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STUDIES IN THE BORAGINACEAE, XXIII A SURVEY OF THE GENUS LITHOSPERMUM

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With three plates

SOME MONTHS AGO I began a study of the genus *Arnebia* for the purpose of determining whether or not the eastern Asiatic species *A. Hancockiana* (Oliver) Johnston had been properly assigned to that genus. As the study progressed questions arose as to precisely how *Arnebia* could be distinguished from *Lithospermum*. As a basis for the solution of this problem dissections were made of representative species of *Lithospermum*. This gave me reasons for doubting the naturalness of that genus as currently defined. Methodical study of all the species of *Lithospermum* was then commenced, and the investigation eventually extended to members of other obviously related genera. From an examination of a few Asiatic species my study has gradually widened into a critical re-examination and redefinition of *Lithospermum* and all the other genera of the Lithospermeae characterized by coarsely bracted inflorescence.

The present paper is concerned only with *Lithospermum*. The species of the genus are enumerated, their principal synonymy given, and a key for their identification provided. My chief concern, however, has not been with the details of species-classification, but rather with the over-all composition of the genus, and in its units only so far as they reveal morphological traits pertinent to the definition of the genus and the major grouping of its species. The observations given concerning the species are primarily those significant in establishing the relationship and the precise position of the species in a natural classification. They are mostly concerned with the inner structures of the corolla, for the most part described only imperfectly, if not completely ignored, by previous writers. The related genera will be given similar treatment in the next paper of this series. Their relationships with *Lithospermum* will there be discussed at length, and new generic descriptions, keys, and tabular synopses useful in evaluating and distinguishing them will be provided.

As here treated *Lithospermum* includes *Arnebia* and *Macrotomia*, but excludes *Lithodora*, *Moltkia* and *Stenosolenium*, as well as *Lithospermum*

apulum L., *L. microspermum* Boiss., *L. cinerascens* (DC.) Johnston, *L. revolutum* Robins., and the species allied to *L. arvense* L. and *L. purpureo-coeruleum* L. The genus thus delimited is a very natural one, readily distinguished from its closest relatives by decisive characters of fundamental importance. Its species are many and diverse, and, though prevailingly well marked, exhibit in all degrees of expression and in many combinations the various evolutionary modifications that distinguish them. As a result of a wealth of intermediates, and the freedom with which characters are combined, there are no clear-cut large groupings of the species within the genus. The genus has great internal coherence. It is exasperatingly lacking in lines of cleavage. There are no sharply defined natural major divisions. Even artificial divisions useful in a key are difficult to find. The genus contains so many well-marked species that even the naming of species-groups (series) seems impractical, since the majority of them would be monotypic. Accordingly I have proposed no subgeneric divisions in *Lithospermum*. This is not because I have made no attempt to discern them, but only because I have been forced to the belief, reluctantly, that no useful, natural, definable ones are present.

The latest comprehensive study of *Lithospermum* and *Arnebia* is that published in 1846 in the 10th volume of De Candolle's *Prodromus*. Subsequent publications concerning the genera have been mostly regional, most of them relating to only a limited number of species. Four papers, however, have sufficiently broad scope to be especially useful to the student of *Lithospermum*. One by Helene Spengler, *Oesterr. Bot. Zeitschr.* 68: 111–123, f. 1–41 (1919), is a study of the form and internal organization of the corollas of *Lithospermum*. Many species were examined and described, and the dissected corollas (and frequently also the nutlets) were illustrated. While her observations do not always conform with my findings, her paper is a stimulating and useful one. The many American *Lithospermums* have been treated by Johnston, *Contr. Gray Herb.* 70: 18–31 (1924) and 78: 6–11 (1927). The species are keyed and their synonymy given. Incidental to the publication of additional species, another key to the American species was later published by A. Brand, *Fedde Repert.* 28: 10–17 (1930). The synonymy of the American species has been rather completely covered by Johnston and by Brand. Synonymy for the species of Eurasia and Africa is to be found in the purely bibliographic paper by G. Stroh, *Beih. Bot. Centralbl.* 58^B: 203–211 (1938).

The present study is based primarily on the material in the large and very representative world-wide collection of the Boraginaceae assembled at the Gray Herbarium by my efforts during the past twenty-five years. From that source suites of specimens representative of practically all species have been available for dissection and repeated examination and comparison. Supplementary material of great usefulness has also been received on loan from other institutions: Mexican and African collections from the Missouri Botanical Garden, Mexican and South American from the Chicago Museum of Natural History and from the United States National Museum; and Asiatic ("*Arnebia*") from the Natural History Museum,

Stockholm, and from the Botanical Museum of the University of Lund. The type of *Arnebiola* was also sent for my examination from the Botanical Institute, Florence. Through the courtesy of the curators of the institutions mentioned I have had a very large and representative series of specimens for study. For this help I wish to express again, now publicly, my grateful appreciation.

GENERAL OBSERVATIONS ON THE FLOWER AND FRUIT

Most species of *Lithospermum* have yellow or orange, or at least yellowish corollas. Albino variants of these, if they exist, are apparently extremely rare. Pure white corollas, entirely so or yellow only in the throat, are characteristic of about seventeen species. Blue or pink or brownish corollas are characteristic of a few other species, mostly Asiatic. In general, closely related species agree in corolla-color. Among the Asiatic species formerly placed in *Arnebia* a number (*L. decumbens*, *L. Griffithii*, *L. Szechenyi*, *L. guttatum* and *L. Tournefortii*) have five black or blue spots on the yellow or orange corolla-limb. These decorative spots, one adjacent to the base of each sinus on the limb, are evanescent, being dark and conspicuous on the newly expanded corolla but soon fading after prolonged exposure to sunlight. They occur on the corollas of species sharing general relationships but no immediate affinity.

The corolla-lobes usually have entire margins. Erode or lobulate or lacerate margins, however, are characteristic of the Asiatic *L. fimbriatum*, *L. fimbriopetalum*, and *L. Bungei*, all former members of *Arnebia*, and also of the American species *L. incisum* and *L. calycosum*.

The throat of the corolla may bear five well-developed invaginate appendages, or these may be imperfectly developed or entirely lacking. The faucal invaginations may be trapeziform, gibbose, lunate, or mere convexities. They may be velvety, velvety with intermixed stipitate glands, or merely glanduliferous. When present their location is marked on the outside of the corolla by slits that open into pocket-like recesses or merely by convex depressions of varying depth. Minute stipitate glands are common features in and about the throat of the corolla. They may occur on the faucal appendages, when these are present, but are usually most abundant on the inner side of the appendages and especially just below their base. Frequently they are abundant on the walls of the corolla-tube as far down as the filament-attachments. In many species they decorate the decurrent base of the filaments. In some of the species lacking faucal appendages (*L. discolor*, *L. viride*, *L. californicum*) the glands are abundant and generally distributed in the throat, and in others (*L. multiflorum*, *L. obovatum*, and *L. calcicola*) they may form sharply circumscribed congregations that take the place of the appendages. The species which have the corolla-throat unappendaged and sparingly or not at all glanduliferous are mostly Asiatic. Most of them were formerly placed in *Arnebia*. Indeed, lack of such appendages and glands has been used as the crucial character in attempts to distinguish *Arnebia* from *Lithospermum*. It is to be noted,

however, that among these Asiatic species glands are not completely absent in the corolla-throat. In species such as *L. Hancockianum*, *L. Sewerzowi*, *L. Szechenyi*, *L. guttatum*, *L. densiflorum*, and *L. Griffithii* the glands may occur only in very moderate quantity or be very sparse, but they are present and are evident when looked for.

The inner wall of the corolla-tube is glabrous in most species or at most has only very minute hairs on the basal nectary. The tube is distinctly hairy, however, in *L. hispidissimum*, *L. Tournefortii*, and *L. discolor*, as well as in the three related species *L. cobrense*, *L. obovatum*, and *L. tubuliflorum*. The development has diagnostic value but little importance as an indicator of relationship. The species with hairy corolla-tubes are all heterostylic. In some the hairs are more abundant in the short-styled flowers than in the long-styled ones. An extreme condition occurs in *L. obovatum*, in which only the long-styled flowers have hairs, the tube of the short-styled corollas being glabrous.

Another feature of the corolla of *Lithospermum* is the nectary located inside the tube 1–2 mm. above the base. This appears in a variety of forms and has various degrees of development. In some species the nectary appears to be undifferentiated (*L. Tournefortii*, *L. Benthami*, *L. euchromon*, *L. tetrastigma*) or marked only by minute hairs (*L. densiflorum*, *L. incisum*). In other species it is hardly more than a tumid band (*L. californicum*, *L. rudemale*) or a lineate ridge (*L. fimbriatum*). Frequently it becomes a prominent annulate ridge or flange (*L. officinale*) or even collar-like and as much as 1 mm. high (*L. guttatum*, *L. Aucherii*). Not uncommonly it is more or less lobulate. In some species (*L. multiflorum*, *L. cobrense*, *L. caroliniense*) it is divided into ten proximate quadrate lobes. Related species tend to have similar nectaries.

The anthers are oblong or narrowly oblong with obtuse or rarely somewhat acute or even apiculate tips. In non-heterostylic flowers they are borne near the summit of the corolla-tube or below it at a distance not exceeding their own length. When the tube is short, as in *L. officinale*, they may be attached near the middle of the tube, but in flowers with elongate tubes, such as are present in most species, they are always borne in the upper quarter of the tube. In corollas with faucal appendages the tip of the anther commonly reaches up to the appendage-base and is never more than an anther-length below it. This is the normal condition in the genus. Most departures from it are associated with heterostyly. In long-styled flowers the anthers are usually borne at or near the middle of the tube even when the latter is very elongate. In *L. obovatum*, *L. cobrense*, and *L. tubuliflorum* they are extremely low, being borne on the lower third of the tube. In short-styled flowers the anthers are found very high in the tube and frequently partially exerted from it. In this genus any corolla bearing anthers near the middle of its tube almost certainly belongs to a long-styled flower of a heterostylic species.

The filaments are usually short, less than one half and usually only a third or a quarter of the length of the anther. Two species show notable departure from this norm. The stamens on the short-styled flower of *L.*

hispidissimum have filaments nearly as long as the anther. In the long-styled flowers, however, the relation of filament to anther is normal. One of the most aberrant filaments, however, is that present in some of the plants I have referred to *L. tschimganicum*. This will be discussed under that species.

The attachment of the stamens in most species is whorled, i.e., within the individual corolla all are attached at the same level on the corolla-tube. In *L. Tournefortii*, however, although always confined within definite zones on the tube, the stamens are affixed at several differing levels. In *L. decumbens*, western forms have whorled stamens or may have one stamen borne slightly below the other four. In eastern forms, however, the stamens within a corolla are frequently borne at several loosely spaced superimposed levels, with two anthers at the mouth of the tube, another pair below, and a single anther lower down. In both *L. Tournefortii* and *L. decumbens*, accordingly, there is a departure from radial symmetry in the androecium. Such departures are present in a number of genera closely related to *Lithospermum*. Stamens attached at unequal heights in the tube are developed by species of *Stenosolenium*, *Lithodora*, and *Alkanna*. In *Moltkia* the filaments become unequal in length. Zygomorphy associated with stamens of various length and heights of attachment occurs in *Echium* and *Halacsya*. The sporadic appearance of aberrant stamen-attachments in *Lithospermum* is not surprising.

The behavior of the style in the non-heterostylic species deserves some comment, since its length relative to that of the corolla-tube may change between the time pollen is shed in the flower-bud just before opening and the time when the flower is completely expanded. In mature flower-buds the style is usually sufficiently long to carry the stigmas up between the dehiscent anthers or just above them. In species such as *L. officinale*, *L. distichum*, and *L. ruderale* the relative position of stigma and anthers remains similar in the expanded corolla. In some species there is evident elongation of the corolla-tube subsequent to anther-dehiscence. When this is accompanied by comparable elongation of the style, as in *L. calycosum*, the relative position of anthers and stigmas is maintained. In *L. Nelsonii* and *L. strictum*, however, the style elongates less, and although the stigmas are between the anthers at dehiscence, they assume a position below them when the corolla is completely expanded. In some of the Mexican species (*L. oblongifolium*, *L. viride*, *L. Muelleri*, and forms of *L. calcicola*) the style has become very elongate in the unopened bud. At the time the anthers dehisce the stigmas are held well above the anthers and the style itself is somewhat contorted in order to accommodate its length in its cramped quarters. When the corolla eventually opens the style straightens and the stigmas become exerted from the corolla-tube. Were the corolla-lobes of these species not strongly imbricate, but valvate as in *Onosmodium*, the style could force a way out through the tip of the unopened corolla and be precociously exerted in the manner characteristic of that related genus. A very different condition exists among the annual species of the Old World. In some plants of *L. detonsum* the stigmas and anthers are

juxtaposed at the time pollen is shed, but by the time the corolla is fully expanded the stamens are carried high above the stigmas. The corolla-tube has apparently elongated more rapidly than the style. In *L. decumbens* and other plants of *L. detonsum*, even when pollen is shed, the stigmas are well below the anthers. Interestingly, they become even more widely separated by the time the corolla is fully expanded.

The style usually bears two stigmas; only in *L. tetrastigma* and *L. decumbens* is the number increased to four. Among some of the Asiatic species, particularly the annual ones, the style is apically forked and the stigmas terminate the short branches. In most species, however, the stigmas are sessile on the upper end of a simple style. Though usually terminal, in some American species they are distinctly subterminal, being affixed laterally slightly below a convex or conic, and sometimes notched sterile tip of the style. The latter condition is usually well developed in *L. Nelsonii*, *L. mediale*, and *L. oblongifolium*. The stigmas are usually distinct, but in such species as *L. strictum*, *L. Muellieri*, *L. fimbriatum* and *L. Szechenyi* they are crowded together on the tip of the style and their juxtaposed bases may become somewhat joined. Most stigmas are more or less globose, but in species such as *L. guttatum* and *L. multiflorum* they may become flattened and broadened and even obscurely lobed. Two species have the style more or less evidently twice forked and frequently bearing a stigma terminating each of the four ultimate branches. This remarkable condition, unique among the Boraginoideae, no doubt arose by division of stigmas borne on a simply forked style. Indeed, a suggestion of the condition is not infrequent in *L. guttatum*. In some individuals of that species the two stigmas may be very deeply bilobed and even nearly divided. With such evidence that an incipient stage actually exists, the further evolutionary steps for the formation of a bis-bifid style bearing four stigmas is not difficult to imagine. In any case the two species with this extreme development give indications in all other structures that they are not immediately related. The peculiarities they share are probably parallelisms and not the direct product of shared immediate ancestry. In this regard it is to be noted that the stigmas of *L. tetrastigma* are narrow and elongate, a form unique in this genus.

Heterostylic flowers are developed by at least eighteen species of *Lithospermum*. The two types of flowers in these species differ not only in position of stamens and length of style, but also in the size and frequently even in the shape of the pollen grains. Among most of these species the anthers in the long-styled flowers are borne near the middle of the corolla-tube. In *L. obovatum* and *L. tubuliflorum*, however, the anthers are in the lower third of the tube, while in *L. fimbriatum*, *L. densiflorum*, and *L. hispidissimum* they are borne in its upper third. The style in such flowers usually reaches the summit of the corolla-tube and may be even slightly exerted from it. In *L. densiflorum* long styles may be exerted as much as 5 mm. The anthers of short-styled flowers are borne near the summit of the tube, either entirely included or partially exerted from it. Their style reaches the middle of the tube or slightly beyond. Very short styles,

less than a quarter of the length of the tube, are present only in *L. discolor* and *L. canescens*.

Associated with the major differences relating to style-length and stamen-height, there are also the correlated minor ones usually present in well-developed heterostyly. The anthers of long-styled flowers are usually smaller than those of short-styled flowers. In some species, e.g., *L. densiflorum*, the corollas with short styles are perceptibly larger than those with long styles. In most of the species the corolla-tube differs in form also. It is usually cylindric or very gradually ampliate in short-styled flowers. In the long-styled flowers there is usually a slight but abrupt increase in diameter at above the level of the stamen-attachments, with the result that the upper half of the tube is differentiated into an elongate cylindric throat. The corollas of *L. obovatum* present an unusual difference, perhaps unique among heterostylic flowers. The inner surface of the tube is hairy in the long-styled flowers but glabrous in those with short styles. The manifestations of heterostyly in *L. Tournefortii* are also unusual and perhaps unique. In that species the stamens in the individual corolla are not borne at one level, whorled, as is usual in most *Lithospermums* and other regular flowers. Rather, they are attached at several different heights on the corolla, and so occupy a zone rather than a single level on the tube. These staminiferous zones behave as do simple whorls of stamens. They have very different positions in the two types of flowers, being located below the middle of the tube in long-styled corollas and near its summit in the short-styled.

The pollen grains of the eighteen species with well-marked heterostyly have size-differences correlated with the two types of flower, those of the short-styled flowers always being the larger (Plates I and II). In nine of these species (*L. Griffithii*, *L. Tournefortii*, *L. densiflorum*, *L. discolor*, *L. canescens*, *L. multiflorum*, *L. cobrense*, *L. obovatum*, and *L. californicum*) the grains in the two floral types, though obviously different in size, are otherwise very similar. This is normal and is the condition present in all genera in which marked heterostyly has been studied. The pollen of the remaining nine heterostylic species is not of this conventional sort. The grains in the two types of flower differ not only in size but in shape as well. This is a most unusual condition. Indeed, it seems to be a type of pollen dimorphism previously unreported. The flowers of those species of *Lithospermum* in which it occurs present heterostyly in one of its most highly elaborated states. Two of the nine species having dimorphic pollen are American (*L. tubuliflorum* and *L. caroliniense*) and seven are Asiatic (*L. fimbriatum*, *L. Sewerzowi*, *L. Szechenyi*, *L. guttatum*, *L. Benthami*, *L. euchromon*, and *L. hispidissimum*). If classed according to the intimacy of their relationship, these nine species fall into eight groups as follows: 1. *L. tubuliflorum*; 2. *L. caroliniense*; 3. *L. fimbriatum*; 4. *L. Sewerzowi*; 5. *L. Szechenyi*; 6. *L. guttatum*; 7. *L. Benthami* and *L. euchromon*; and 8. *L. hispidissimum*. Most of these have their closest affinities not with each other but with species or species-groups having pollen little or not at all differentiated in shape. Furthermore, their closest

relations are intra-continental, the American species having a basically different type of pollen than that of the Asiatic species. Heterostylic species with dimorphic pollen do not form a natural group.

With heterostyly so strongly developed in some species, it is surprising that the other members of the genus show so few tendencies of that nature. Some evidence of incipient heterostyly occurs among some of the many puzzling forms of *L. decumbens*. Throughout the wide range of that species plants within a collection may or may not show differences in style-length, and moderate differences in the distance below the corolla-lobes at which the stamens are attached. In some collections of the large-flowered forms of the species from Central Asia, the differences can be more marked and even involve the shape of the corolla-tube. In all these forms, however, pollen shows no variation in size or shape. If tendencies towards heterostyly do exist, they have only weak and uncertain expression.

Within the Boraginaceae heterostyly is known in *Lithodora*, *Pulmonaria*, *Anchusa*, *Symphytum*, *Amsinckia*, *Cryptantha*, *Oreocarya*, and *Paracaryum*. Of these genera only *Lithodora* is closely related to *Lithospermum*. Most of its species have dimorphic flowers differing in style-length and height of stamen-attachment, and in some, even in the form of the corolla-tube. Unlike *Lithospermum*, however, the two types of flowers in *Lithodora* show no differences in pollen.

Cleistogamy is present in *Lithospermum incisum*, *L. Parksii*, *L. confine*, and *L. mirabile*, all members of a closely intrarelated group, and also in *L. calycosum*. In *L. incisum* the plant first produces clusters of large, very attractive chasmogamic flowers, mostly infertile, and subsequently only large numbers of cleistogamic flowers which fruit prolifically. Chasmogamic flowers may be completely suppressed in *L. confine*. In the other species the cymes produce conspicuous chasmogamic flowers until late in the growing season, and then only minute cleistogamic ones. Both types of flowers appear to be equally fertile. In all of the five species mentioned the cleistogamic flowers are very similar. The corolla is calyptrate, usually 1–3 mm. long, and eventually falls without opening. Faucal appendages and stiped glands that may be present in the large open flowers are not developed in the corollas of the cleistogamic flowers. The pollen produced by open and closed flowers is indistinguishable, or at most very slightly smaller in the closed flowers. Since the style of the closed flowers is extremely short, the fruit produced by each of the two types of flowers is readily distinguished by the length of the persisting style associated with it.

It is surprising that cleistogamy is not a more common development in *Lithospermum*. Anyone seeking pollen in this genus for examination soon discovers that the anthers of expanded flowers are nearly always empty. Although the books report that *Lithospermum* is proterogynous, without exception I have found that normal anthers in this genus shed their pollen before the corolla opens. The pollen is dumped out and adheres in masses on the inner sides of the faucal appendages and on the glanduliferous wall of the throat. In some species masses of pollen adhere to the stigma, in the bud frequently surrounded by the anthers, and these masses are later

carried up into the mouth of the corolla by stylar elongation. The physical conditions are extremely favorable for self-pollinization. Indeed, only if the flowers are self-sterile can it be prevented. Investigation of heterostyly in many other genera has indicated that the condition is usually accompanied by a high degree of self-sterility. Possibly this is also present in most of the non-heterostylic species of *Lithospermum*.

