, in my treatment of the "Sino-Indian Species of Onosma," Jour. Arnold Arb. 32: 206, 356–67 (1951). With the validity of the genus *Maharanga* now recognized, the following new binomials are required:

Maharanga verruculosa (Johnston), comb. nov.

Onosma verruculosum Johnston, Jour. Arnold Arb. **32:** 356 (1951).

Maharanga Borii (Fischer), comb. nov.

Onosma Borii Fischer, Kew Bull. **1940:** 38 (1940).

Maharanga lycopsioides (Fischer), comb. nov.

Onosma lycopsioides Fischer, Kew Bull. **1940:** 39 (1940).

Maharanga microstoma (Johnston), comb. nov.

Onosma microstoma Johnston, Jour. Arnold Arb. **32:** 360 (1951).

Maharanga dumetorum (Johnston), comb. nov.

Onosma dumetorum Johnston, Jour. Arnold Arb. **32:** 361 (1951).

Maharanga egregia (Johnston), comb. nov.

Onosma egregium Johnston, Jour. Arnold Arb. **32:** 366 (1951).

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