The nutlets of most species of *Lithospermum* are ellipsoidal or ovoid and usually have a smooth lustrous white surface. There are, however, many deviations from this common type. The surface may be smooth and porcelain-like or more or less pitted, or, particularly in Asiatic species, tuberculate, verrucose, or rugose. It may be white or stained with yellow-brown or brown, or, in Asiatic species, gray, brownish, or even olivaceous. Occasionally it is rubiginous (*L. tetrastigma*) or minutely mottled with purplish (*L. Tournefortii*). The prevailing shapes are ovoid or ovoid-ellipsoidal with rounded dorsum, rounded or obtusely angled venter, and blunted obtusish apex. Sharply pointed, subrostrate nutlets, however, occur in *L. euchromon* and *L. Sewerzowi*. In *L. tetrastigma* the nutlets are compressed, having a broad, flat or slightly concave back and convex venter. In *L. fimbriatum* and *L. detonsum* the broad nutlets have a wide depression down the middle of the lower half of the dorsum.

American species frequently have a well-developed ventral keel. This is commonly low and rounded, but in *L. strictum* it is narrow and acute. It may extend even over the apex of the nutlet and onto the dorsum. Among Mexican species the ridge down the middle of the venter is frequently made more prominent by a line of pits or slit-like depressions in the pericarp on either side of it. In most American species the ventral angle of the nutlet is traversed from top to bottom by a fine lineate sulcus representing the ventral suture. Among the Asiatic species other than *L. Tournefortii* and *L. tschamganicum* there is little or no evidence of this suture. The venter of their nutlets may be angled but is never obviously keeled, nor does it bear lines of pits and slits. In most species the nutlets are gradually narrowed to the base. In some, however, as the result of a lineate suprabasal constriction, the nutlet may develop a collar-like base (*L. matamorensis*, *L. incisum*) and in others, because of a much broader suprabasal constriction (*L. ruderale*, *L. viride*) it may have a short stout neck just above a flaring base.

The nutlets have a basal attachment surface, commonly rounded and about as broad as long. It is usually flat or slightly concave or convex. In *L. incisum*, however, it is very deeply concave, almost excavated, and furthermore bears a spur-like projection. In *L. guttatum* the attachment has a broad lateral prolongation extending a short but evident distance up the venter of the nutlet-body and then outward under the truncate base of the ventral keel. A comparable upward prolongation of the attachment surface occurs also on the very aberrant nutlets of *L. tetrastigma*. The dorso-ventrally compressed nutlets of that species have a cordate base. The attachment is transversely elongate and depressed at the center and has a quadrate lobe extending upwards on the ventral side of the nutlet-body.

The gynobase in *Lithospermum*, traditionally described as flat, is, as a matter of fact, usually depressed pyramidal. When all four nutlets have been matured and shed, the gynobase usually bears four plane or somewhat concave and upcurved surfaces that slope towards the base of the style at angles of ten to forty-five degrees. In those species with nutlets that have a ventral upward extension of their attachment-scar (*L. guttatum*, *L. tetrastigma*, and to a less extent *L. Sewerzowi*) the gynobase may even take the form of a strongly truncated pyramid. Among most American species the surfaces on the gynobase (the scars or pads left by the fallen nutlets) usually have an upturned or thickened cartilaginous margin and tend to be joined laterally by cartilaginous tissue. In most Asiatic species, however, as well as in a very few American (*L. Nelsonii*, *L. Berlandieri*) the attachment pads on the gynobase are unmarginated and, though juxtaposed, remain distinct. In *L. oblongifolium* and *L. strictum*, in which the pyramidal gynobase is about as high as broad, the cartilaginous tissue between the margined attachment-pads becomes very prominent and even continues upward to the base of the style as narrow wings along the angles of the gynobasic pyramid.

POLLEN

In this genus I first examined pollen for the purpose of determining if there were size-differences associated with heterostyly. When the surprising variety of forms was revealed, the pollen of *Lithospermum* and related genera was methodically examined. It proves to be an extremely good indicator of relationships, generic as well as specific, and hence of great usefulness in classification, particularly so in *Lithospermum*. Since my purpose has been to examine pollen from as many herbarium specimens as possible (about five hundred were sampled in *Lithospermum*) my technique has been a simple one. Dehiscent anthers with pollen, taken from the flower-bud just before the expansion of the corolla when possible, have been macerated on a slide in a drop of 85% lactic acid and then protected by a coverglass. The grains expand rapidly and reach permanent form in a minute or two. Labeled, unsealed mounts have been used repeatedly over a period of six months. Those which dried out have been quickly repaired by the addition of more lactic acid. Comparison of such old mounts with freshly made ones shows no difference in pollen size or form. The grains were studied and measured under 450 magnification. It is obvious that a refined technique, and especially the use of stains and higher magnifications, would reveal much more concerning the pollen than the gross features, the size and form, and the position and number of pores which I have observed. That, however, is left to a better microscopist than I. In the present study of *Lithospermum* a wide survey of pollen-types is more useful than one that is limited because it is detailed.

The pollen of *Lithospermum* is notable in several respects. In the heterostylic species the grains of long-styled and short-styled flowers differ not only in size but frequently in shape as well. Differences in size are

not unexpected. They have been found associated with heterostyly in genera of many families. Darwin, indeed, was inclined to consider them as the ultimate proof that true heterostyly was present. Differences in shape, however, are a different matter. I have, in fact, been unable to discover any previous report of such a condition. This pollen dimorphism which is associated with the heterostyly in some species of *Lithospermum* may be unique.

The two kinds of pollen produced by the various heterostylic species of *Lithospermum* are illustrated in Plates I and II. It is to be seen that size differences occur in all the species. Dimorphism is extreme in *L. tubuliflorum* (fig. 10) and *L. caroliniense* (fig. 12), moderate in *L. Hookeri* and *L. euchromon* (fig. 3), *L. fimbriatum* (fig. 4), *L. guttatum* (fig. 5) and *L. hispidissimum* (fig. 7), and only weak or variable in *L. californicum* (fig. 9), *L. cobrense* (fig. 15), and *L. canescens* (fig. 11).

The pollen of five species (*L. incisum*, *L. Parksii*, *L. confine*, *L. mirabile*, and *L. Tournefortii*) is almost perfectly spherical. In a few others it is subglobose with the sides slightly angulate when viewed in lateral profile (*L. viride*, *L. Macbridei*, *L. strictum*, *L. Muelleri*). In most species, however, it is distinctly elongate with the length twenty-five to two hundred per cent greater than the maximum thickness. In polar view and in transverse sections perpendicular to the axis, the grains have a circular outline or sometimes a slightly polygonal one if prominent pores are included. In lateral view the profile varies greatly. The sides may be convex or outwardly angled, concave or inwardly angled, or straight and parallel or somewhat convergent. What is most unusual, the outline of the upper half of the grain may differ greatly from that of the lower half. As a result, the grains have a wide variety of forms. They may be spherical, ellipsoidal, barrel-shaped (cylindric with rounded ends), ovoid in various modifications, or, as a result of a medial or submedial constriction, achieve a lateral outline suggestive of an hourglass or a shoe-print in the snow. In size they also vary widely, from 65–72 μ in *L. densiflorum* down to 13–16 μ in *L. officinale*. As observed by me under 450 magnification, the grains appear smooth; I have detected no furrows. The pores are small and usually inconspicuous or even invisible. Only in a few species are they noticeably protrudent in lactic acid (*L. Pringlei*, *L. indecorum*). Their position and number is usually most readily determined by a study of shrunken or collapsed grains.

Two fundamentally different types of pollen, best distinguished by the position of the pores, are recognizable in the genus. One is represented by fifteen of the species formerly referred to *Arnebia* and *Macrotomia*; the other by the remaining twenty-nine species here referred to *Lithospermum*. In the latter type the pores are in a single row, equally spaced around the grain. Their number may be six, seven, eight, or nine, the particular number being relatively constant in the pollen of a given plant, but usually varying over two or three numbers among individuals of the species. When the grain of this type is spheric, ellipsoidal, or barrel-shaped, the pores are on the equator or at least equidistant from the two poles. There

is, however, in this type of pollen, a tendency for the upper and lower halves of the grain to differ in size and form. When such asymmetry is present the band of pores may occur at levels below the middle of the grain. In the subcylindric grains of *L. calcicola* the pores are only slightly below the middle. They are more so in the somewhat ovoid grains of *L. tuberosum* and very conspicuously so in grains having the hourglass or shoe-print profiles. In such medially constricted grains the pores are located where the lower half of the grain is broadest, or, in other words, at the point where the evenly rounded curve of the base of the grain terminates and constriction begins. When these grains are viewed in lateral profile, the constriction just above the pores is by sloping, straight (not curved) lines. The convergent straight lines of this constriction form the distinctive shoulders recognizable in many grains of this type. As landmarks, even in grains of the hourglass form, these sloping shoulders distinguish the lower from the upper half of the grain and are always an indicator as to the location of the single band of pores.

The other type of pollen in *Lithospermum*, that which is characteristic of most species formerly placed in *Arnebia* and *Macrotomia*, is always perfectly symmetric, with the bottom and top halves alike. It may be cylindric or nearly so, or weakly to strongly constricted medially and hence sometimes subcylindric with slightly concave sides or more or less clearly of the hourglass form. The pores are very indistinct. They appear to be arranged about the convex ends of the grain, five (or rarely four) in the row at each end. Possibly there may be additional pores, one at each pole. In this type of pollen there are no pores on or near the equator. In three species, *L. densiflorum*, *L. detonsum* (fig. 29) and *L. Aucherii*, the grains sometimes appear to be serrulate at the constricted equator. When empty, or dry and shriveled, they have an unusual form, being somewhat basket-like and consisting of superimposed rings joined by five (or four) equally spaced ribs. The ribs are usually verrucose at the middle and presumably form the serrulations previously mentioned. The empty or shrunken grains of the other species in this type are not ribbed nor basket-like. Commonly they appear subcylindric or bag-like. If they burst open, it is usually at one or more places at the ends, never at or near the middle. The pollen-walls are evidently thicker and more rigid in these grains than in the other type of pollen.

The developmental history of the asymmetric pollen grains deserves study. Prepared sections of the anther at various stages of development should reveal exactly how the unusual grain-shapes arise and how, for example, grains with the hourglass form can be efficiently packed together in the theca. Until the matter is investigated we can only suspect that the peculiarities in the form of the grains must be a manifestation occurring late in their ontogeny.

Of the two types of pollen in the genus, the more common one, that with six to nine pores in a single row, shows the greatest diversity in outline. The many forms assumed by this pollen type can be homologized, however, as modifications of a spheric grain with equatorial pores. From a spheric

grain, by equal enlargement of both hemispheres, ellipsoidal and barrel-shaped grains can be derived. The asymmetrical grains, those bearing the row of pores below the middle, are probably the result of hypertrophy of one hemisphere. In the very asymmetric pollen with the hourglass or foot-print profile, in which the row of pores is near one end, one half of the original basic spherical form is to be recognized in the rounded base of the grain. The major portion of the grain, that above the band of pores, is the other hemisphere excessively enlarged and greatly modified in outline (fig. 1).

TEXT-FIG. 1. Relation of the forms in the two types of pollen in *Lithospermum*. Levels at which rows of pores are borne indicated by arrows and broken lines. Type with two rows of pores (upper figures) always symmetrical, differing in the degree of medial constriction. Type with one row of pores (lower figures), probably all modifications of a sphere, becoming ellipsoidal or subcylindric by equal modifications of the two hemispheres or becoming ovoid or achieving more asymmetric form by excessive modification of only one hemisphere.

What relations this type of pollen may have with that which has the pores in two rows is obscure. The two different types remain distinct and their variants give no clues as to how one of the types might have given rise to the other or how they might both be derived from a common ancestral form.

THE RELATIONS OF LITHOSPERMUM AND ARNEBIA

In a subsequent paper I will discuss the nature and relations between *Lithospermum* and the numerous allied genera and give reasons why certain species previously classified under *Lithospermum* should be excluded. Some justification must be given at this time, however, for the inclusion within *Lithospermum* of species which other authors have believed generically separable. The species concerned are those which constituted the genus *Arnebia* or its segregate *Macrotomia*. For convenience in discussion I have listed below all the species that recent authors have classified under these two genera. Those genera other than *Arnebia* under which the species have been classified are named within brackets.

1. *Arnebia tinctoria*
2. *Arnebia decumbens*
3. *Arnebia Griffithii*
4. *Arnebia hispidissima*
5. *Arnebia Bungei*
6. *Arnebia fimbriopetala*
7. *Arnebia minima*
8. *Arnebia linearifolia*
9. *Arnebia* [*Macrotomia*] *euchroma*
10. *Arnebia* [*Macrotomia*; *Leptanthe*] *Benthami*
11. *Arnebia* [*Macrotomia*] *densiflora*
12. *Arnebia fimbriata*
13. *Arnebia obovata*
14. *Arnebia Szechenyi*
15. *Arnebia guttata*

16. *Arnebia* [*Macrotomia*] *echioides*
17. *Arnebia* [*Lithospermum*] *Hancockiana*

Among the seventeen species that botanists have assigned to *Arnebia*, the first fifteen in the above list share the greatest number of significant characters. The two at the end of the list, although giving evidence of relationship with the others, deviate from them in important details. Below I have given the characters of "*Arnebia*," deriving them only from the first fifteen species in the list. The aberrant characters of the two species at the end of the list are not included. For comparison, a characterization of *Lithospermum* (exclusive of *Arnebia* and *Macrotomia*) is also provided.

ARNEBIA, p.p.

Annual or perennial; flowers frequently heterostyled; corolla yellow, orange, blue, pink, or brownish, sometimes with an evanescent spot between the bases of adjacent corolla-lobes; corolla-throat without appendages, usually also lacking stipitate glands or these sparse if present; corolla-tube glabrous or rarely hairy; corolla-nectary present or absent, weak or well developed; style simple, forked or twice forked, stigmas two or four; stamens whorled in corolla-tube (except in *A. decumbens*); pollen cylindric or constricted medially, symmetric, bearing a row of four or five pores at each end; nutlets roughened, more or less tuberculate, verrucose or rugose, gray, brown, olivaceous or rubiginous, never white. — Asia and north Africa.

LITHOSPERMUM, p.p.

Perennial or rarely annual; flowers sometimes heterostyled; corolla yellow, orange, or white, never spotted; corolla-throat with or without intruding appendages, more or less glanduliferous; corolla-tube glabrous or rarely hairy; nectary weak or well developed; style simple; stigmas two; stamens whorled in the corolla-tube; pollen globose, cylindric, ellipsoidal, more or less ovoid, or more or less constricted medially, bearing six to nine

pores in one row at or below the middle of the grain or near one end; nutlets usually smooth, white and lustrous, but sometimes brownish or pitted, rough only in a few species. — America, Eurasia, and Africa.

Even with its two aberrant species eliminated, *Arnebia* differs sharply from *Lithospermum* only in one character, nature of pollen. The annual habit is well developed in *Arnebia*, but a few examples of it exist in *Lithospermum* (*L. matamorensis*, *L. Pringlei*). The corolla of *Arnebia*, unlike that of *Lithospermum*, is sometimes spotted, and may be blue, pink, or brownish, but it may also be yellow or orange and unspotted as in *Lithospermum*. The corolla-throat has no appendages or at most very weak ones (*A. euchroma*), but many species of *Lithospermum* are similarly lacking in faucal appendages. Most species of *Arnebia* have no stipitate gland in the corolla-throat, but *A. obovata*, *A. guttata*, *A. Szechenyi*, and *A. densiflora* have them in limited numbers. The style can be forked in *Arnebia*, but it can also be simple and consequently similar to that of *Lithospermum*. None of the fifteen *Arnebias* have the smooth, polished, frequently white nutlets common in *Lithospermum*. They are brown, gray, greenish, or reddish, and roughened. Brown or gray roughened nutlets, however, do occur in some *Lithospermums* (*L. cinereum*, *L. mirabile*, *L. Parksii*).

The fifteen species of *Arnebia* cannot be distinguished from *Lithospermum* more readily if the practice of some authors be followed and the coarse perennials (*A. euchroma*, *A. Benthami*, and *A. densiflora*) be assigned to *Macrotomia* and the remaining twelve species be left in a restricted *Arnebia*. According to some authors *Macrotomia* is distinguishable from *Arnebia* by its simple style, lack of nectary in the corolla-tube, and its coarse habit. The authors who have used these characters had not dissected all the species of *Arnebia*. Simple styles also occur on *A. fimbriata*, *A. obovata*, and *A. Szechenyi*, and the nectary is also lacking in *A. tinctoria*, the type of the genus *Arnebia*. Furthermore, the coarseness of habit supposed to distinguish *Macrotomia* from *Arnebia* becomes only a vague matter of degree when forms of *Macrotomia euchroma* and *Arnebia guttata* are compared. *Macrotomia* is not a readily definable or useful concept, furthermore it is unnatural, for *Macrotomia euchroma* and *M. Benthami* are not immediately related to *M. densiflora*.

The two *Arnebias* recognized as aberrant, and as yet undiscussed, remain to be considered. The first of these, *A. Hancockiana*, combines characters of *Arnebia* and *Lithospermum*. Its blue or pink unappendaged corollas are more suggestive of *Arnebia*. In having ellipsoidal pollen with a row of pores at the equator, a glanduliferous corolla-throat, a simple style with subterminal stigmas, and smooth lustrous white nutlets, it has the characters of *Lithospermum*. The other aberrant species, *A. echioides*, has a yellow, spotted corolla devoid of appendages and glands in the throat, which is very characteristic of *Arnebia*. So also is the shape of its broadly affixed nutlets. Its globose pollen, with the pores on the equator, as well as the nearly smooth surface of its nutlets, are, however, characteristic of

Lithospermum. Its hairy corolla-tube is duplicated in both genera, as is also its simple style. In bearing stamens at unequal heights within the corolla-tube, it is dissimilar to *Lithospermum* but suggestive not only of *Arnebia decumbens* but also of species in other genera related to *Lithospermum*, such as *Stenosolenium*, *Lithodora*, and *Alkanna*. The suppressed nectary is to be compared only with that of *A. tinctoria*. In most of its characters the species is more closely allied to *Arnebia* than to *Lithospermum*.

Even when *A. echioides* and *A. Hancockiana* are not considered, the difference between *Lithospermum* and the fifteen species of *Arnebia* is weak and uncertain. When the aberrant species are taken into consideration, the differences between the supposedly different genera entirely disappear. If *A. echioides* be assigned to *Arnebia*, then there is no longer any difference in type of pollen. On the other hand, if the species be placed in *Lithospermum*, then the spotted corolla or the corolla devoid of glands in the throat is no longer found only in *Arnebia*. If *Arnebia Hancockiana* be treated as an *Arnebia*, then the two genera again lose their differences in type of pollen, and furthermore, the smooth, white, polished nutlets are no longer distinctive of *Lithospermum*. Should *A. Hancockiana* be treated as a *Lithospermum* that genus no longer has only orange, yellow, or white corollas, but also pink or blue.

The distinctive developments which occur singly or collectively in species of *Arnebia* and can give them an aspect so different from species of *Lithospermum* occur in only some, not all the species of that group. The spotted corolla-limb of *Arnebia* occurs in only five of the seventeen species assigned to that genus. Only six of the seventeen have colors other than yellow or orange, such as pink, blue, or brown. The forked style is found in only half the species. Pollen of the type with two rows of pores is found in only fifteen of the seventeen. Since these characters are not universal in the group and are frequently combined in species with traits characteristic of *Lithospermum*, it seems futile to make further attempts at distinguishing *Arnebia* from *Lithospermum*.

Happily, most of the species of *Arnebia* retain their familiar specific epithets when the group is submerged in *Lithospermum*. The five exceptions are as follows: *Lithospermum tetrastigma* (*Arnebia tinctoria*), *L. detonsum* (*A. minima*), *L. Aucherii* (*A. linearifolia*), *L. Sewerzowi* (*A. obovata*), and *L. Tournefortii* (*A. echioides*).

I have not recognized *Arnebia* because it cannot be sharply defined or decisively separated from *Lithospermum*. Another reason for not doing so involves nomenclature. As pointed out by Rothmaler, Fedde Repert. 49: 56 (1940), the generic name, *Arnebia* Forsk. Fl. Aeg.-Arab. 62 (1775), typified by *Arnebia tinctoria*, is antedated by *Echioides* [Tourn.] Ortega, Tabulae Botanicae 7 (1773), typified by *Arnebia echioides*. If the group known as *Arnebia* is to be given generic recognition, *Echioides* must be substituted as the correct generic name.

I have seen only the second edition of Ortega's Tabulae Botanicae (1783), on page 16 of which the genus *Echioides* is keyed out in the synopsis

under the following final item, "Flore infundibuliformi, sed isoperimetro. Seminibus capitis viberini aemulis." No species, no locality, no reference, nor other means of further identifying the plant are given. However, Ortega makes it very clear that he used the Institutiones of Tournefort as the model of his synopsis. The name "Echioides" appears in Tournefort's "Corollarium Institutionum," page 46 (1703), where it is associated with the following description: "Echioides est plantae genus, flore monopetalo, infundibuliformi, sed isoperimetro, qua notâ differt ab Echio. Pistillum enim abit in fructum ex quatuor seminibus compositum, caput viperinum aemulantibus. — Echioidis speciem unicam novi. — Echioides Orientale, Buglossi folio, flore luteo, maculis atropurpureis notato. — *Echioides quasi planta ad Echium accedens*." The similarity between Ortega's short diagnosis and the longer one of Tournefort leaves no doubt that the same plant is intended. The generic name *Echioides* Ortega (1773), applied to *Arnebia echioides*, fulfils all the requirements for legitimate publication. This is not the case with *Echioides* J. Agosti, *De Re Bot. Tractatus* 193 (1770), a name for *Nonnea*, recently put forward by Schwarz, *Mitt. Thuring. Bot. Ges.* 1¹: 113 (1949). Agosti's book, also an adaptation of Tournefort, has descriptions of the genera, but the numerous species mentioned bear only polynomials. Agosti, unlike Ortega, was not a follower of Linnaeus nor a user of binomial nomenclature. Because binomial nomenclature was not adopted, Agosti's "Echioides" may be ignored. The name *Echioides* Ortega remains the acceptable one for the genus formerly known as *Arnebia*. Confronted with the choice of transferring all the species of *Arnebia* either to *Echioides* or to *Lithospermum*, I much prefer the latter.

KEY TO THE SPECIES

Pollen encircled by 2 rows of pores, one at each end of the grain, the rows each with 4 or 5 pores, upper and lower half of pollen grain similar in size and outline; corolla orange, yellow, pink, blue or brownish, throat only very obscurely if ever appendaged, glandless or very sparingly glanduliferous; nutlets roughened, rugose or tuberculate or papillate, gray, brown, olivaceous or rubiginous, never white and porcelain-like; plants mostly Asiatic, with outliers in Greece and North Africa.

Plants annual.

Stigmas 4, style frequently twice forked.

Mature calyx not developing an enlarged, indurate, pentangular tube; corolla blue or bluish, lacking a nectary in the tube; stigmas elongate; nutlets with cordate base, flat dorsum, and convex venter.....1. *L. tetrastigma*.

Mature calyx with tube enlarged, indurate and prominently veined and angulate; corolla orange or yellow, with a membranous collar-like nectary in tube; stigmas subcapitate; nutlets with a broad nearly flat base, rounded back and angulate venter.....2. *L. decumbens*.

Stigmas 2, style simply forked.

Corolla-tube villulose inside near middle; filaments in short-styled flowers more than half as long as the anthers; flowers strongly heterostylic; pollen strongly dimorphic.....3. *L. hispidissimum*.

Corolla-tube glabrous inside; filaments always less than half as long as the anthers; pollen monomorphic.

Calyx not strongly accrescent, mature lobes slender, 10–15 mm. long and 0.5–1 mm. broad; corolla-limb with 5 evanescent black spots; flowers always heterostylic.....4. *L. Griffithii*.

Calyx strongly accrescent, mature lobes lanceolate or lance-ligulate, 10–28 mm. long and 2–5 mm. broad; corolla-limb not spotted; flowers weakly heterostylic or monomorphic.

Corolla-lobes fimbriate, margins lobulate or lobulate-lacerate.....5. *L. fimbriopetalum*.
.....6. *L. Bungei*.

Corolla-lobes with margins entire or practically so.

Mature calyx 20–28 mm. long; leaves with lower surface glabrous or nearly so; nutlets nearly as broad as long, dorsum with medio-longitudinal depression below the middle and more or less definitely carinate above the middle....7. *L. detonsum*.

Mature calyx 12–17 mm. long; leaves strigose beneath; nutlets evidently longer than broad, back rounded and neither depressed nor carinate along the medial line....8. *L. Aucherii*.

Plants distinctly perennial.

Corolla-lobes with conspicuously fimbriate margins, pink changing to blue; nectary in corolla-tube a villose lineate ring.....9. *L. fimbriatum*.

Corolla-lobes entire or practically so.

Nectary in corolla-tube a well-developed villose collar.

Corolla blue.....10. *L. Sewerzowi*.

Corolla yellow or orange, limb usually bearing 5 black evanescent spots. Bracts of cymes broad, more or less elliptic, foliaceous, not simulating the narrow calyx-lobes; style not forked.....11. *L. Szechenyi*.

Bracts narrow, simulating the calyx-lobes in size and form; style usually forked at apex.....12. *L. guttatum*.

Nectary in corolla-tube obscure or absent.

Corolla yellow or orange, very large, limb 20–25 mm. broad, tube 20–37 mm. long; stamens borne at or near the mouth of the corolla-tube; corolla-tube sparsely villulose just above the base inside; pollen homomorphic, very large; Greece and Turkey...13. *L. densiflorum*.

Corolla pink, purple or brownish, limb less than 15 mm. broad, tube less than 15 mm. long; stamens in long-styled flowers borne near the middle of the corolla-tube; corolla-tube glabrous inside; pollen dimorphic; n.w. Himalayas to eastern Iran and north into Central Asia.

Inflorescence cylindric, much longer than broad; calyx-lobes slender, very elongate and flexuous, usually much longer than the corolla-tube; leaves usually evidently 3–5-ribbed from the base.....14. *L. Benthami*.

Inflorescence subglobular, tending to become broader than long; calyx-lobes lanceolate, coarse and rigid, usually equalling the corolla-tube or surpassed by it; leaves usually with only a strong midrib.....15. *L. euchromon*.

Pollen encircled at the middle, below the middle, or near one end with a single row of 6–9 pores, upper and lower halves of the grain similar or differing in outline and size; corolla orange, yellow or white (or exceptionally bluish,

in *L. Hancockianum*), with or without evident faucal appendages, usually bearing abundant minute stipitate glands in and below the throat; nutlets prevalingly polished and porcelain-like, completely smooth or with scattered punctate pits, white or more or less stained with brownish (or minutely mottled in *L. Tournefortii*; rough and dull only in *L. mirabile*, *L. Parksii*, *L. matamorensis*, *L. papillosum*, and *L. cinereum*); plants of America, Eurasia and Africa.

Corolla orange, yellow, yellowish or greenish, not white.

Flowers heterostylic or dimorphic, the two types of flowers differing in the height at which the stamens are affixed in the corolla-tube.

Pollen broadest at the equator, pores medial.

Flowers not truly heterostylic, pollen (ellipsoidal) of one size, length of style not correlated with the position of the stamens; Central Asia.....16. *L. tschimganicum*.

Flowers strongly heterostylic, the two types of flowers differing not only in position of stamens but also in the length of the style and in the size of pollen.

Stamens affixed at three different levels on the corolla-tube; corolla-limb bearing 5 evanescent black spots; corolla-tube minutely hairy inside; pollen globose; basal leaves well developed; Caucasus.....17. *L. Tournefortii*.

Stamens all affixed at the same level on the corolla-tube; corolla-limb without spots; pollen longer than broad; America.

Stems not arising from a leaf rosette, lower cauline leaves small and poorly developed, very much smaller than the middle and upper ones; corolla-tube always glabrous within.....18. *L. multiflorum*.

Stems arising from the center of a well-developed leaf-rosette; basal leaves much larger than the middle and upper cauline leaves; corolla-tube hairy inside or at least so in long-styled flowers.

Basal leaves large, obovate to elliptic, 15-25 mm. broad, upper surface with coarse appressed hairs only; corolla-tube not hairy within in short-styled flowers.....19. *L. obovatum*.

Basal leaves narrow, elongate, oblanceolate, 5-15 mm. broad, upper surface bearing long and short hairs; corolla-tube always hairy inside.

Corolla funnelform, usually almost as broad as long; plant cinereous, evidently hairy.....20. *L. cobrense*.

Corolla tubular funnelform, usually about twice as long as broad; plant green, inconspicuously hairy.....21. *L. tubuliflorum*.

Pollen constricted at the middle or evidently broader at one end, bearing the pores below the middle.

Basal leaves larger than the middle cauline ones; stems arising from center of leaf-rosette; pollen of long-styled flowers ovoid, of short-styled flowers ellipsoid; Mexico.....21. *L. tubuliflorum*.

Basal cauline leaves small and imperfectly developed, much smaller than the middle cauline ones; stems arising directly from a bud on the caudex; pollen never ellipsoidal.

- Nutlets strongly constricted just above base, 5 mm. long; nectary in corolla-tube a glabrous tumid ring; herbage glaucescent; fruiting calyx usually recurved; California..... 22. *L. californicum*.
- Nutlets not constricted just above base; nectary in corolla-tube 10-lobed, villulose; herbage not glaucescent; fruiting calyx remaining erect; eastern United States.
- Corolla orange-yellow, 13–25 mm. long, faucal appendages glanduliferous ridges not invaginate; mature calyx-lobes 6–13 mm. long; nutlets 3.5–4.5 mm. long..... 23. *L. caroliniense*.
- Corolla yellow, 10–18 mm. long, faucal appendages invaginate, gibbose; mature calyx-lobes 5–6 mm. long; nutlets 2–3 mm. long..... 24. *L. canescens*.
- Flowers not heterostyled, monomorphic.
- Stamens borne at middle of corolla-tube; pollen neither ellipsoidal nor globose.
- Stems arising from a cluster of thickened fusiform roots, developing a basal rosette of leaves which persists at least until anthesis; pollen distinctly ovoid; southeastern United States... 25. *L. tuberosum*.
- Stems arising directly from a strong sparingly branched, dye-stained tap-root; basal leaves small and imperfectly developed, not forming a rosette; pollen constricted at middle or rarely subcylindric.
- Stems with slender, loosely appressed or spreading hairs..... 26. *L. erythrorhizon*.
- Stems short-strigose, the hairs closely appressed.
- Mature leaves 5–15 (–20) mm. broad, firm, acute, veins 1 or 2 on either side of midrib, not obviously anastomosing nor branched; calyx at most only shortly surpassing the corolla-tube, commonly shorter, in fruit 3–5 (–8) mm. long; nutlets commonly 3 mm. long; Eurasia..... 27. *L. officinale*.
- Mature leaves 15–45 mm. broad, thin, frequently somewhat acuminate, veins 2–4 on either side of midrib, obviously anastomosing and usually branched; calyx distinctly longer than the corolla-tube, in fruit 9–13 mm. long; nutlets 4.5–5 mm. long; America..... 28. *L. latifolium*.
- Stamens borne near summit of corolla-tube; pollen ellipsoid to globose or practically so.
- Pollen perfectly globose, 33–42 μ ; plant always developing some cleistogamic flowers; chasmogamic flowers with an elongate corolla-tube and well-developed invaginate faucal appendages.
- Nutlets angulate, much punctate and roughened, narrowed to the base; attachment-scar flat, without a subulate projection; tap-root short-lived, fusiform..... 29. *L. mirabile*.
- Nutlets rounded, ellipsoidal-ovoid, usually somewhat constricted just above base to delimit a basal collar that surrounds the markedly concave attachment-scar, scar bearing a prominent subulate projection; taproot not fusiform, usually strong and perennial.
- Corolla-lobes erose or fimbriate; fruiting calyx usually nutant or cernuous; nutlets smooth or somewhat pitted; cleistogamous flowers very abundant..... 30. *L. incisum*

- Corolla-lobes with entire margins; fruiting calyx erect.
 Nutlets roughened, strongly verrucose or rugose; chasmogamic flowers abundant, large.....31. *L. Parksii*.
 Nutlets smooth and shiny; chasmogamic flowers few or none, plant commonly almost completely cleistogamic.....
32. *L. confine*.
 Pollen ellipsoidal, if subglobose usually with angulate sides when viewed in lateral profile; cleistogamic flowers produced in only one species (*L. calycosum*).
 Corolla small, less than 10 mm. long.
 Pollen cylindric, sides straight and parallel in lateral profile; stems very elongate, 5-10 dm. long; Central Africa.....
33. *L. afromontanum*.
 Pollen ellipsoidal, sides rounded or angulate in lateral profile; stems 1-5 dm. long; America.
 Stems bearing numerous floriferous branchlets from the uppermost leaf-axils, the inflorescence, hence, an elongate cylindrical thyrses, individual cymes even in advanced maturity usually less than 5 cm. long, obscurely racemose; nutlets 4-6 mm. long, strongly constricted just above base; western United States and adjacent Canada.....34. *L. ruderales*.
 Stems loosely branched, the cymes not aggregated into a cylindrical thyrses, scattered, usually becoming very elongate and racemose at maturity; nutlets not strongly constricted just above base; Mexico.
 Margin of corolla-lobes erose-dentate or -lobulate or crisped; fruiting calyx 8-19 mm. long; corolla-throat with scattered glands but no invaginate intrusions; corolla very variable in size, the later ones small and sometimes cleistogamic..
35. *L. calycosum*.
 Margin of corolla-lobes entire or practically so; fruiting calyx 4-9 mm. long; corolla-throat with gibbous invaginations or definite congregations of glands.
 Leaves evidently veined; corolla-tube 5-9 mm. long, surpassing the calyx 1-3 mm., corolla-throat with well-defined gibbous invaginations; pollen $33-37 \times 25-27 \mu$, pores prominent.....36. *L. Pringlei*.
 Leaves obscurely veined or veinless; corolla-tube 3-5.5 mm. long not surpassing the calyx; corolla-throat with obscure convex areas bearing congregations of glands.
 Plant green, hispidulous, hairs spreading or loosely appressed; larger leaves 6-12 mm. broad; pollen with prominent pores, $30-33 \times 26-28 \mu$
37. *L. indecorum*.
 Plant with a dense soft gray indument, abundantly appressed villulose-hispidulous; largest leaves 2-3 mm. broad; pollen $20 \times 16 \mu$, pores obscure.....
38. *L. jimulcense*.
 Corolla large, 10-40 mm. long.
 Throat of corolla bearing 5 sharply defined invaginate appendages, tube usually constricted at the summit.

- Cauline leaves large, 10–30 mm. broad, evidently veined; corolla 20–40 mm. long; pollen evidently longer than broad. 39. *L. oblongifolium*.
- Cauline leaves 1–8 mm. broad, veinless; corolla 10–20 mm. long; pollen subglobose, about as long as broad.
- Taproot abruptly swollen, fusiform; lower leaf-face more or less strigose; corolla-lobes evidently longer than broad, narrowly obovate or oblong; style not exserted. 40. *L. strictum*.
- Taproot not abruptly thickened, lower surface of leaves glabrous except on midrib; corolla-lobes as broad or broader than long, broadly attached, not narrowed at the base; style becoming evidently exserted. 41. *L. Muelleri*.
- Throat of corolla without well-defined invaginate appendages, glanduliferous with the glands scattered or congregated.
- Corolla bluish; leaves silky white-strigose beneath; plant with a sprawling very loosely branched woody caudex; southwestern China. 42. *L. Hancockianum*.
- Corolla yellow or yellowish; lower surface of leaves not white nor silky strigose; caudex small and compact; America.
- Margin of corolla-lobes erose, denticulate or crisped; corolla varying widely in size, becoming reduced in size as the season advances, late one small and frequently cleistogamic; Mexico. 35. *L. calycosum*.
- Margin of corolla-lobes entire; flower never cleistogamic; style becoming tardily exserted.
- Corolla-tube gradually expanding, evidently broader above the middle than at the base, lobes ascending; pollen ellipsoid. 43. *L. guatemalense*.
- Corolla-tube subcylindric, lobes divaricate or recurved; pollen subglobose, about as long as broad.
- Cauline leaves 10–35 mm. broad, evidently veined; nutlets constricted just above the base; northern Mexico and adjacent United States. 44. *L. viride*.
- Cauline leaves 3–7 mm. broad, veinless; nutlets gradually narrowed at base; Peru. 45. *L. Macbridei*.
- Corolla white or with only the faucal appendages yellow.
- Pollen constricted at the middle.
- Flowers heterostylic; corolla-tube villose inside. 46. *L. discolor*.
- Flowers monomorphic; corolla-tube glabrous inside.
- Nutlets with a constriction just above the base; America.
- Plant annual; nutlets usually conspicuously pitted and more or less brownish. 47. *L. matamoreense*.
- Plant perennial; nutlets smooth and white.
- Corolla-tube 10–15 mm. long, 2–3 times as long as calyx, limb 10–14 mm. in diameter. 48. *L. Nelsonii*.
- Corolla-tube 2.5–3.5 mm. long, equalling or barely surpassing the calyx, limb 4–6 mm. broad. 49. *L. Berlandieri*.
- Nutlets narrowed to a rounded base; Eurasia.
- Stem strigose, the hairs closely appressed; fruiting calyx 3–5 (–8) mm. long; corolla longer than broad, lobes elongate, ascending. 27. *L. officinale*.

- Stems with spreading or loosely appressed hairs, fruiting calyx 5–10 mm. long; corolla about as broad as long, lobes broad and spreading.....26. *L. erythrorhizon*.
- Pollen not constricted at the middle.
- Plants of South Africa.
- Leaves broadest just above the base, sparsely appressed hispid, "nutlets rugose.".....50. *L. papillosum*.
- Leaves broadest at or above the middle.
- Stems 4–8 dm. tall, lower leaves 6–12 cm. long and 15–20 mm. broad; nutlets with smooth rounded back.....51. *L. diversifolium*.
- Stems 1–3 dm. tall, largest leaves less than 7 cm. long and 10 mm. broad.
- Herbage with a smooth grayish indument of very abundant short closely appressed hairs; nutlets tumulose on back; corolla-tube not surpassing calyx.....52. *L. cinereum*.
- Herbage villose-hispid, hairs mostly spreading; nutlets with smooth rounded back; corolla-tube elongate becoming about twice as long as calyx.....53. *L. scabrum*.
- Plants of tropical America.
- Stems very slender, elongate and prostrate; pollen ellipsoid.....54. *L. peruvianum*.
- Stems erect or ascending, not prostrate.
- Corolla-throat bearing 5 congregations of glands but lacking definite invaginations; pollen ellipsoid or more commonly somewhat ovoid.....55. *L. calcicola*.
- Corolla-throat with well-developed glanduliferous and velvety more or less invaginate gibbose appendages.
- Stems erect, 3–8 dm. tall; pollen ellipsoid.....56. *L. mediale*.
- Stems erect to loosely decumbent, less than 3 dm. tall; pollen cylindric.
- Plant with loosely appressed or spreading hairs; stems erect, arising from a short-lived thickened fusiform taproot; basal leaves broad.....57. *L. sordidum*.
- Plant closely strigose; stems spreading, numerous, arising from a small more or less well-developed caudex crowning a strong perennial taproot.....58. *L. distichum*.
-59. *L. Gayanum*.

1. *Lithospermum tetrastigma* (Forsk.) Lam. Encyc. 3: 30 (1789), Tab. Encyc. 1: 398 (1791).

Arnebia tetrastigma Forsk. Fl. Aeg.-Arab. 63 (1775); C. Christ. Dan. Bot. Arkiv 4^o: 17 (1922); Steud. Nom. ed. 2, 1: 56 (1840).

Arnebia tinctoria Forsk. Fl. Aeg.-Arab. 63 (1775); Coss. & Kral. Bull. Soc. Bot. Fr. 4: 404 (1857); Boiss. Fl. Orient. 4: 214 (1879).

Lithospermum tinctorium (Forsk.) Vahl, Symb. 2: 33, t. 28 (1791), not L. (1753).

Echioides tinctorium (Forsk.) Rothm. Fedde Repert. 49: 56 (1940).

Lithospermum Arnebia Delile, Fl. Aegypt. Ill. 7 (1813); Lehm. Asperif. 2: 316 (1818); R. & S. Syst. 4: 45 (1819).

A small, compactly branched cinereous herb, 3–9 cm. tall, of Egypt and northern Arabia. Root annual, slender and dye-stained. Cymes dense,

becoming 2–5 cm. long at maturity, bracts longer and broader than the calyx-lobes. Corolla small, 5–8 mm. long, blue or bluish, scarcely longer than the calyx; limb small, formed of small ascending ovate or cuneate lobes; tube 4–7 mm. long; throat glabrous, without glands or appendages; base of tube glabrous inside, nectary completely absent. Stamens borne at or just below summit of corolla-tube. Pollen (fig. 28) cylindric, in lateral profile with rounded ends and straight parallel sides, $41\text{--}46 \times 33 \mu$. Style reaching to the height of the stamens, bis-bifid at the apex and bearing 4 minute cylindric stigmas. Nutlets strongly compressed dorsi-ventrally, rubiginous or brownish, obscurely tuberculate or nearly smooth, somewhat lustrous, ca. 2 mm. long and nearly 2 mm. broad above the distinctly emarginate base, cordate in outline, plano-convex in cross-section, with a decidedly flat or slightly concave dorsum angled at the margin and a low-convex ventrum with a low broad medial keel. Attachment surface on the narrow retuse base of the nutlet, depressed and bearing a pit at the middle, 3-lobed, the lobes quadrate, the middle one extending upward on the ventral face of the nutlet. Seeds cordate. Gynobase with 4 distinct attachment faces, elevated and truncate at the center.

This very distinct species is the type of the genus *Arnebia*. It has general relationships with the other annuals of the Near and Middle East and perhaps its closest affinities with *L. Aucheri*. It presents several especially noteworthy developments. The dorsi-ventrally compressed, plano-convex nutlets, with a 3-lobed attachment on the cordate base, are unique. They are aberrant in this genus and deserve recognition as one of the very extreme types of nutlets in all the Boraginaceae. In having four stigmas *L. tetragigma* resembles *L. decumbens*, but from that and all other congeners it differs in having elongate stigmas and not capitate, flabellate, or reniform ones. Another unusual feature of the plant is the complete suppression of the nectary in the corolla-tube.

2. *Lithospermum decumbens* Vent. Descr. Pl. Nov. Jard. Cels, t. 37 (1801).

Arnebia decumbens (Vent.) Coss. & Kralik, Bull. Soc. Bot. Fr. 4: 402 (1857).

Echioides decumbens (Vent.) Rothm. Fedde Repert. 49: 56 (1940).

Lithospermum cornutum Ledeb. Fl. Altai. 1: 175 (1829), Icon. Fl. Ross. 1: t. 25 (1829) and Fl. Ross. 3: 139 (1847).

Arnebia cornuta (Ledeb.) F. & M. Ind. Sem. Hort. Petrop. 1: 22 (1835) and Ann. Sci. Nat. ser. 2, 5: 126 (1836); DC. Prodr. 10: 95 (1846); Boiss. Fl. Orient. 4: 213 (1879).

Arnebia orientalis [Pallas] Lipsky, Acta Hort. Petrop. 26: 513 (1910). — Based on a misidentified drawing without analyses; "*Onosma orientale*" sensu Pallas, not Linnaeus; cf. Bornm. Beih. Bot. Centralbl. 33²: 174 (1915).

The name *L. decumbens* is here applied to a bewildering assemblage of very diverse plants occurring from Algeria, across north Africa, and in Asia from Palestine and the Caspian area eastward to Songoria and Afghanistan. Only a few of its many synonyms are given above. The group is one that must be studied in the field before its many forms can be interpreted

properly. In the present paper I can only circumscribe it, establish its general relations with other congeners, and indicate some of its more striking features. The plants with which we are concerned are all annuals, characterized by a combination of unusual features relating to the stigmas, the attachment of the stamens, and the form and behavior of the fruiting calyx.

The stigmas, four in number, are borne paired terminally on the two branches of the simply forked style or solitary and terminal on the four branches of the twice-forked style. They are globose in form. The stamens are not borne in perfect whorls, or in other words not all at the same level in the corolla-tube. In some plants, particularly the western ones and especially those from North Africa, the deviation from a whorled arrangement may be slight, only one anther being slightly though distinctly lower than the other four. In plants from the region east of Mesopotamia and the Caspian, however, the anthers are attached at very different heights on the corolla-tube. Commonly they are borne in three well-spaced superimposed groups, with a pair in the throat, another pair below, and the fifth anther lowest down in the tube, 2–4 mm. below the pair in the throat. This arrangement of the anthers at differing heights can be ascertained without dissection by simply viewing the corolla with transmitted light.

The calyx is strongly accrescent. At maturity it becomes a tough rigid bur-like structure which eventually detaches from the rhachis of the inflorescence with the nutlets still enclosed. As in species of *Cryptantha* and *Myosotis*, the bur-like calyx appears to have some role in dissemination. At maturity it has thick prominent indurate veins and an enlarged very prominently pentangular tube. The slender lobes are rigid and appressed. Between the ten indurate ribs the tube becomes membranous or opaquely vitreous. The five more prominent ribs, at times narrowly cristate, bear coarse warts or slender papillae, each terminated by a pungent hair.

In the forms of the species growing in Mesopotamia and westward, the corollas are usually subtubular and 10–15 mm. long and have a limb 2.5–4 mm. broad and a tube 8–12 mm. long. The stamens, as already mentioned, are crowded towards the summit of the corolla-tube and frequently deviate from a perfectly whorled arrangement only by having the base of one anther projecting below the bases of the other four. In some plants the stamens are borne in three groups differing in the level at which they are attached, but unlike the anthers in the plants of Central Asia, the tip of the lowest anther in the western forms is never below the level of the base of the anther attached directly above. In other words, the distance between the attachment-levels of superimposed stamens is always less than the length of the anther, and frequently only half as long. The stigmas are always carried distinctly below the level of the lower stamens.

The western plants of *L. decumbens* occur in two well-marked forms. One is found in the whole of the region from Transcaucasia and Mesopotamia to Algeria. It is a small low plant, frequently branching at the base and decumbent, having corollas ca. 10 mm. long, and mature calyces 7–10 mm. long. It is the form represented by the type of *L. decumbens*. The other form of the western plant is restricted to Algeria and Tunis. It is

conspicuously more robust, having corollas 12–15 mm. long and mature calyces 15–20 mm. long, and has been distinguished as *Arnebia decumbens* var. *macrocalyx* Coss. & Kral. Before giving it a close study I had suspected that it might prove to be specifically separable. It has been a surprise to discover that it lacks distinctive structures and that it differs from true *L. decumbens* only in the matter of degree.

The forms of the species occurring east of Mesopotamia and the Caspian Sea differ from the western ones in being commonly much taller (1–6 dm.), more erect plants with very much larger corollas and very unequal stamen-attachment. In size the corolla varies widely. At times it is no larger than in western forms (10–15 mm.), but commonly it approaches 20 mm. in length and develops a limb 6–8 mm. in diameter. In extreme forms, however, it can attain as much as 25 mm. in length and may develop a limb 15–20 mm. broad. The corolla-limb seems to be always slightly oblique. It is yellow or orange (or exceptionally blue or bluish?) and frequently bears five black evanescent spots. Selected forms of this plant can differ greatly in size, shape, and coloration of the corolla. In any large representative series of specimens, however, the corolla-variations are found in all combinations and degrees of development. Lipsky, *Acta Hort. Petrop.* 26: 513–26 (1910), did select out and give varietal names to some of the extreme forms but stated definitely that transition between them was complete and that many specimens were intermediate in character and difficult to place.

As mentioned previously, the stamens in the large-flowered eastern forms are usually attached at unequal heights in the corolla-tube. Commonly the attachments of the superimposed anthers are separated by a distance equivalent to $1\frac{1}{2}$ –2 anther-lengths. This departure from radial symmetry in the androecium associated with the slightly oblique corolla-limb allows the corolla to be described as somewhat zygomorphic. The style in such forms commonly reaches up to slightly below the lowest stamen or, at times, to about the same height. Occasionally (e.g. *Spiridonow 167* from Golodnaja Steppe) the flowers seem to be heterostylic, the uppermost anthers on some plants being 3–4 mm. below the summit of the corolla-tube and surpassed by the style, while in other plants, as is common in the species, the upper stamens are just below the summit of the tube and the style is short. There is, however, no associated difference in size or shape of pollen.

Some of the structures relatively constant and shared by all forms of *L. decumbens* remain to be mentioned. The nectary in the corolla-tube is a membranous collar about 0.5 mm. high. The pollen (fig. 27), despite the inordinate diversity in size and form of corolla, is relatively constant in form. It is elongate, in lateral profile has concave sides, and measures $43\text{--}61 \times 30\text{--}41 \mu$. Within the limits given there is a rough correlation between pollen-size and size of corolla, particularly as to the smaller sizes. The nutlets are 2.5–3 mm. long, brownish, and scantily to abundantly tuberculate. They are roughly ovoid in form and have a rounded back and angulate venter. The attachment surface is rounded and basal.

3. *Lithospermum hispidissimum* [Sieber] Lehm. Icones 1: 23, t. 39 (1821).

Arnebia hispidissima (Lehm.) DC. Prodr. 10: 94 (1846); Wight, Icones 4: t. 1393 (1848); Jaubert & Spach, Ill. Pl. Orient. 4: 100, t. 363 (1852); Boiss., Fl. Orient. 4: 213 (1879).

Anchusa hispidissima Sieber ex Lehm. Icones 1: 23 (1821), in synonymy.

Dioclea hispidissima [Sieber] Spreng. Syst. 1: 556 (1825).

Echiochilon hispidissima Tausch, Flora 12²: 643 (1829).

Strobila hispidissima G. Don, Gen. Syst. 4: 327 (1837).

Anchusa asperrima Delile, Fl. Aegypt. Ill. 7 (1813), nomen.

Arnebia asperrima (Del.) Hutch. & Dalz. Fl. W. Afr. 2: 201 and 608, f. 246 (1931).

Echioides asperrimum (Del.) Rothm. Fedde Repert. 49: 56 (1940).

Lithospermum vestitum Wall. Numerical List. no. 941 (1829), nomen; Benth. in Royle, Ill. 305 (1836); Don, Gen. Syst. 4: 325 (1837).

Toxostigma luteum A. Rich., Tent. Fl. Abyss. 2: 86 (1850).

Arnebia lutea (Rich.) Armari in Pirotta Ann. Ist. Bot. Roma 8: 161 (1904).

Toxostigma purpurascens A. Rich., Tent. Fl. Abyss. 2: 87, t. 77 (1850).

Arnebia purpurascens (Rich.) Baker, Fl. Trop. Africa 4²: 56 (1906).

Anchusa polygama Hamilton ex Don, Gen. Syst. 4: 325 (1837), in synonymy.

Arnebiola migiurtina Chiov. Fl. Somala. 227, t. 24, f. 1 (1929).

A hispid annual herb of the deserts of northern Africa and across southern Asia to Pakistan. It grows 5–50 cm. tall and has erect to decumbent stems and a slender dye-stained root. Cymes scorpioid, numerous, terminating the main stem and the numerous branches, simple, elongating, becoming 8–12 cm. long and racemose at maturity. Calyx with very unequal lobes, usually much shorter than the corolla-tube, 2.5–10.5 mm. long. Corolla 10–16 mm. long, retrorsely villulose outside; limb blue, funnelform, 4–7 (–8) mm. broad; tube 7–13 mm. long, inside villulose in a band ca. 1 mm. broad near the middle; throat glabrous, without glands or appendages, tube-nectary a very narrow lobulate sparingly villulose ring. Flowers heterostylic. Stamens borne in the upper middle quarter of the tube on filaments less than half as long as the anthers, or borne at the summit of the tube on filaments as long or nearly as long as the anthers. Style reaching the middle of the corolla-tube or reaching its summit or even somewhat exserted, evidently forked, more deeply so on long styles. Stigmas reniform or in long-styled flowers flabellate-reniform and somewhat lobed. Pollen (fig. 7) of long-styled flowers constricted at the middle, $25\text{--}33 \times 16\text{--}25 \mu$. Pollen of short-styled flowers short cylindric, sides straight and parallel in lateral profile, $37\text{--}46 \times 30\text{--}37 \mu$. Nutlets 1–2 mm. long, broadest at base, ovoid, brown or rubiginous, nearly smooth or more or less abundantly tuberculate.

A bristly desert herb varying greatly in habit, apparently in response to the varying rigors of its habitat. It may be an erect, loosely and ascendingly branched herb nearly 5 dm. tall, but is usually lower and more compactly branched. The type of *Arnebiola* is the plant in its most depressed and compact form.

The species has several unusual features. The corolla is villulose inside

the tube and perhaps has a slightly zygomorphic limb. The filaments of the short-styled flowers are at least twice as long as those of the long-styled flowers. In the long-styled flowers, as characteristic in most species of this genus, the filament is distinctly less than half as long as its anther. In the short-styled flowers of *L. hispidissima*, however, the filaments are usually 0.9–1.2 mm. long and the anthers 1.2–1.8 mm. long. The species is well marked but is not as distinct as the repeated attempts to give it generic recognition might suggest. Surprisingly, four different generic names have been proposed for it: *Dioclea* Spreng., *Strobila* G. Don, *Meneghinia* Endl., and *Arnebiola* Chiov.

4. *Lithospermum Griffithii* (Boiss.), comb. nov.

Arnebia Griffithii Boiss. Diag. ser. 2, 3: 135 (1856) and Fl. Orient. 4: 213 (1875); Hook. Bot. Mag. 87: t. 5266 (1861); Clarke, Fl. Brit. Ind. 4: 176 (1883).

Echioides Griffithii (Boiss.) Rothm. Fedde Repert. 49: 56 (1940).

A slender annual of Pakistan and Afghanistan, having erect hispidulous simple or ascendingly branched stems 1–3 dm. tall. The very slender root is only slightly stained with dye. Calyx-lobes slender, linear, hispid-villose, weakly accrescent, 1 mm. wide or less. Corolla yellow or orange, 20–23 (–30) mm. long; limb spreading, 10–15 (–20) mm. broad, with 5 black evanescent spots; tube slender, much surpassing the calyx, 15–18 mm. long; throat glabrous or scantily glanduliferous, without appendages; tubenectary a narrow villulose collar. Flowers heterostyled. Stamens borne either just above middle of corolla-tube or at the summit and almost exserted. Style reaching to above the middle of the tube or reaching the summit or even shortly exserted, forked at the apex; stigma compressed reniform or somewhat flabellate, entire or obscurely lobed. Pollen (fig. 6) somewhat constricted at middle, in lateral profile with concave sides, in long-styled flowers $33\text{--}41 \times 20\text{--}26 \mu$ and in short-styled flowers $43\text{--}49 \times 23\text{--}28 \mu$. Nutlets 2 mm. long and nearly as broad at the base, brown or rubiginous, somewhat lustrous, sparsely and coarsely tuberculate, back somewhat cordate at base.

5. *Lithospermum fimbriopetalum* (Stocks), comb. nov.

Arnebia fimbriopetala Stocks in Hook. Jour. Bot. & Kew Misc. 3: 180, t. 6 (1851); Boiss. Fl. Orient. 4: 205 (1879).

Echioides fimbriopetalum (Stocks) Rothm. Fedde Repert. 49: 56 (1940).

A species of eastern Persia and Baluchistan known to me only from the references cited above. It is most closely related to *L. Bungei* and perhaps has a synonym in that species. According to Bornmüller, Beih. Bot. Centralbl. 33: 176 (1915), *Arnebia leptosiphonoides* Vatke (1875) is a synonym of the present species.

6. *Lithospermum Bungei* (Boiss.), comb. nov.

Arnebia Bungei Boiss. Fl. Orient. 4: 215 (1879).

Echioides Bungei (Boiss.) Rothm. Fedde Repert. 49: 56 (1940).

Only duplicates of the original collection, from middle eastern Persia, have been seen. These plants are in full flower but lack fruit. They represent the long-styled form of the species. The calyx at anthesis is 10–15 mm. long and has very slender linear lobes 0.5–1 mm. broad. The yellow or orange corolla becomes 25–28 mm. long and has a spreading limb 10–14 mm. in diameter. The corolla-lobes have distinctly lobulate and hence more or less fringed margins. The tube is 20–23 mm. long and is glabrous and devoid of appendages in the throat. Its nectary is a papery collar ca. 0.5 mm. high. The anthers are borne 15–17 mm. above the base of the tube. The style reaches the summit of the tube, is shortly forked at the very summit, and bears 2 simple or bilobed reniform stigmas. The pollen grains have slightly constricted sides and measure $45\text{--}49 \times 28\text{--}30 \mu$.

The species is closely related to *L. fimbriopetalum* of Baluchistan and eastern Persia and perhaps is not distinct. Boissier stated that his species differed in its short pubescence, slender less elongated fruiting calyx, and its crenate rather than fimbriate corolla-lobes. The isotype of *L. Bungei* dissected by me, however, has the margin of the corolla-lobes not merely crenate, but distinctly and narrowly lobulate.

7. *Lithospermum detonsum*, nom. nov.

Arnebia minima Wettstein in Stapf, Denkschr. Acad. Wiss. Wien **50**: 30 (1885); Bornm. Bull. Herb. Boiss. **7**: 783 (1907). Not *Lithospermum minimum* Moris. (1827).

A sparingly and loosely branched herb of Transcaucasia and northern Iran. Its thickish leaves are glabrous or subglabrous on the lower surface. The slender root is dye-stained. The scorpioid cymes become very elongate (to 10 cm. long) and very conspicuous at maturity. Calyx conspicuously accrescent at maturity, 20–28 mm. long, tuberculate and hispid at the base; lobes ligulate or lanceolate. Corolla yellow or orange, subtubular, 19–25 mm. long; lobes ascending; limb only 4–6 mm. in diameter; tube 17–20 mm. long, usually about 3 mm. longer than the calyx; throat glabrous, without glands or appendages; nectary a lobed papery collar 0.3–0.8 mm. high, glabrous. Anthers borne at or just beneath the summit of the tube, not exerted. Style reaching up to 1–3 mm. below the anthers, short, forked at apex; stigmas 2, compressed, globular or reniform. Pollen (fig. 29) with concave sides, usually somewhat dentate at the middle, $49\text{--}59 \times 30\text{--}40 \mu$. Nutlets brownish, 3–3.5 mm. long, ca. 3 mm. broad near the base, coarsely tuberculate, constricted above the middle, lower half of dorsum swollen on either side of a medio-longitudinal depression, upper half usually with a rounded medial keel.

The description given above is based on three collections: Ulja Norashen, Nakhichevan ASSR, May 9, 1947, *Grossheim, Iljinskaja & Kirpitschnikas* (G); Transcaucasia, *Heideman* (Stockholm); and Patschinar, Iran, *Bornmüller 7711* (G). They appear to represent the short-styled form of the species. Another collection from Patschinar, *Bornmüller 7708* (G, Stock.) appears to be the long-styled form. Its coarser corolla is 25 mm. long and has a limb up to 12 mm. in diameter. Its tube (20 mm. long)

does not surpass the calyx. The anthers are borne 5–6 mm. below the summit of the corolla-tube and the style (surpassing the anthers 2–3 mm.) reaches up to 3–4 mm. below the summit of the tube. In other respects, however, and this includes pollen, as well as nectary and nutlets, the plant is similar to the short-styled form described. If the plant is heterostylic such dimorphy is unaccompanied by differences in size of pollen.

This plant of Transcaucasia and northern Iran has been confused with *L. Aucherii* (*Arnebia linearifolia* DC.), a related but apparently distinct species of the deserts of Egypt, Sinai, and southern Palestine. It is a more northern plant with a more robust habit, scanty indument, larger cymes, larger calyx, and larger bigibbose nutlets.

8. *Lithospermum Aucherii*, nom. nov.

Arnebia linearifolia DC. Prodr. 10: 95 (1846); Boiss. Fl. Orient. 4: 214 (1875); Coss. & Kralik, Bull. Soc. Bot. Fr. 4: 404 (1857). Not *Lithospermum linearifolium* Goldie (1822).

Echioides linearifolium (DC.) Rothm. Fedde Repert. 49: 56 (1940).

Arnebia flavescens Boiss. Diagn. 11: 117 (1849), a substitute for *A. linearifolia* DC. Not *Lithospermum flavescens* Mey. ex Steud. (1841).

A compactly branched herb 5–10 cm. tall, arising from a slender dye-stained annual taproot. The plant is known from Egypt and eastward into northern Arabia and southern Palestine. Its cymes, glomerate at anthesis, remain short (1–3 cm. long) and dense even in fruit. The calyx is strongly accrescent; mature lobes lanceolate, 10–17 mm. long, 2–3.5 mm. broad, and coarsely tuberculate and hispid at base. The yellow corolla is subtubular, 10.5–13.5 mm. long, and has a limb of small ascending lobes 2–3 mm. in diameter; tube slender, 9–12 mm. long, usually surpassing the calyx 2–3 mm.; throat glabrous, without gland or appendages; nectary a papery lobulate collar ca. 0.5 mm. high. Anthers borne at summit of corolla-tube, included. Style reaching up to 1–3 mm. below the anthers, short-forked at apex, bearing 2 compressed reniform stigmas. Pollen measuring $43\text{--}52 \times 33\text{--}37 \mu$, with sides slightly concave, frequently seeming to be dentate near the middle. Nutlets 2.5–3 mm. long, about 2 mm. broad near the base, rubiginous, sparingly punctate and tuberculate and sometimes rugose, back rounded.

If this be a heterostylic species, the five collections dissected and described all represent the short-styled form of the species. This plant has its closest relative in *L. detonsum* of northern Iran and Transcaucasia.

9. *Lithospermum fimbriatum* (Maxim.), comb. nov.

Arnebia fimbriata Maximovicz, Bull. Acad. St. Petersb. ser. 3, 27: 507 (1881); Diels in Fütterer, Durch Asien 3ⁱ: 19 and 28, t. 3 (1911).

A low perennial with a purple-stained woody root and a pallid indument of stiff straight loosely appressed hairs. The plant is known only from western Outer Mongolia and adjacent Kansu. Leaves all cauline, numerous, acute, mostly oblanceolate and 2–5 mm. broad; those at the base of

the stem imperfectly developed. Inflorescence coarsely and loosely glomerate, terminal, bracts narrow and commonly not surpassing the subtended calyx. Corolla pink changing to dark blue when dry, 16–24 mm. long; limb 10–17 mm. broad; lobes ovate, spreading, with conspicuously erose or shallowly lacerate margins; tube 13–17 mm. long, surpassing the calyx 2–8 mm.; throat without appendages or glands; tube-nectary a villulose linear ring (not a collar!). Flowers heterostylic. Stamens borne low in the upper third of the corolla-tube (10–12 mm. above the base) or borne at the summit of the tube and partially exerted. Style reaching to beyond the middle of the corolla-tube or shortly exerted from it; stigmas 2, sessile, obovate, strict, compressed, usually somewhat united dorsally. Pollen in long-styled flowers (fig. 4) measuring $26\text{--}31 \times 20\text{--}23 \mu$, evidently constricted at middle. Pollen of short-styled flowers (fig. 4) $35\text{--}38 \times 33 \mu$, short-cylindric with the sides in lateral profile parallel or nearly so. Nutlets dorsi-ventrally compressed, 2.5–3 mm. long and below the middle nearly as broad, 1.5 mm. thick, broadest at base, dull, gray or olivaceous, with scattered coarse tuberculations, attachment large, nearly flat.

10. *Lithospermum Sewerzowi* (Regel), comb. nov.

Arnebia ["Amebia"] *Sewerzowi* Regel, Descr. Pl. Nov. a cl. O. Fedtsch. 57 (1882).

Arnebia obovata Bunge, [Lehmann rel. bot.] Mem. savants étrang. St. Petersb. 7: 407 (1851); Lipsky, Acta Hort. Petrop. 26: 526 (1910). Not *Lithospermum obovatum* Macbr. (1916).

Echioides obovatum (Bunge) Rothm. Fedde Repert. 49: 56 (1940).

Arnebia Olgae Regel, Descr. Pl. Nov. a cl. O. Fedtsch. 57 (1882).

I have seen only two collections possibly referable to this blue-flowered species of southeastern Turkestan. The two differ to a surprising degree in shape of leaves, indument, tip of style, and relative length of calyx-lobes and corolla-tube. One, *von Knorring* 128 from Namangan dist., Uzbek S.S.R., has obovate or obovate-oblongate obtuse leaves, a hispid-villous indument with the slender hairs arising from thickened bases, long-styled flowers with the corolla-tube twice as long as the calyx, and the style with a forked apex. The other collection, *G. Balabajew s.n.* (July 12, 1915) from Iskanderaul, Serawschen dist, Tadzhik S.S.R., has narrow very elongate acute oblongate leaves, an indument of minute retrorse hairs, short-styled flowers with the elongate calyx-lobes as long or even longer than the corolla-tube, and a style not forked at the apex. The collection from Namangan, except as to indument, agrees most closely with the emended description of *Arnebia obovata* given by Lipsky, l.c. The elongate calyx-lobes of Balabajew's collection appear to be aberrant.

The salient features of the species appear to be as follows: — A perennial with a woody root and loosely branched stems 1–3 dm. tall. Cymes terminal and very elongate in age; bracts simulating the calyx-lobes in size and form. Corolla blue, 20–23 mm. long, with a spreading limb 8–10 mm. broad; tube 14–20 mm. long and usually much surpassing the calyx; throat not appendaged, glanduliferous in a narrow band at the summit; tube-

nectary well developed, a densely villous collar 0.8–1 mm. high. Stamens affixed either at the middle of the corolla-tube or at its summit. Style extending up to the middle of the tube or shortly exerted, sometimes forked at the summit. The two reniform stigmas are either sessile or terminate the short branches of the style. Pollen of long-styled flowers measures $28\text{--}33 \times 16\text{--}20 \mu$, and is evidently constricted at the middle. The pollen of short-styled flowers measures $35\text{--}41 \times 26\text{--}30 \mu$, is subcylindric, in lateral profile with sides straight and parallel or nearly so. Nutlets longer than broad, 2.5–3 mm. long, dull, gray, or olivaceous, tuberculate, and broadest at the base.

11. *Lithospermum Szechenyi* (Kanitz), comb. nov.

Arnebia Szechenyii A. Kanitz, Pl. Exped. Szecheny 42, t. 5 (1891) and Wiss. Ergebn. Reise Szechenyi Ostasien 2: 719, t. 5 (1895).

Plant suffrutescent, perennial, 15–35 dm. tall, known only from western Kansu. Stems erect or loosely spreading, simple or ascendingly branched, 1.5–2.5 mm. thick. Root woody, not stained with dye. Leaves firm, veinless, oblanceolate to elliptic, mostly 7–15 mm. broad, slightly cinereous, bearing hairs of two distinct types, scattered stout bristles (1–1.5 mm. long) arising from a discoid or bulbous base, and rather abundant minute slender pallid hairs (0.2–0.5 mm. long) which tend to be antrorse on the upper leaf-face and more or less retrorse on the lower face. Lower cauline leaves smaller than the middle and upper cauline ones. Inflorescence terminal, scorpioid with coarse leafy bracts, in age racemose and 3–7 cm. long. Corolla yellow, 15–20 mm. long; limb 7–10 mm. broad, with 5 evanescent black spots; lobes minutely puberulent on upper face; tube 11–15 mm. long, shortly but distinctly surpassing the calyx; throat puberulent and also bearing scattered glands, unappendaged; tube-nectary a well-developed villose collar ca. 0.6 mm. high. Flowers heterostylic. Stamens borne either at the middle of the corolla-tube or at its summit. Style simple, reaching the middle of the corolla-tube or to its summit; stigmas 2, cordate-reniform, sessile, distinct nearly to the base or more or less united along their medio-dorsal line. Pollen of long-styled flower not seen. Pollen of short-styled flowers measuring $39\text{--}44 \times 23\text{--}30 \mu$, moderately constricted at the middle. Nutlets broadly attached basally, tuberculate, only immature ones seen.

The original description and plate of this species is based on the long-styled plant from "Tschung-pe-shien in valle Si-ning-fu," Kansu. I have had for study a short-styled plant collected near Hsuein Hwa Hsien, Kansu, *Ching* 731. The species is very distinct. Notable among its distinctive features are the large foliaceous bracts in its inflorescence.

12. *Lithospermum guttatum* (Bunge), comb. nov.

Arnebia guttata Bunge, Ind. Sem. Hort. Dorpat. p. vii (1840) and Linnaea 15: Litteratur Bericht 85 (1841); Ledeb. Fl. Ross. 3: 139 (1847); Lipsky, Acta Hort. Petrop. 26: 530 (1910); Krylov, Fl. Siberiae Occ. 8: 2282 (1937). *Macromeria guttata* Farrer, English Rock Garden 1: 469 (1919).

Arnebia tibetana Kurz, Jour. Asia. Soc. 43²: 189 (1874); Clarke, Fl. Brit. Ind. 4: 176 (1883).

Arnebia Thomsoni Clarke, Fl. Brit. Ind. 4: 176 (1883).

Ranging from Kashmir north and northeastward in the mountains of Central Asia to the Mongolian Altai and westernmost Kansu. Plant 1–2.5 dm. tall, flowering the first year but becoming perennial; stems one to several, simple or bearing short ascending floriferous branches, arising from a dye-stained taproot. Leaves thickish, oblanceolate, 3–8 mm. broad, with obtuse or rounded apex; basal leaves well developed but usually disappearing before time of anthesis. Cymes terminal, at first glomerate and 1–2 cm. in diameter, in age elongating and 5–10 cm. long; middle and upper bracts simulating the calyx-lobes in size and form. Corolla orange or yellow, 14–19 mm. long, commonly with 5 black evanescent spots on the limb and occasionally with a purpureous tube; limb spreading, 8–12 mm. broad; tube 10–15 mm. long, evidently surpassing the calyx; throat without appendages or glands, or at times (especially in short-styled flowers) with a narrow transverse band of glands below each corolla-lobe; tube-nectary a well-developed villose collar. Flowers heterostylic. Stamens borne just above middle of tube or near its summit and partially exerted. Style reaching up to middle of tube or short-exserted, usually distinctly forked with the branches once to several times as long as the stigmas; stigmas 2, reniform, entire or more or less bilobed. Pollen of long-styled flowers (fig. 5) measuring $25\text{--}32 \times 13\text{--}20 \mu$, narrowed at the middle. Pollen of long-styled flowers (fig. 5) measuring $33\text{--}37 \times 23\text{--}26 \mu$, sub-cylindric, in lateral profile with sides straight and parallel or slightly concave. Nutlets 2–3 mm. long, dull, gray or olivaceous, more or less tuberculate, broadest at the base; attachment surface large, rough, usually with a quadrate prolongation upward and outward in the recessive angle beneath the base of the ventral keel of the nutlet.

The species is very distinct. Although to be classed as a perennial, its root is not as strong nor apparently as long-lived as the other perennials of this affinity. Among the many collections examined there are frequent individuals which appear to have flowered when less than a year old. Another character suggestive of some relationship with the annual species is the forked style. That type of style prevails among the related annual species, but among the perennial species is consistently developed only in *L. guttatum*. A tendency for the nutlets to be slightly excised ventrally at the base and for the attachment-surface to be upwardly prolonged there, is observable in related perennials, but never to the degree characteristic of *L. guttatum*. Indeed, a well-developed ventral upward extension of the basal attachment is known in only one other species, the annual *L. tetrastigma*.

13. *Lithospermum densiflorum* Ledeb. ex Nordmann, Bull. Acad. St. Petersb. 2: 312 (1837).

Arnebia densiflora Ledeb. Fl. Ross. 3: 140 (1847).

Munbya densiflora (Ledeb.) Boiss. Diag. 11: 116 (1849).

- Macrotomia densiflora* (Ledeb.) Macbride, Contr. Gray Herb. 48: 56 (1916); Farrer, English Rock Garden 1: 469 (1919).
Arnebia cephalotes DC. Prodr. 10: 96 (1846).
Munbya cephalotes (DC.) Boiss. Diag. 11: 116 (1849).
Macrotomia cephalotes (DC.) Boiss. Fl. Orient. 4: 612 (1879); Köhler, Medizinal Pfl. 3: t. 25 (1898); Ball, Gard. Chron. ser. 3, 98: 319, f. 126 (1935).
Munbya conglobata Boiss. Diag. 11: 116 (1849).
 ? *Arnebia macrothyrsa* Stapf, Wiener Ill. Gart. Zeitung 16: 128 (1891); Gard. Chron. ser. 3, 9: 148 and 180 (1891).

A montane plant of Turkey and Greece. The coarse caudex and the strong perennial root are rich in purple dye. Stems 1–3 dm. tall, 3–6 mm. thick at the base, simple below the inflorescence. Basal leaves oblanceolate, 10–15 cm. long. Cauline leaves lanceolate, 4–8 cm. long, lower and middle one about equal in size. Inflorescence globular or corymbose, 6–10 cm. broad, a dense aggregation of coarse, very short-pedunculate cymes arising terminal on the stem and from its uppermost leaf-axils; bracts simulating the calyx-lobes in size and form. Corolla yellow or orange, very large and attractive; limb spreading 20–25 mm. broad; tube 20–37 mm. long, commonly ca. 10 mm. longer than the large calyx, without a nectary but scantily villulose inside just above the base; throat scantily glanduliferous, without appendages. Style forked at apex, with branches 0.5–1 mm. long; stigmas 2, rounded, compressed. Flowers heterostylic. Corolla of long-styled flowers slightly smaller than those with short style; tube 20–27 mm. long and limb ca. 20 mm. broad; anthers borne slightly below mouth of tube with their apices 1–2 and their bases 3.5–4.5 mm. below the mouth; style 22–32 mm. long, exserted 2–5 mm. from the tube; pollen (fig. 2) constricted at middle, $46\text{--}50 \times 26\text{--}31 \mu$. Corolla of short-styled flowers with tube 32–37 mm. long and limb 20–25 mm. broad; anthers borne partially exserted in the mouth of the tube with their bases 1–2 mm. below the top of the tube; pollen (fig. 2) constricted at the middle, similar in form to that of the long-styled flower but much larger, measuring $65\text{--}75 \times 38\text{--}43 \mu$, in lateral profile frequently appearing serrate at the middle; style 20–23 mm. long, reaching up to beyond the middle of the tube. Nutlets 5–6 mm. long, broadest at base, gray, dull, abundantly and very minutely papillate, coarsely rugose.

This very well marked species is notable for having the largest flowers and the largest pollen-grains in the genus. Its nutlets, floral organization, and pollen type are obviously those of the *Arnebia* group. Although heterostyly is well developed in the species, being expressed in differences of corolla-size and -form, length of style and pollen size, the anthers differ very little as to the level at which they are borne in the very elongate corolla-tube. In both types of flowers the anthers are high in the tube, in the short-styled only 2–3 mm. higher than in the long-styled flowers. In the former they are partially exserted and in the latter they have their tip only 1–2 mm. below the mouth of the tube.

14. *Lithospermum Benthami* (Wall.), comb. nov.

Echium Benthami Wall. Numerical List. no. 931 (1829), nomen; G. Don, Gen. Syst. 4: 333 (1838).

Macrotomia Benthami (Wall.) A. DC. Prodr. 10: 27 (1846); Clarke, Fl. Brit. India 4: 177 (1883); Hooker, Bot. Mag. 114: t. 7003 (1888); Coventry, Wild Flowers Kashmir 1: t. 37 (1923); Blatter, Beautiful Flowers of Kashmir 2: t. 45 (1929).

Leptanthe macrostachya Klotzsch, Bot. Reise Prinz. Waldemar. 95, t. 62 (1862).

A coarse perennial of northwestern Himalaya. Its underground parts contain much purple dye. The flowering stems are 1–8 dm. tall and 5–10 mm. thick, and arise from the center of a leaf-cluster. The lower cauline leaves are accordingly larger than the middle and upper ones. Leaves usually 3–5-ribbed from the base. A very distinctive feature of the plant is its elongate slender long-attenuate bracts and calyx-lobes and its elongate cylindrical flower cluster. The inflorescence is a dense cylindrical thyrses 4–7 cm. thick and 5–30 cm. long. The calyx, 13–25 mm. long at anthesis, becomes 25–35 mm. long in fruit. Its very slender flexuous lobes are 0.5–1 mm. broad at the base and very gradually attenuate. Corolla elongate, pink to purple or maroon, 20–25 mm. long, usually shorter than the calyx; throat without glands or appendages; tube-nectary not developed. Flowers heterostyled. Stamens borne either at the middle of the corolla-tube or partially exerted at its summit. The style reaching up to the middle of the tube or nearly to its summit; stigmas 2, rounded, broader than long. Pollen of long-styled flowers strongly constricted at middle, $30\text{--}37 \times 16\text{--}20 \mu$. Pollen of short-styled flowers subcylindric, $39 \times 25\text{--}26 \mu$, in lateral profile with sides nearly parallel or somewhat concave. Nutlets 3–4 mm. long, dull, abundantly and very minutely papillate, and also coarsely and irregularly rugose and more or less tuberculate, broadest near middle, the ventral keel continuous over the beaked apex, the attachment scar frequently with 2 distinct dorsal traces.

Previously, Contr. Gray Herb. 73: 48 (1924), I stated that the corollas of this species were slightly zygomorphic and possessed a ventral longitudinal plication. These observations are entirely false and the result of misinterpretation of the poor and inadequate material then available for study.

No material of *Arnebia speciosa* Aitchison & Hemsl. (1880) from Afghanistan, or *Arnebia inconspicua* Hemsl. & Lace (1891) from Baluchistan, has been available for analysis. These two species are close relatives of *L. Benthami*, but are probably sufficiently distinct to be worthy of recognition.

15. *Lithospermum euchromon* Royle ex Benth. in Royle, Ill. Bot. Himal. 305 (1836).

Macrotomia euchroma (Royle) Paulsen, Bot. Tidsschr. 27: 216 (1906) and Studies Veg. Pamir 58, f. 20 (1920); Lipsky, Acta Hort. Petrop. 26: 505 (1910).

- Arnebia euchroma* (Royle) Johnston, Contr. Gray Herb. 73: 49 (1924).
Stenosolenium perenne Schrenk ex Fischer & Meyer, Enum. Pl. Schrenk 1: 34 (1841).
Arnebia perennis (Schrenk) DC. Prodr. 10: 95 (1846).
Munbya perennis (Schrenk) Boiss. Diag. 11: 115 (1849).
Macrotomia perennis (Schrenk) Boiss. Fl. Orient. 4: 212 (1879).
Macrotomia endochroma Hook. & Thom. ex Henders. & Hume, Lahore to Yarkand 328 (1873); Aitchison, Jour. Linn. Soc. 18: 81 (1880), nomen; cf. Clarke, Fl. Brit. India 4: 177 (1883).
Macrotomia onosmoides Regel & Smirn. Acta Hort. Petrop. 2: 624 (1878).
Macrotomia euchroma var. *subacaulis* Lipsky, Acta Hort. Petrop. 26: 510 (1910).
Macrotomia ugamensis Popov in Baranov, Jour. Turkest. Branch, Russian Geogr. Soc. 17: 26, t. 3 (1925).
Arnebia tingens A. DC. Prodr. 10: 96 (April, 1846).
Lithospermum cyanochroum Boiss. Diag. 7: 33 (1846).
Munbya cyanochroa Boiss. Diag. 11: 115 (1849).
Macrotomia cyanochroa Boiss. Fl. Orient. 4: 212 (1879).
Macrotomia grandis Bornm. Oesterr. Bot. Zeit. 47: 289 (1897).

A coarse, hirsute, frequently glanduliferous perennial. In typical form it ranges from the northwestern Himalaya northward in the mountains of Central Asia to the Dzungarian Ala-tau. A pungently hirsute form also occurs in the mountains of eastern Iran. This latter may deserve at least varietal recognition. The last five names listed above apply to it. The underground parts of all forms of the species contain an abundance of purple dye. The flowering stems are 1–5 dm. tall and arise from the axils of leaves that formed a sterile basal cluster the previous season. The basal cauline leaves are small and imperfectly developed and much smaller than the middle cauline ones. The terminal inflorescence is congested and tends to be broader than long. The corolla is purplish white to purple or brownish, 16–22 mm. long; limb 8–16 mm. broad, with ascending lobes; throat usually unappendaged and glandless, but, particularly in long-styled flowers, occasionally developing 5 small weakly invaginate swellings; nectary not developed. Flowers heterostyled. Anthers borne either at middle of tube or at its summit. The style reaches up to the middle of the tube or is short-exserted, and is usually forked at the very summit; stigmas 2, compressed, rounded, broader than long. Pollen in long-styled flowers (fig. 3) strongly constricted at middle, $26-30 \times 16-20 \mu$. In short-styled flowers (fig. 3) pollen somewhat cylindric, in lateral profile the sides nearly parallel or only slightly concave, $33-43 \times 25-28 \mu$. The gray or dusky nutlets are 3–4 mm. long, irregularly and coarsely tuberculate and more or less rugose, the surface dull, covered with crowded microscopic papillae. The nutlet is broadest near the middle and has a well-developed keel on the venter which extends up and over the beaked apex and continues down the back of the nutlet. The attachment scar is flat and frequently bears 2 ventral traces.

The species has its closest relative in *L. Benthami* and agrees with that species in pollen, fruit, coloration, and general organization of the corolla.

16. *Lithospermum tschimganicum* B. Fedtsch. Bull. Jard. Bot. St. Petersb. 5: 42 (1905); Lipsky, Acta Hort. Petrop. 26: 510 (1910).

A very distinct and unusually interesting species of Central Asia, endemic in the mountains east and southeast of Tashkent. It is a perennial with stems 15–60 dm. tall. The numerous evidently veined leaves, 1–5 cm. broad, increase in size upward along the stems, the lowest one being small and imperfectly developed. The cymes, terminal on the main stem and on a few upper branches, are conspicuously bracted, and are small in size, even in fruit being less than 7 cm. long. The nutlets are lance-ovoid, 4–5 mm. long, and white. They are completely smooth or only sparingly punctate. In general appearance and nutlets, and also in pollen, the plant is more suggestive of the large-flowered American species than of any of the other species of the Old World. The corollas, however, particularly in having an unappendaged very sparingly glanduliferous throat, are perhaps more suggestive of the Asiatic “*Arnebias*” than of American species.

Of the five collections available for study, three have provided corollas for dissection, viz., *von Knorring* 180 from Osch dist., Kirghiz S.S.R., *von Minkwitz* 752 from Kokand dist., Uzbek S.S.R., and *von Knorring* 359 from Namangan dist., Uzbek S.S.R. Though apparently all representing one species and though indistinguishable in all other structures, these three collections show surprising differences inside their corollas. The corollas from Kokand and Namangan districts are 17 mm. long and have a gradually ampliate tube ca. 9 mm. long. The anthers (ca. 1.5 mm. long) are borne on slender filaments 0.2–0.3 mm. long attached 5 mm. above the base of the corolla. The unappendaged throat is sparingly and inconspicuously glanduliferous. The glands occur very sparingly from the throat down to the middle of the corolla-tube, with most of them confined to the principal veins. More occur, locally abundant, just below the attachment of each filament. The collections from Kokand and Namangan agree very closely in all details save only the length of the style. In the former the style is 15–17 mm. long and is shortly exerted from the corolla-tube. In the collection from Namangan, however, it is only 5.5 mm. long and reaches upward in the corolla-tube only to the tip of the anthers.

The dissection of the corolla on the plant from Osch, on the other hand, reveals a very different condition. The corolla is 20 mm. long and is tubular below the middle and gradually ampliate above. The anthers (2 mm. long) are borne on uncinat-cuneate filaments 1.7–1.9 mm. long affixed in the corolla-throat 13.5–14 mm. above the base of the corolla and only 3 mm. below the base of the corolla-lobes. The filaments are most unusual, not only in size but also in form. They are 0.5–0.6 mm. broad at the base, gradually narrowed, curved, very strongly compressed laterally, and provided with an evident excentric vein. There are no glands clustered at their base. Glands, however, do occur scattered in the corolla-throat. The style is 5–6 mm. long. As in the collections from Kokand and Namangan, the 2 stigmas are obcordate in form and divergent from the

tip of the style. In all three collections the nectary in the corolla-tube is glabrous and obscurely developed, at most only a vaguely defined tumid annular area just above the corolla-base.

Since the collections from Kokand and Namangan have anthers borne low in the corolla-tube and that from Osch has slightly larger anthers borne high in the tube, heterostyly can be suspected. The flowers in the collections from Kokand and Namangan, however, have low-placed stamens associated with a short, as well as a very long style. Furthermore, the pollen in all the three collections mentioned is similar in size and form and shows no correlation with the differences in style-length or stamen-attachment. In all collections mentioned the grains are ellipsoidal, $20\text{--}25 \times 16\text{--}18 \mu$, and in lateral profile have rounded or slightly angled sides (fig. 30). They bear their very obscure pores at the middle and are broadest there. Heterostyly, certainly of the strongly developed type characteristic of other congeners, is not present in *L. tschimganicum*. If heterostyly is not present, then the collections must represent another type of floral dimorphism or two distinct species must be represented. I find it impossible to believe that two species with such floral differences could be so all-prevailingly similar in all other structures. I am also aware of the fact that in this genus, among species with elongate corollas, the stamens are always borne above the middle of the corolla-tube when only monomorphic flowers are produced. Stamens borne low in the corolla-tube are found only in long-styled flowers of heterostylic species. It is not unreasonable to believe, therefore, that, though *L. tschimganicum* may not now be heterostylic, it may have been derived from such an ancestor. Though now without correlated differences of pollen and style, it may have retained only the corolla-dimorphism of its heterostylic ancestry. If so, the condition is very unusual, and certainly unique in this genus. The matter should be investigated by someone who can observe the plants in the field, or at least by one who has access to many more specimens than have been available to me.

17. *Lithospermum Tournefortii*, nom. nov.

Lycopsis Echioides L. Sp. Pl. ed. 2, 199 (1762).—Based on *Echioides*, Tourn. Coroll. Inst. 46 (1703) and Buxbaum, Cent. 1: 1, t. 1 (1728). Not *Lithospermum echioides* Benth. in Royle (1836).

Arnebia echioides (L.) DC. Prodr. 10: 96 (1846); Bot. Mag. 74: t. 4409 (1848); Gartenfl. 25: 259, t. 877 (1876).

Anchusa echioides (L.) M. v. B. Fl. Taur.-Cauc. 1: 123 (1808).

Macrotomia echioides (L.) Boiss. Fl. Orient. 4: 211 (1879); Farrer, English Rock Garden 1: 469 (1930).

Aipyanthus echioides (L.) Stevens, Bull. Soc. Nat. Moscou 26: 600 (1851).

Arnebia longiflora C. Koch, Linnaea 22: 640 (1849). Not *Lithospermum longiflorum* Salisb. (1796), nor Spreng. (1825).

A handsome and very distinct species of Armenia and the Caucasus, frequently cultivated as a rock-garden plant. The large yellow corolla becomes 2–3 cm. long and has a tube usually twice as long as the calyx.

The tube is villose inside and the broad limb has an evanescent black spot at the base of each sinus. The throat has neither appendages nor glands and the tube neither nectary nor rudiments of it. The stamens are affixed on the corolla at several superimposed levels, in the long-styled flowers in a zone below the middle of the tube and in the short-styled flowers in a zone high in the throat. In these antheriferous zones there appear to be two stamens that are uppermost, an alternating pair that are lowermost, and a fifth stamen at an intermediate level. Furthermore, very close examination reveals that in both upper and lower pair one member has a slight but still perceptibly lower attachment than its companion. Accordingly, in various degrees, the stamens are all attached at differing levels. The androecium appears to have no plane of symmetry. The style reaches either to the middle of the corolla-tube or to its summit. The two stigmas are broad and terminal and tend to be somewhat united, sometimes to form a single obconic stigmatic mass. The pollen (fig. 8) is globose or very slightly longer than broad. There are 9 obscure pores spaced about its equator. In long-styled flowers the grains measure 30–35 μ in diameter and in the short-styled flowers 40–50 μ . The large nutlets are smooth or only inconspicuously and minutely tuberculate towards the apex. They are brownish, minutely mottled with purple, and not lustrous. The ventral side is sharply angled. The attachment surface is broad, rounded, and basal. The gynobase is very broadly pyramidal.

18. *Lithospermum multiflorum* Torr. in Gray, Proc. Am. Acad. 10: 51 (1874).

Lithospermum cognatum Greene ex Spengler, Oesterr. Bot. Zeit. 68: 118, f. 31 (1919).

A species of western United States (Colorado and Utah south to western Texas and Arizona) and adjoining Mexico. Flowers are clearly heterostylic. The corollas have 5 glanduliferous slightly swollen (but not invaginate) areas in the throat and a well-developed basal nectary composed of 10 quadrate villulose lobes. The corolla-tube is glabrous within. In short-styled flowers the stamens are borne in the throat of the corolla and the style reaches up to the middle of the tube. In long-styled flowers the style is nearly exerted and the stamens are borne at the middle of the corolla-tube and the tube above them is glanduliferous. In flowers of both types the filaments are usually somewhat glanduliferous at and just below their base. The pollen (fig. 14) is characteristically ellipsoid and broadest at the equator, but occasionally may become almost cylindric with the sides nearly parallel. The pores are in a single medial row. In long-styled flowers the grains measure 16–20 $\times$ 8–13 μ and in short-styled flowers 25–33 $\times$ 20–28 μ . The two terminal stigmas are somewhat semicircular or flabellate and frequently bilobulate. They tend to be spreading or even slightly reflexed. Commonly they are umbonate at the base just above their attachment to the end of the style. I have had a great number of specimens of this species for study, among them, surprisingly, are very few in the fruiting state.

19. *Lithospermum obovatum* Macbride, Contr. Gray Herb. 48: 56 (1916).

Lithospermum gentianoides Brand, Fedde Repert. 28: 15 (1930).

A well-marked species having obvious relations with *L. cobrense*. It is known only from the Sierra Madre Occidentale of northern Mexico (Chihuahua and Durango). The thickish basal leaves are very broad, obovate to elliptic, and form a conspicuous rosette. They are conspicuously veined, with the veins not merely prominent beneath but also strongly sulcate on the upper face. Their indument consists of slender elongate hairs only, not of a mixture of long and short hairs as in *L. cobrense*. The corolla resembles that of *L. cobrense* in form but differs in a number of other respects. The glands in the throat of the corolla tend to form small but evident aggregations below the base of each corolla-lobe. The corolla-tube inside is hairy only in long-styled flowers. In short-styled flowers the tube is glabrous. The stamens in the long-styled flowers are borne in the lower third of the corolla and hence lower proportionately than in *L. cobrense*. The pollen (fig. 16) is ellipsoid and broadest at the equator. It measures $14-18 \times 10-13 \mu$ in long-styled flowers and $25-28 \times 18-23 \mu$ in the short-styled flowers. The nutlets of this species are unknown.

20. *Lithospermum cobrense* Greene, Bot. Gaz. 6: 157 (1881).

A species known only from Arizona, New Mexico, and western Texas, and in the mountains of northern Mexico, in Chihuahua and Durango. The flowers are strongly heterostylic. The funnelform orange or yellow corollas have the tube hairy inside and possess a well-developed basal nectary composed of 10 crowded quadrate lobes. The throat is unappendaged but evidently glanduliferous. The glands are numerous and generally distributed. They are not aggregated as in *L. obovatum*. In the short-styled flowers the stamens are borne in the throat and the style is very short, usually not half the length of the calyx. In the long-styled flowers the stamens are borne just below the middle of the corolla and the style reaches up into the glanduliferous throat. The two stigmas are terminal, spreading, and semicircular or obovate. The pollen (fig. 15) is ellipsoidal and usually broadest at the equator. In the two types of flowers it differs only in size and in the position of the 7-9 pores. In the long-styled flowers the pores tend to be slightly submedial rather than exactly medial in position. The grains of the long-styled flowers measure $21-25 \times 12-20 \mu$, and those of the short-styled flowers $26-39 \times 23-31 \mu$.

21. *Lithospermum tubuliflorum* Greene, Pittonia 1: 155 (1888).

Lithospermum lasiosiphon Johnston, Contr. Gray Herb. 70: 22 (1924).

A species showing relationship with *L. cobrense* and *L. obovatum*. It is known only from the east base of the Sierra Madre Occidentale in Chihuahua and Durango in northern Mexico. The foliage is thin, light green, and inconspicuously hairy. The basal leaves form a rosette and, like those of *L. obovatum*, have the veins evident on both surfaces. The

flowers are strongly heterostylic. The corolla is tubular-funnelform with ascending lobes and most resembles that of *L. multiflorum* in general form. The throat is very sparingly glanduliferous and completely lacking in appendages. The tube is always hairy inside. The nectary is similar to that of *L. cobrense* but is less prominent. The stamens of the long-styled flowers are borne extremely low, in the lower third of the tube. The pollen (fig. 10) in the two types of flower differs in shape as well as size. That of long-styled flowers is broadest and shouldered just below the middle. It measures $26-30 \times 16-25 \mu$. The pollen of short-styled flowers measures $33-40 \times 26-32 \mu$ and is ellipsoidal and broadest at the equator. There are apparently 8 pores. The nutlets resemble those of *L. cobrense* but are slightly smaller and perhaps more sharply keeled.

22. *Lithospermum californicum* Gray, Proc. Am. Acad. 10: 51 (1875).

A species known only from northern California and adjacent Oregon. Although in many ways very suggestive of *L. ruderale*, and especially so in form and organization of corolla and nutlets, *L. californicum* differs in type of inflorescence, pollen, and presence of heterostyly. Distinctive features of the species are its slightly glaucescent herbage and its recurved fruiting calyx. The elongate yellow corolla is gradually ampliate, 10–15 mm. long, and has a limb of loosely ascending lobes 5–10 mm. in diameter. The throat is glanduliferous and sometimes bears very obscure swellings below each of the corolla-lobes, but is otherwise unappendaged. The stamens are borne either slightly above the middle of the glabrous corolla-tube or near its summit. The style reaches up to near the middle of the tube or is nearly exerted from it. The two stigmas are terminal. The pollen on the long-styled flowers (fig. 9) measures $25-28 \times 10-18 (-22) \mu$. It tends to be rather variable in form, sometimes resembling that of the short-styled flower and sometimes being distinctly constricted at the middle. The pollen of the short-styled flowers (fig. 9) measures $33 \times 20-25 \mu$ and is nearly ovoid or is ovoid with distinct shoulders. The nectary in the corolla-tube is an obscurely lobed glabrous tumid ring. The smooth white ovoid nutlets, ca. 5 mm. long, are rather pointed and have a strong constriction just above their base.

23. *Lithospermum caroliniense* (Walt.) MacMill. Metasp. Minn. Valley 438 (1892).

Anonymos caroliniense Walter, Fl. Carolina 91 (1788).

Batschia caroliniensis (Walt.) Gmel. Syst. 1: 315 (1791).

Lithospermum carolinianum Lam. Tab. Encyc. 1: 397 (1791).

Onosmodium carolinianum (Lam.) A.DC. Prodr. 10: 70 (1846).

Batschia Gmelini Michx. Fl. Bor. Am. 1: 130 (1803).

Lithospermum Gmelini (Michx.) Hitchc. Spring Fl. Manhattan 30 (1894).

Anchusa hirta Muhl. Cat. 19 (1813), nomen.

Lithospermum hirtum (Muhl.) Lehm. Asperif. 2: 304 (1818).

Lithospermum strigosum Raf. New Fl. No. Amer. 4: 18 (1836).

Lithospermum bejariense A. DC. Prodr. 10: 79 (1846).

Lithospermum croceum Fernald, Rhodora 37: 329, t. 376 (1935).

A well-known species, widely distributed in eastern United States. Plant 3–10 dm. tall, arising from a strong dye-stained root, and commonly becoming very dark in drying. Flowers heterostyled. Corolla orange-yellow, 13–25 mm. long, with a funnelform limb nearly as broad. Corolla-tube cylindric, in long-styled flowers 7–8 mm. long, about equalling the calyx; in short-styled flowers 10–12 mm. long, surpassing the calyx by as much as 3–4 mm. The corolla-throat is very obscurely if at all invaginate, its appendages are represented only by 5 arcuate clusters of glands at the summit of the tube. Inside the tube is sparingly glanduliferous above the middle but otherwise glabrous. The anthers are borne either above the middle of the tube or just below its summit. The style reaches almost to the middle of the tube or almost to the summit. The 2 stigmas are terminal. The corolla-nectary is 10-lobed and minutely villulose. The pollen (fig. 12) has 7–9 pores, and in the two types of flowers differs in size as well as shape. In long-styled flowers it is elongate, constricted at the middle, and measures $33 \times 13\text{--}18 \mu$. In short-styled flowers the pollen is ovoid, with shoulders, and is broadest at one end. It measures $33\text{--}39 \times 25\text{--}33 \mu$. It may be noted in passing that the floral differences used by Fernald to distinguish *L. croceum* from *L. carolinense* are those which distinguish the short- and long-styled flowers of the species.

24. *Lithospermum canescens* (Michx.) Lehm. Asperif. 2: 305 (1818).

Batschia canescens Michx. Fl. Bor. Am. 1: 130, t. 14 (1803).

Anchusa canescens Muhl. Cat. 19 (1813).

Anchusa virginiana L. Sp. Pl. 133 (1753). Not *Lithospermum virginianum* L. (1753).

Lithospermum sericeum Lehm. Asperif. 2: 306 (1818).

Batschia sericea (Lehm.) R. & S. Syst. 4: 743 (1819).

Batschia conspicua R. Br. in Richardson, Bot. Append. to Frankl. Jour. 732 (1823).

A native of eastern United States. Stems 1–4 dm. tall, arising from a strong dye-stained root. When young the plant has a very distinctive vesture of slender, appressed, somewhat silky hairs. The flowers are heterostylic. The yellow corolla is 10–18 mm. long and has a funnelform limb 11–15 mm. in diameter. Its tube is cylindrical, 7–8 mm. long, and evidently longer than the small calyx. The throat bears weakly invaginate appendages which are usually gibbose and somewhat velvety as well as glanduliferous, especially on the sides. The tube is glanduliferous above the middle, and most abundantly so in long-styled flowers. Its nectary is 10-lobed and minutely villulose. The anthers are borne either just below the middle of the corolla-tube or near its summit. The style is either very short, 1–2 mm. long and less than a third of the tube-length, or surpasses the stamens and becomes 5–9 mm. long. It is terminated by 2 small stigmas. The pollen (fig. 11) of the long-styled flowers is constricted at the middle and measures $20\text{--}25 \times 10\text{--}13 \mu$. That of the short-styled flowers (fig. 11) is shouldered-ovoid, broadest at one end, and measures $25\text{--}33 \times 14\text{--}23 \mu$.

25. *Lithospermum tuberosum* Rugel ex DC. Prodr. 10: 76 (1946).

A species of southeastern United States readily recognized by its rosette of basal leaves and clustered fleshy fusiform roots. The flowers resemble those of *L. officinale* and allies. *Lithospermum tuberosum* probably has its closest relations with those species. The yellow or yellowish corolla is 4.5–6 mm. long and has a tube 3–4 mm. long. The corolla-lobes, 1.5–2 mm. long, are longer than broad and ascending. The throat bears 5 small intruding velvety trapeziform appendages formed by invagination. Below the appendages the throat is sparingly glanduliferous. The calyx is shorter than the corolla-tube or at most equals it in length. The filaments are attached at the middle of the corolla-tube and have no glands at their base. The nectary is a narrow glabrous flange. The style is 2–3 mm. long and bears 2 small terminal stigmas. The pollen (fig. 20) is somewhat ovoid, being broadest towards one end and commonly measuring $20 \times 16 \mu$. The nutlets are small, 1.5–2.5 mm. long, and may be abundantly punctate.

26. *Lithospermum erythrorhizon* Sieb. & Zucc. Abh. Bayer, Akad. Wiss. 4³: 149 (1846); Hara, Bot. Mag. Tokyo 51: 50 (1937) and Enum. Spermatoph. Japon. 1: 176 (1948).

Lithospermum officinale β *erythrorhizon* (Sieb. & Zucc.) Maxim. Bull. Acad. St. Petersb. 17: 441 (1872).

Lithospermum officinale subsp. *erythrorrhizon* (Sieb. & Zucc.) Hand.-Mazz. Symb. Sin. 7⁴: 817 (1936).

Lithospermum murasaki Siebold, Syn. Pl. Oecon. Jap. 32 (1830), nom. subnud.

Lithospermum officinale var. *japonica* Miquel, Ann. Mus. Lugd.-Bat. 2: 94 (1865).

Lithospermum albiflorum Vaniot, Monde de Plantes ser. 2, 7: 42 (1905).

This species is a very close relative of *L. officinale* and occurs beyond the eastern limit of the latter in China and northward in Korea and Japan. It differs in having spreading rather than closely appressed hairs on the herbage, a larger, somewhat differently shaped corolla, and a larger, more strongly accrescent calyx. Its root appears to contain larger quantities of purple dye than that of *L. officinale*. The corolla has been illustrated as pure white, and collectors have so reported it. Unlike that of *L. officinale*, the limb of the corolla is spreading and formed of rounded lobes about as broad as long. Its diameter is commonly about equal to the total length (5–9 mm.) of the corolla. The corolla-tube, 3–4 mm. long, is usually equalled or shortly surpassed by the calyx-lobes. The faucal appendages are trapeziform invaginations which are velvety on the summit and glanduliferous on the side. The filaments are affixed at the middle of the tube and are glanduliferous at the base. The nectary is a glabrous flange. The pollen, $13\text{--}16 \times 8\text{--}10 \mu$, is constricted at the middle or rarely has near straight and parallel sides. The fruiting calyx is commonly 5–10 mm. long and usually several times longer than the nutlets.

Plants from Afghanistan, Pakistan, and Kashmir agree with those from

eastern Asia in having spreading hairs on the stems. In characters of calyx and corolla, however, they agree with typical *L. officinale* and probably deserve to be classed as variants of that species.

27. *Lithospermum officinale* L. Sp. Pl. 132 (1753).

Native in Europe and east to central Asia. In Afghanistan, Kashmir and Pakistan it is replaced by a variety with spreading hairs, and in China, Korea, and Japan by the closely related *L. erythrorhizon*. Over its wide range *L. officinale* remains a reasonably constant species. Its stems are closely strigose and have no spreading hairs. The yellowish or greenish, or sometimes nearly white corollas are 4–6 mm. long. The corolla-limb is at most 4 mm. broad and consists of ascending usually oblong lobes 1–1.5 mm. long. The tube is 2.5–3.5 (or rarely 4) mm. long. The calyx may be shorter than the corolla-tube or slightly longer, but commonly it has about the same length. The corolla-throat bears 5 trapeziform, intruded, distinctly invaginate appendages which are densely velvety on top and glanduliferous, particularly on the sides. Below the level of the faucal appendages glands are scattered. The filaments, attached at the middle of the corolla-tube, are usually glanduliferous at the base. The style is 1–2 mm. long and bears 2 small terminal stigmas. The nectary on the corolla-tube is a glabrous, entire, or obscurely lobed flap. The pollen (fig. 32) is constricted at the middle and measures $13-16 \times 8-10 \mu$. The nutlets (2.7–3.8 mm. long) are most commonly about 3 mm. in length and more than half as long as the fruiting calyx.

28. *Lithospermum latifolium* Michx. Fl. Bor. Am. 1: 131 (1803).

Lithospermum officinale β *latifolium* Lehm. Asperif. 2: 311 (1818).

Cyphorima latifolia (Michx.) Raf. in DC. Prodr. 10: 76 (1846).

Cyphorima lutea Raf. Cat. 13 (1824).

Lithospermum luteum (Raf.) House, Bull. N. Y. State Mus. 243–4: 61 (1923).

Lithospermum lutescens Coleman, Cat. Pl. Grand Rapids 29 (1874).

A species of northeastern United States very closely related to the Eurasian *L. officinale*. The pale yellow corolla is 5–7 mm. long and has ascending lobes nearly as broad as long. Its tube is 2.5–3.5 mm. long and is evidently shorter than the slender calyx-lobes. The throat has 5 intruded velvety trapeziform appendages formed by invagination. The inner face of the appendages is glanduliferous and so also is the throat directly below them. The filaments arise at the middle of the corolla-tube and usually bear some glands at their base. The style is very short, usually only 1 mm. or less long, and bears two small terminal stigmas. The nectary is a glabrous flange. The pollen (fig. 25) resembles that of *L. officinale* but is slightly larger and less constricted. It measures $16-20 \times 8-14 \mu$. The nutlets, 4.5–5 mm. long, are usually much surpassed by the calyx-lobes.

29. *Lithospermum mirabile* Small, Fl. Southeast. United States 999 and 1337 (1903).

Lithospermum longiflorum var. *mirabile* (Small) Brand, Fedde Repert. 28: 14 (1930).

A very distinct species which is most closely related to *L. incisum* and *L. Parksii*. It is confined to the eastern half of Texas. The plant is a biennial or a short-lived perennial and has a thickened, dye-stained, fusiform taproot. The stems, usually few, bear elongating cymes that produce only conspicuous chasmogamic flowers or first chasmogamic flowers and then later cleistogamic ones. Both types of flowers are fertile. The conspicuous flowers have corollas similar in form, size, and organization to those of *L. incisum*, but differ in their darker coloration and in the entire margin of their lobes. The nutlets are very distinctive and are readily separable not only from those of related species but from those of all other members of the genus. They are brown, dull, abundantly punctate, rough, and distinctly angulate. They have only a weakly defined collar at the base and their attachment-scar is flat. The gynobase is depressed pyramidal or nearly horizontal. The pollen resembles that of *L. incisum* in form and size (33–44 μ), but unlike that species tends to have its pores slightly visible. These pores are 7 or more commonly 8 in number and are equally spaced about the equator.

Meriting publication are some interesting field observations concerning *L. mirabile* contained in a letter addressed to me on Aug. 5, 1937, by Dr. H. B. Parks, then Chief of the Apicultural Research Laboratory, San Antonio, Texas. "This is the plant that sent me on the quest to find out something about this genus. I noted that in travelling through the country in early spring there were two colors of flowers among the *Lithospermums* seen by the roadside. A casual investigation revealed the fact that the darker yellow one had smooth edges to the corolla, while the light yellow one was toothed or crisped. On investigation I became convinced that the yellow flowered one was *L. mirabile* and now after having raised the plant and produced the seeds I am sure of this determination. *Lithospermum mirabile* does produce a few small cleistogamous flowers which sometimes develop fruits, however the most of its fruits come from perfect flowers. This plant contrary to statements is not restricted to the vicinity of San Antonio. It seems to be restricted to the Eocene plains which stretch across Texas south of a line from Texarkana to Del Rio. The plants are generally found in poor, gravelly or clay soils. They commence to bloom by the latter part of March and will stay in bloom until the first of July. From a distance, with the exception of color in the flowers, there is little to distinguish this plant from *L. incisum*; however, the whole manner of growth, the shape of the leaves, and the shape of the seed show it is a good species. I have collected it from Bexar County on the north to Brooks County on the south and from Medina County west to Anderson County on the east. In many places it is more abundant than *L. incisum*, a thing which I think is due to the difference in soil requirement."

30. *Lithospermum incisum* Lehm. Asperif. 2: 303 (1818).

Lithospermum angustifolium Michx. Fl. Bor. Am. 1: 130 (1803), not Forsk (1775).

Lithospermum linearifolium Goldie, Edinb. Phil. Jour. 6: 322 (1822).

Batschia longiflora Nutt. in Pursh, Fl. Sept. Am. 1: 132 (1814).

Lithospermum longiflorum (Pursh) Spreng. Syst. 1: 544 (1825), not Salisb. (1796).

Batschia decumbens Nutt. Gen. 1: 114 (1818).

Lithospermum decumbens (Nutt.) Torr. Ann. Lyceum N. Y. 2: 225 (1826), not Vent. (1800).

Lithospermum cryphtanthiflorum Brand, Fedde Repert. 28: 13 (1930).

Lithospermum boreale Brand, Fedde Repert. 28: 13 (1930).

A species widely distributed in the United States, chiefly on the Great Plains and along the Rocky Mountains, and extending into adjacent Canada and Mexico. The plant has been given many names. Only the older and the most recent ones are given above. For additional synonymy see Johnston, Contr. Gray Herb. 70: 24 (1924).

In the spring the plant produces compact terminal clusters of very conspicuous yellow flowers. The tube of the corolla is 20–35 mm. long, 2–3 mm. thick, and two to three times as long as the calyx. The limb is 8–15 mm. in diameter, and its broad rounded lobes have erose-fimbriate margins. There are five evident faucal appendages. These are invaginate, trapeziform, and moderately glanduliferous. The stamens are always borne high in the corolla-tube, 1–2 mm. below the base of the appendages. The style varies considerably in length, from half as long as the corolla-tube to slightly longer. There is some evidence for believing that the style may change in length between anthesis and the time the corolla is shed. The two stigmas are semicircular or ovate and terminal. The nectary at the base of the corolla-tube is very weakly developed or absent and commonly consists only of five very minute tufts of hairs.

The nutlets are elongate, 2.5–3 mm. long, broadest near the middle and smooth or somewhat punctate. A lineate constriction just above the base gives the nutlet a more or less well defined basal collar. This collar, commonly slightly different from the rest of the nutlet in color and surface, surrounds the concave or excavated basal attachment-scar. The scar is notable not only for its concavity, but also for bearing a subulate appendage, ca. 1 mm. long, resulting from a projection of tissue surrounding the dorsal vascular bundles of the nutlet. The gynobase is distinctly pyramidal, about one and a half times as broad as high. After the fall of the nutlet each of its attachment-surfaces has a central pit, the socket into which the appendage on the nutlet-scar formerly fitted. As a result of a bend in the pedicels, the fruiting calyces are usually nutant or cernuous.

After the appearance of the bunched large conspicuous vernal flowers, the plant becomes much branched and then produces cleistogamic flowers exclusively, and these in very great abundance. The early flowers with conspicuous corollas mature few fruits, but the later flowers with minute (1–3 mm. long) closed corollas are extremely fertile. This fact is readily established by observing the length of the persistent style. Few fruits are to be found associated with the long (10–30 mm.) style of the conspicuous vernal flowers. The pollen (fig. 17) of this species is spherical and bears 7 or 8 obscure pores equally spaced about the equator. In chasmogamic

flowers it measures 33–42 μ in diameter. In cleistogamic flowers it is slightly smaller, 27–35 μ , but otherwise indistinguishable.

31. *Lithospermum Parksii*, sp. nov.

Herba perennis 2–3 (–5) dm. alta erecta; caulibus pluribus praesertim supra medium adscendenti-ramosis; foliis costatis sed saepissime enervatis griseis adpresse villosis-hispidulis, maturitate margine saepe evidenter revolutis; foliis inferioribus majoribus oblanceolatis 5–10 cm. longis 5–10 mm. latis obtusis; foliis caulinis mediis linearibus obtusis saepe 2–4 cm. longis 2–4 mm. latis; cymis conspicue bracteatis caules ramulosque terminantibus simplicibus, juventute circinatis, maturitate elongatis racemosis ad 10 cm. longis, saepe floribus chasmogamicis abundantibus gestis et solum senescentibus apicem versus flores cleistogamicos paucos gerentibus vel rare a basi usque ad apicem floribus cleistogamicis donatis; floribus chasmogamicis fertilibus, corolla more *L. incisum* sed margine loborum integerrimo, tubo saepe 15 mm. longo 2–3 mm. crasso, limbo 10–12 mm. diametro, lobis rotundis integerrimis, fauce appendiculis trapaeziiformibus glanduliferis instructo, calyce supra medium tubi corollae attingenti, in statu fructifero erecto, lobis calycis linearibus margine revolutis quam nuculis saepe subtriplo longioribus; floribus cleistogamicis fertilibus, corolla 1–3 mm. longa perinconspicua, calyce ei florum chasmogamicorum simili; nuculis elongatis opacis densissime verrucosis et punctatis supra basim aliquantum constrictis, basi tumidis, cicatrice concava.

TEXAS: Edwards County: 25 mi. n.w. of Rocksprings, *Cory* 24195 (G); 7.25 mi. n.w. of Rocksprings, *Cory* 38768 (G); Little Hackberry Creek, 14.5 mi. s.e. of Rocksprings, *Cory* 42962 (G); Pulliam Creek below Blue Hole, *Cory* 43779 (G). Kinney County: 23.7 miles north of Brackettville, *Cory* 645 (G). Sutton County: Substation no. 14, Pasture E, *Corey* 24189 (G). Val Verde County: 6.33 miles south of Loma Alta, *Cory* 41685 (G); Devils Lake, ca. 20 miles n.-n.w. of Del Rio, *McVaugh* 7725 (TYPE, Gray Herb.). Jeff Davis County: Piedra Pinta, 1851, *Wright*, field no. 110 (G); Brewster Glass Mountains, 1936, *Cory* (G); Gage Ranch, Glass Mts., *Warnock* 553 (G); Hess Canyon, Glass Mts., *Warnock* 294 (G); Jim Nichol's Ranch, Old Blue Mt., *Warnock* 567 (G); Sierra del Norte, ca. 10 mi. s.e. of Alpine, *McVaugh* 7856 (G).

Lithospermum Parksii var. *rugulosum*, var. nov.

A varietate genuina differt pilis sparsioribus vestita, radice minus persistente; nuculis subnitidis dense rugosis haud verrucosis.

MEXICO: COAHUILA: near Rancho Encampanada, Sierra Hechiceros, *Stewart* 206 (G); Muzquiz, *Marsh* 2108 (G); Caracol Mts., southeast of Monclova, *Palmer* 897 (G); Soledad, west of Monclova, *Palmer* (G). NUEVO LEON: descent into Alamar, ca. 15 mi. s.w. of Galeana, *Mueller* 598 (TYPE, Gray Herb.). TAMAULIPAS: cliffs s.w. of Victoria, *Runyon* 726 (US).

A species known only from areas of limestone in southwestern Texas and northeastern Mexico. Obviously a close relative of *L. incisum* and native to an area in which that species occurs also. It is, however, certainly

distinct! Among the characters distinguishing it from its relative are the olivaceous rather than gray-green herbage, the loosely appressed hairs of stem and leaves, the entire margins of the corolla-lobes, and the verrucose or rugose nutlets. Unlike *L. incisum* the plant does not become diffusely branched. Its cymes are all elongate and racemose at maturity.

The chasmogamic flowers are usually fertile. They are the flowers first developed in the spring and frequently make up the majority of those developed on the elongating cymes. The last flowers on the cyme, however, are usually cleistogamic. Cymes developed late in the season may bear only cleistogamic flowers. Mature, fully elongate cymes, whether producing open or closed flowers, are similar in size and form. This is very different from the condition in *L. incisum*. The chasmogamic corolla of *L. Parksii* differs from that of *L. incisum* only in its paler yellow color and entire lobes. The appendages, stamens, pollen, and style in the two species are indistinguishable. The nutlets of the two species, though very different in surface features, are rather similar in size, form, and attachment. In *L. incisum* the nutlets are smooth or merely pitted. In *L. Parksii* they are covered with crowded warts or are distinctly rugose. The fruiting calyx is erect and never nutant or cernuous as prevalent in *L. incisum*.

As here defined *L. Parksii* included two recognizable forms, the var. *typicum* of Texas and the var. *rugulosum* of near-by Mexico. Possibly these should be treated as two closely related species. However, until a larger suite of specimens of the Mexican plant becomes available for comparison, and especially until collections showing the fully mature nutlets can be studied, the present disposition of the two plants seems desirable. The Texan plant is much more vigorous and obviously has more numerous, stiffer stems and a stronger and much more persistent root than does the Mexican. All the plants of Texas give the appearance of having grown in sunny exposed places, while those from Mexico seem to have come from partial shade, perhaps from open woodland. The most important difference between the varieties, however, is in the nutlets. The nutlets of the Texan plants are coarsely and densely verrucose. The surface is opaque and covered with very crowded warts which are separated here and there by pits and deep narrow irregular fissures. On the other hand, the nutlets of the Mexican plants are slightly lustrous and are roughened only moderately by crowded irregular ridges.

The species is named for Dr. H. B. Parks, former chief of the Texas Apicultural Research Laboratory, to whom I am indebted for many valuable notes concerning the Texan species of *Lithospermum*, the results of his cultivation and observation of the species over many years. The present plant, which he first called to my attention fifteen years ago, is very fittingly associated with his name.

32. *Lithospermum confine*, sp. nov.

Planta erecta strigosa perennis e radice palari valida erumpens, 2–4 dm. alta; caulibus pluribus erectis praesertim supra medium ramosis foliosis; foliis costatis sed enervatis viridibus utrinque strigosis numerosis obtusis

2–6 cm. longis 1–10 mm. latis, inferioribus oblanceolatis, superioribus lanceolatis vel linearibus, margine anguste revolutis; cymis caules et ramos terminantibus, juventate glomeratis maturitate ad 10 cm. longis racemosis foliosis distantifloris; inflorescentiis a basi fere ad apicem flores chasmogamicos gerentibus solum apice floribus cleistogamicis donatis vel cymis omnino flores cleistogamicos proferentibus; floribus chasmogamicis flavis, tubo 7–10 mm. longo 1–2 mm. crasso calyce subduplo longiori, limbo 5–6 mm. diametro, lobis rotundis margine integris, fauce appendiculis trapeziformibus invaginati glanduliferis donato, stylo 5–10 mm. longo; floribus cleistogamicis inconspicuis 1–3 mm. longis, stylo 1.5–3 mm. longo; calyce subanthesi 4–5 mm. longo, lobis linearibus statu fructifero saepe ad 10 mm. longis nuculis duplo longioribus; pedicello fructifero 2–10 mm. longo erecto; nuculis laevibus nitidis albis supra basim plus minusve constrictis 3–3.5 mm. longis 2–2.5 mm. crassis.

ARIZONA: Chiricahua Mine, 6500 ft. alt., Oct. 17, 1907, *Blumer 1796* (G); 8 m. north of Metcalf, Greenlee Co., June 5, 1935, *Maguire et al. 11805* (G). TEXAS: Smith Canyon, Guadalupe Mts., Culberson Co., 5500 ft., Sept. 15, 1948, *Warnock 113* (G); (?) Little Hackberry Creek, 14.5 mi. southeast of Rocksprings, Edwards Co., Aug. 9, 1943, *Cory 42961* (G).

MEXICO: COAHUILA: Sierra del Pino, mouth of southern canyon, Aug. 26, 1940, *Johnston & Muller 746A* (G). NUEVO LEON: Canyon de los Capulines, above San Enrique, Hacienda San Jose de Raices, Aug. 6, 1935, *Mueller 2378* (TYPE, Gray Herb.) and *2379* (G).

The plants above described agree in gross habit and vegetative characters, in calyx, nutlets and pollen, and in their predominantly cleistogamic flowering. Annotation on the specimens cited gives evidence of my uncertainty and changing opinions concerning their identity. At one time or another they have been questionably identified as *L. obtusifolium*, *L. calycosum*, *L. multiflorum*, *L. cobrense*, and *L. incisum*, and even their possible hybrids, as well. In grouping them in a proposed species I am aware that they are relatively few in number and that they represent a wide and erratic geographic distribution on either side of the United States–Mexican boundary. The specimens come from scattered localities in southeastern Arizona, in western Texas and northeastern Mexico, all areas much visited by botanists. I can only suggest that because the species is pre-vaillingly cleistogamic and accordingly deficient in colorful flowers, it has not attracted the attention of collectors and so is poorly represented in herbaria.

In general appearance *L. confine* closely simulates *L. calycosum*, a Mexican species also developing cleistogamic flowers. It is, however, readily separable from that species by its large spherical pollen, basally constricted nutlets, and chasmogamic corollas with faucal appendages. The same characters also eliminate *L. cobrense* and *L. multiflorum*, as does also the presence of cleistogamy. Cleistogamy is known in *Lithospermum* only in *L. calycosum* and in the group of species containing *L. incisum*, *L. Parksii*, and *L. mirabile*. Our present plant obviously belongs in this latter group.

It has the distinctive pollen of that group, and also similar chasmogamic corollas. Its nutlets, furthermore, are very similar in appearance, size, form, and structure to those of *L. incisum* and, in all except surface markings, to those of *L. Parksii* also. I believe it to be most closely related to *L. incisum*. From that species it differs in its infrequent, much smaller chasmogamic flowers, entire-margined corolla-lobes, erect fruiting pedicels, elongate cymes, and erect, never diffusely branched stems.

33. *Lithospermum afromontanum* H. Weim. Bot. Notiser 1940: 65, f. 7 (1940).

A very distinct plant of central Africa formerly confused with the very different *L. officinale*. From the latter it is easily distinguished by having very different pollen, a more accrescent calyx, and stamens borne high in the more elongate corolla-tube. The stems are very elongate, 5–10 dm. long, and bear numerous sharply acute lanceolate leaves 4–8 cm. long and 7–30 mm. broad. The yellow corolla has a subcylindric tube 5–7 mm. long, which usually surpasses the calyx by 1–2 mm. The spreading limb is about 8 mm. in diameter. The faucal appendages are well developed gibbose invaginations which are minutely hairy and glanduliferous. The nectary is a thickish collar. The style is 1.5–4 mm. long and terminated by two small stigmas. The pollen is cylindric with rounded ends and straight paralleling sides. It measures 20 by 13 μ .

34. *Lithospermum ruderale* Dougl. ex Lehm. Pug. 2: 28 (1830).

Lithospermum pilosum Nutt. Jour. Acad. Philad. 7: 43 (1834).

Batschia pilosa (Nutt.) G. Don, Gen. Syst. 4: 372 (1838).

Lithospermum Torreyi Nutt. Jour. Acad. Philad. 7: 44 (1834).

Batschia Torreyi (Nutt.) G. Don, Gen. Syst. 4: 372 (1838).

Lithospermum ruderale var. *Torreyi* (Nutt.) Macbride, Contr. Gray Herb. 48: 55 (1916).

Lithospermum laxum Greene, Pittonia 3: 263 (1898)

Lithospermum lanceolatum Rydb. Mem. N. Y. Bot. Gard. 1: 333 (1900).

Lithospermum ruderale var. *lanceolatum* (Rydb.) Nelson, Bot. Gaz. 52: 272 (1911).

Lithospermum ruderale var. *macrospermum* Macbride, Contr. Gray Herb. 48: 55 (1916).

Widely distributed in northern portions of western United States and adjacent Canada. A distinctive feature of the species is its cylindric thyrsoid inflorescence. Unlike most species of the genus, there is no large dominant cyme terminating the main stems. Indeed, in *L. ruderale* the terminal cyme is usually less developed than the numerous small lateral cymes that arise from the upper leaf-axils. The aggregation of these numerous small cymes is elongate, very leafy and cylindric. The pale yellow corollas have a cylindric tube not much longer than the calyx. The limb has ascending lobes. The throat bears more or less well defined congregations of glands below each corolla-lobe, but has no intruding appendages. Scattered glands are numerous in the tube above the level of the filament-attachments and

further down, scanty along the principal veins to near the middle of the tube. The nectary is a somewhat tumid obscurely lobed glabrous ring. The style reaches up to the level of the stamens and is usually shorter than the calyx-lobes. The two stigmas are terminal and juxtaposed. The pollen (fig. 23) is ellipsoidal $25 \times 18\text{--}20 \mu$, and in lateral profile has rounded or weakly angulate sides. It is clearly broadest at the equator. The pores are weak or obscure. The nutlets, 4–7 mm. long, are ovoid or globose-ovoid, pointed at the apex, and strongly constricted just above the broad base.

35. *Lithospermum calycosum* (Macbride) Johnston, Contr. Gray Herb. 70: 30 (1924).

Lithospermum strictum var. *calycosum* Macbride, Contr. Gray Herb. 48: 56 (1916).

Lithospermum obtusifolium Johnston, Contr. Gray Herb. 70: 27 (1924).

Lithospermum Galeottii Brand, Fedde Repert. 28: 17 (1930).

A variable species ranging from northeastern Mexico south into the mountains of Guatemala. One of its features is its capacity for developing cleistogamic flowers. Cleistogamy is known in the genus otherwise only in *L. incisum* and its close relatives. The chasmogamic corollas of *L. calycosum* vary widely in size, being largest on vigorous plants and especially in the spring of the year. Late flowers or those on plants in unfavorable habitats tend to be small and frequently cleistogamic. The yellow corollas have a subcylindric tube 5–16 mm. long and 1.5–2.5 mm. thick. When large the tube may be twice the length of the calyx but when small it may scarcely surpass the calyx. The corolla-limb varies from 2 to 7 mm. in diameter. Its lobes are spreading and 1–2 mm. long and are erose or strongly crisped at the margin. The throat lacks invaginate intrusions. It is distinctly glanduliferous with the glands tending to congregate below each of the corolla-lobes. Scattered glands occur down in the tube to about the level of the stamen-attachment. The nectary in the corolla consists of 10 minutely hairy swellings. The style reaches up to the stamens or just beyond them and at times can be almost exerted from the tube. The two stigmas are terminal. The pollen is ellipsoidal and measures $35\text{--}41 \times 24\text{--}33 \mu$, and commonly much resembles that of *L. Pringlei* and *L. indecorum*. In lateral profile it is evidently broadest at the equator and the sides are rounded or somewhat angulate. The pores may be either prominent or obscure.

The corollas of the cleistogamic flowers are 1–3 mm. long. Such flowers may be produced only at the ends of the cymes late in the growing season, or occasionally may be the only flowers produced by the plant. The type of *L. obtusifolium* appears to represent the latter condition. Since nutlets produced by cleistogamic flowers are associated with styles only 1–3 mm. long and those from chasmogamic flowers with styles up to 16 mm. long, the relative fertility of the two types of flowers is readily ascertainable. The two appear to be equally fertile, but the chasmogamic ones are much more numerous.

Plants from southern Mexico and Guatemala tend to be more robust than the more northern plants and have coarser, more spreading hairs. The name *L. Galeottii* is available for them if they prove worthy of recognition.

36. *Lithospermum Pringlei* Johnston, Contr. Gray Herb. 70: 22 (1924).

Lithospermum Seleri Johnston, Contr. Gray Herb. 70: 28 (1924).

A species of central Mexico, probably most closely related to *L. calycosum* and *L. indecorum*. Most of the specimens seen have a weak root which, if not annual, is probably no more than biennial in duration. The yellow corollas have a cylindric tube 5–9 mm. long and 1.5–2 mm. thick, which surpasses the calyx by 1–3 mm. The limb is 3–7 mm. broad. The rounded lobes frequently have a somewhat erose or crispulate margin and hence are suggestive of those of *L. calycosum*. The throat bears 5 definite gibbose invaginations which are densely glanduliferous on the inner side and at times are minutely velvety on the summit. Stiped glands occur only on the faucal appendages and just below them. The nectary in the tube is 5–10-lobed and usually minutely villulose. The style reaches up into the corollathroat and bears two nearly terminal stigmas, left and right on its truncate or convex sterile tip. The pollen (fig. 21) is ellipsoid, $33\text{--}37 \times 25\text{--}27 \mu$, and has prominent pores. The pores seem to be seven in number.

37. *Lithospermum indecorum*, sp. nov.

Herba perennis 1–4 dm. alta; caulibus simplicibus vel laxe ramosis basim versus 1–2.5 mm. crassis hispidulis vel villosis-hispidulis (pilis 0.5–2.5 mm. longis saepe adpressis) et pilulis inconspicuis 0.1–0.3 mm. longis saepe incurvatis obsitis, internodiis saepe 1–3 cm. longis; foliis basalibus tempore florendi delapsis; foliis costatis sed saepissime enervatis, eis infra medium caulis gestis oblanceolatis 1.5–4 cm. longis 4–10 mm. latis, eis supra medium caulis gestis plus minusve oblongis vel lanceolatis 3 cm. longis et 4 mm. latis vel minoribus, supra viridibus vix abundante adpresseque hispidulis (pilis gracilibus 1–4 mm. longis et pilulis 1–2 mm. longis praeditis), subtus pallidioribus sparse adpresse hispidulis vel secus costam et marginem adscenderet hispidulis; floribus inter folia apicem versus caulis et ramulorum dispositis in inflorescentiam distinctam haud collectis; calyce adpresse hispidulo, lobis lanceolatis tubo corollae aequilongis vel eum breviter superantibus maturitate 6–9 mm. longis; corolla flava extus sparse strigosa, limbo 2–3.5 mm. diametro, lobis rotundis 1–1.2 mm. latis, tubo subcylindraco 4–5.5 mm. longo ad 2 mm. crasso, fauce appendiculis prominulis debiliter invaginatibus sparse glanduliferis praeditis; antheris 0.8 mm. longis, filamentis 3–3.5 mm. supra basim tubi corollae affixis; nectario tubi annulato tumido lobulato, lobulis villulosis; stylo 2.5–4 mm. longis; stigmatibus 2 parvis terminalibus vel paulo subterminalibus saepe compressis et divaricatis; nuculis ovoideis ca. 3.5 mm. longis supra medium subconicis saepe brunnescentibus et sparse punctatis.

MEXICO: NUEVO LEON: Canyon Los Capulines above San Enrique, Hacienda San Jose de Raices, shaded situations on slopes, fl. cream-yellow, *Mueller* 2380

(TYPE, Gray Herb.; Mo, FM). TAMAULIPAS: between Marcella and Hermosa, burned-over area, fl. cream-yellow, *Stanford, Lauber & Taylor* 2637 and 2649 (G).

Probably most closely related to *L. Pringlei*, from which it is distinguished by smaller veinless or nearly veinless leaves and smaller corollas that have weak faucal appendages and a tube not surpassing the calyx.

38. *Lithospermum jimulcense*, sp. nov.

Planta perennis indumento griseo vestita; caulibus erectis pluribus 10–15 cm. longis e rhizomate lignoso orientibus supra medium sparse breviter ramosis pilis rectis adpressis pallidis 1–2.5 mm. longis obtectis; foliis numerosissimis, infimis oblanceolatis 5–10 mm. longis 1–2.5 mm. latis tempore florendi delapsis, ceteris (eis parte medionali caulis majoribus) anguste oblongis vel lanceo-oblongis 2–4 mm. latis 1–5 mm. distantibus, apice obtusis, basi abrupte contractis sessilibus, margine anguste revolutis, in facie superiore pilis gracilibus hispidulo-villosis 1–2.5 mm. longis griseo-vestitis, in facie inferiore tomentulosis (pilulis contortis 0.1–0.3 mm. longis) et adpresse hispidulo-villosis; floribus parvis inter foliis minoribus supremis dispositis; calyce 3–4 mm. longo 0.3–1 mm. longe pedicellato, lobis 0.6–1 mm. latis tubo corollae brevissime longioribus; corolla lutea, extus supra medium dense adpresseque villulosa, tubo 3.5–4 mm. longo a basi ca. 1 mm. crasso sursum gradatim ampliato summum ad apicem aliquantum constricto, limbo 3–4 mm. diametro, lobis rotundis 1.5 mm. latis longisque, fauce glandulifero (glandulis dispersis) nullo modo invaginato-appendiculato; antheris 1.3 mm. longis in tertiam partem superiorem tubi positis apice mucronulatis; pollina late ellipsoidea $20 \times 16 \mu$ a latere viso rotunda poris uniseriatis obscuris donata; filamentis 2.5 mm. supra basim tubi affixis; nectario tubi annulato lobulato, lobis inconspicue minuteque villulosis; stylo 2–4 mm. longo stigmatibus 2 minutis terminalibus donato; nuculis ignotis.

MEXICO: COAHUILA: summit of Mt. Jimulco, 3100 m., thick underbrush with oak, pine and juniper, fl. yellow, June 29, 1941, *Stanford, Retherford & Northcraft* 100 (TYPE, Gray Herb.; Mo).

A very distinct species which has a gross habit more suggestive of *Heliotropium* than *Lithospermum*. The short subsimple stems are very numerous and crowded and arise from a very well developed loosely branched caudex growing in rock-crevices or among loose rocks. Among its notable features are its very abundant crowded small elongate leaves and its rather dense grayish indument of appressed slender hairs. The corolla is also noteworthy, being not only unusually small, but also very densely tomentulose-villulose outside. Until the fruit of the plant becomes available for study, the relations of *L. jimulcense* will remain questionable. However, its closest relationship is probably with *L. indecorum*.

39. *Lithospermum oblongifolium* Greenm. Proc. Am. Acad. 32: 300 (1897).

Lithospermum euryphyllum Brand, Fedde Repert. 28: 16 (1930).

This well-marked species probably has its closest affinities among the large-flowered Mexican species with ellipsoid pollen, and particularly with *L. viride*, *L. guatemalense*, *L. strictum*, and *L. Muelleri*. Among its more distinctive features are its well-developed faucal appendages and its cylindric or somewhat ovoid pollen. The plant is confined to the central plateau of Mexico. It is a relatively coarse perennial with stems 3–10 dm. tall. The leaves are large and evidently veined. The greenish yellow corollas have a gradually expanded tube 15–30 mm. long and a small limb of broad rounded lobes 5–10 mm. in diameter. The throat has evident invaginate, emarginate, somewhat trapeziform appendages that are short-hairy and glanduliferous. Inconspicuous, very scattered glands are also present in the throat below the appendages and frequently also on the vein below the filament-attachment. The nectary is an ill-defined slightly swollen glabrous band. The style eventually becomes exerted 3–8 mm. from the throat and bears its two stigmas terminally or subterminally. In some plants the semicircular or transversely oblong stigmas arise from the tip of the style, but in others they are decidedly below and lateral to the obscurely lobed prolonged sterile tip of the style. The pollen, $25\text{--}27 \times 16\text{--}20 \mu$, is cylindric with rounded ends or somewhat ovoid. In lateral outline the sides of the grains are usually straight and accordingly may be either slightly convergent or parallel. The pollen is not ellipsoidal or subglobose nor distinctly broadest at the middle, as is that of closely related species. Nevertheless, as in the latter, its pores are medial. They are apparently six in number and are evident only in collapsed grains.

40. *Lithospermum strictum* Lehm. Asperif. 2: 303 (Nov.–Dec. 1818).

Anchusa tuberosa HBK. Nov. Gen. et Sp. 3: 92 (Sept. 1818). Not *Lithospermum tuberosum* Rugel (1846).

Heliotropium lithospermoides R. & S. Syst. 4: 737 (1819).

Heliotropium mexicanum Sessé & Moc. Pl. N. Hisp. 20 (1888); Johnston, Jour. Arnold Arb. 30: 109 (1949).

Lithospermum rosmarinifolium Sessé & Moc. Pl. N. Hisp. 20 (1888), not Boiss. (1879).

Lithospermum angustifolium Sessé & Moc. Fl. Mex. 32 (1893), not Forsk. (1775).

A readily recognizable species of central Mexico. From a slender taproot, which has a conspicuous fusiform swelling just below the surface of the soil, the plant produces one to many slender stems 2–4 dm. tall. The stems bear numerous slender leaves and terminate in elongate scorpioid cymes bearing numerous flowers and many small bracts. The yellow-green corolla is firm in texture, has a slender tube 6–15 mm. long and a slightly zygomorphic limb 3–6 mm. in diameter. The upper surface of the obovate or elliptic ascending lobes is microscopically velvety-puberulent and frequently also coarsely strigose. The slender corolla-tube is very gradually

ampliate for most of its length but at the very summit is perceptibly constricted. The throat bears five evident faucal appendages. These are weakly invaginate convexities bearing a prominent arcuate ridge of tissue across their upper end. Like the corolla-tube below them, they are glabrous and lustrous. A cluster of glands is usually present at the base of the corolla-lobes just above each arcuate ridge, but below the ridges glands are very few and inconspicuous. The nectary in the corolla-tube consists of a 10-lobed very narrow flap which is very minutely, scantily, and inconspicuously villulose. The style is variable in length, in some plants reaching only to the middle of the corolla-tube but in others as high as the top of the anthers. The two stigmas are terminal, strictly ascending, and at times appear to be joined at the base. The lustrous, very smooth nutlets are distinctive. They have a very sharp and prominent keel which extends up the venter over the apex and partially down the back of the nutlet-body. Below the middle of the nutlets the dorsum is noticeably flattened or very low-convex. The pollen is globose or globose-ellipsoidal, as long as broad or slightly longer than broad. It measures $33\text{--}37 \times 33\text{--}35 \mu$. In lateral outline the sides are rounded or angulate. The grain is clearly broadest at the equator. The pores (apparently 8) are very obscure.

41. *Lithospermum Muelleri* Johnston, Jour. Arnold Arb. 16: 187 (1935).

A very distinct species known only from the mountains of northeastern Mexico. It seems to be most closely related to *L. strictum*. The lower surface of the leaves in *L. Muelleri* bears some appressed hairs along the midrib, but otherwise the surface is glabrous or practically so. This condition is very uncommon in the genus. The elongating scorpioid cymes, as in *L. strictum*, have relatively small bracts and are produced, singly or geminate, terminal on the simple very leafy stems. The greenish yellow corolla has an elongate subcylindric tube 15–20 mm. long which is abruptly constricted at the top and bottom. The small limb, 2–3 mm. broad, is composed of broad, short, rounded ascending lobes. The throat has five small but well-defined faucal appendages. Each consists of a small low-convex area delimited above by an arcuate or somewhat trapeziform intrusion formed partially by an invagination and partially by a thickened ridge of epidermal cells. They are glabrous and somewhat lustrous below the intrusion. On the upper side of the intrusion stipitate glands are numerous. Below the appendages glands are very scattered and tend to be most numerous along the vein just below the filament-attachment. The style eventually becomes exerted from the corolla-tube, commonly by 1–3 mm. The two stigmas are terminal, strict, closely juxtaposed, and frequently more or less confluent. The nectary in the corolla-tube consists of a thin ridge bearing minute tufts of hairs. The pollen (fig. 18), $25\text{--}30 \mu$ broad, is globose or very slightly longer than broad. In lateral profile the sides are rounded or somewhat angled. The grain is broadest at the equator. The pores, apparently 8 in number, are very slightly evident or are obscure. The fruit has not been seen.

42. *Lithospermum Hancockianum* Oliver in Hooker Icones 25: t. 2457 (1895); Hand.-Mazz. Naturbilder aus S.W. China 116, t. 2 (1927).

Lithodora Hancockiana (Oliver) Hand.-Mazz. Sym. Sin. 7: 818 (1936).

Arnebia Hancockiana (Oliver) Johnston, Jour. Arnold Arb. 18: 21 (1937).

Lithospermum Mairei Lévl. Fedde Repert. 12: 286 (1913).

A very distinct species of China, known only from limestone ledges in eastern Yunnan. The functional leaves are borne clustered at the ends of the trailing branches of a very loose shrubby caudex and directly above a skirt-like mass of dead reflexed leaves persistent from previous seasons. They are very elongate and are covered with lustrous white silky appressed hairs beneath. The inflorescence, at first glomerate, later becomes somewhat racemose but is always shorter than the leaves in the cluster from which it arises. The salverform corolla is pinkish or bluish to purplish-red, but usually becomes yellowish in drying. The tube, 2–3 mm. thick, is cylindric and 18–25 mm. long. The spreading limb is 14–20 (–“25”) mm. broad. The throat bears numerous scattered glands above the level of the filament-attachment. There are no faucal appendages. The anthers are borne either 2–3 mm. below the summit of the tube or at the summit and partially exerted from it. The nectary in the tube is a glabrous flange. The style is exerted 2–5 mm. from the tube. The two stigmas are terminal or subterminal. The pollen (fig. 31) is subglobose (26–33 μ in diameter) to ellipsoidal (26–30 $\times$ 23–26 μ), as long as broad to evidently longer than broad. In lateral profile the sides are rounded or angled. The grains are clearly broadest at the equator. The pores (7, or less commonly 6) may be evident or obscure. The nutlets (only submature seen) are white, smooth, bony, and ovoid.

In its non-yellow corolla devoid of faucal appendages, and in its partially exerted stamens, the plant suggests the Asiatic members of the genus formerly referred to *Arnebia*. It differs, however, in its smooth white nutlets and ellipsoid or globose pollen. The plant is one in which heterostyly might be expected. Evidence of it, however, has not been found in the five collections dissected. All the plants studied have elongate, shortly exerted styles, and stamens borne high in the corolla-tube. To be sure there are slight differences in the level at which the anthers are carried. On some plants the anthers are borne just low enough to be included in the corolla-tube, while in others they are borne just enough higher so that they are half exerted from the tube. Such a small difference in level of stamen-attachment is associated with heterostyly in *L. densiflorum*, but in *L. Hancockianum* there appears to be no correlation between stamen-position and a particular length of style or size of pollen.

43. *Lithospermum guatemalense* Donn. Sm. Bot. Gaz. 27: 436 (1899).

A coarse perennial native in the mountains of northern Guatemala and adjacent Mexico. The yellow corollas have a gradually ampliate tube

which is 18–25 mm. long and at least twice the length of the calyx. The rounded lobes are 2–3 mm. long and ascending. The throat bears slightly convex, densely glanduliferous areas below each corolla-lobe. There are no strong invaginations. Glands are scattered over the inner surface of the tube above the level of the filament-attachments. The style becomes eventually exerted, usually as much as 2–3 mm. The two stigmas are terminal. The nectary in the tube consists of 5–10 sparsely villulose very minute swellings. The pollen is ellipsoidal and measures $28 \times 25 \mu$. In lateral profile it has slightly angled sides and is evidently broadest at the equator. The pores, 7–8 in number, may be either obscure or evident. The nutlets are ovoid, ca. 4 mm. long, and usually grayish or tawny rather than white. They are usually very conspicuously sulcate and punctate adjacent to the ventral keel and generally punctate on the back also.

44. *Lithospermum viride* Greene, Bot. Gaz. 6: 158 (1881).

Lithospermum Palmeri Wats. Proc. Am. Acad. 18: 122 (1883).

A species of northeastern Mexico and adjoining United States (Arizona to Texas). Its closest affinities appear to be with *L. Macbridei* of Peru. The tubular corollas are yellowish or greenish and have a relatively small limb of divergent or recurved elliptic to broadly ovate lobes. The tube, 15–35 mm. long, is cylindric with a constriction at the summit. Inside, the throat is devoid of swellings or invaginations, but is abundantly glanduliferous. The nectary is represented by 5–10 very minute, usually villulose swellings. The pollen is subglobose to ellipsoidal and as long or very slightly longer than broad. It measures $16\text{--}23 \times 16\text{--}22 \mu$. In lateral outline it is evidently broadest at the equator and its sides are angulate. There are 7 or 8 very obscure pores about the equator. The style is tardily exerted 1–5 mm. from the tube. It bears 2 terminal stigmas. The mature fruiting calyx becomes 10–20 mm. long. Its very narrow and elongate lobes greatly surpass the nutlets.

45. *Lithospermum Macbridei* Johnston, Contr. Gray Herb. 78: 8 (1927).

This Peruvian plant seems to be most closely related to *L. viride* of Mexico, but is readily distinguished by having crowded, very numerous, much smaller, narrow veinless leaves as well as a neat pallid strigose indument. The greenish yellow corolla has a conspicuous subcylindric tube 10–14 mm. long and a small limb of diverging or recurving lobes. The throat has no intrusions. It is, however, densely glanduliferous with the glands in greatest concentration below each of the corolla-lobes. The nectary is represented by 5–10 minute villulose swellings. The style is eventually exerted 2–5 mm. from the throat and is terminated by 2 stigmas. The pollen is subglobose or nearly spherical, $16\text{--}20 \mu$ in diameter. In lateral profile it is as broad as long, broadest at the equator, and with rounded or slightly angulate sides. There are 8 obscure pores on the equator. The mature fruiting calyx is 5–8 mm. long, and at most only twice as long as the nutlets.

46. *Lithospermum discolor* Mart. & Gal. Bull. Acad. Brux. 11: 337 (1844).

Lithospermum discolor a *candicans* Kuntze Rev. Gen. 2: 439 (1891).

Lithospermum obtusiflorum Sessé & Moc. Fl. Mex. 32 (1893); Johnston, Jour. Arnold Arb. 30: 109 (1949).

Lithospermum chersinum Macbride, Contr. Gray Herb. 49: 22 (1917).

Lithospermum hypoleucum Johnston, Contr. Gray Herb. 70: 23 (1924).

A plant with erect, subsimple to loosely branched, usually hispid stems 5–15 dm. tall, frequently becoming suffrutescent. It is native to central and western Mexico. The evidently veined, usually lanceolate leaves are pale green above and white from a dense appressed indument beneath. The flowers are strongly heterostylic. The white corolla is 1–2 cm. long and has a limb 8–15 mm broad. The tube, slightly to conspicuously longer than the calyx, has the middle three-fifths of its length appressed villose inside. The throat bears abundant scattered glands but is devoid of appendages. The nectary is a tumid obscurely lobed glabrous ring. The stamens are borne below the middle of the corolla-tube or just below its summit. The style is either a quarter to a third the length of the tube or nearly as long as the tube. The two stigmas are terminal. The elongate pollen (fig. 13) is much constricted at the middle, most strongly so in the long-styled flowers. In the latter it measures $22\text{--}28 \times 10\text{--}15 \mu$. In the short-styled flowers it is larger, $33\text{--}39 \times 18\text{--}20 \mu$. There are 7–9 pores. The smooth white nutlets are elliptic-ovoid and are rounded and unkeeled ventrally.

47. *Lithospermum matamorensense* A. DC. Prodr. 10: 76 (1846).

Lithospermum prostratum Buckley, Proc. Acad. Philad. 1861: 462 (1861).

A species known only from northeastern Mexico and adjacent Texas, which is probably most closely related to *L. Berlandieri*. It is an annual, with a juicy taproot and several ascending loosely branched hispidulous stems. The basal leaves are largest. The corolla has a spreading limb 4–6.5 mm. broad. Outside it is very minutely and sparingly strigulose. The tube, 1–1.5 mm. long, is about half the length of the calyx. The throat is provided with trapeziform invaginate appendages which are velvety on top and glanduliferous on the sides. Some glands occur also on the throat below the appendages. The minute anthers are borne on filaments attached at the middle of the corolla-tube. The nectary is a tumid ring, entire or 5–10-lobulate, which is glabrous or very inconspicuously puberulent. The pollen is constricted at the middle and measures $16\text{--}20 \times 10\text{--}13 \mu$. The nutlets of the species are distinctive. They are 2.5–3 mm. long, usually brownish and conspicuously punctate. The ventral keel is broad and rounded and continues up over the apex and down onto the dorsum. The back of the nutlet is not only pitted but frequently also somewhat tuberculate or tumulose. As the result of a lineate constriction above its base the nutlet has a more or less well defined basal collar. The attachment-scar is concave. The funicular canal is evident, but the dorsal traces usually evident on the attachment-scar of the nutlets in other species are very

vague or absent in *L. matamorensis*. The gynobase is obscurely pyramidal, in fact almost plane.

48. *Lithospermum Nelsonii* Greenm. Proc. Am. Acad. 40: 31 (1904).

A species local to northeastern Mexico. The corolla is large, white, and salverform. The limb is 10–14 mm. broad. The tube is 12–15 mm. long, commonly 2–3 times as long as the calyx, and though abruptly expanding at the very base it is cylindric for most of its length. The throat bears small but evident faucal appendages which are invaginate, trapeziform, and glanduliferous. Glands occur also in the throat below the appendages, and others are present at the base of the filaments. The nectary is a glabrous, obscurely lobed flange. The pollen (fig. 26) is medially constricted and measures $15-23 \times 10-13 \mu$. It is similar in size and appearance to that of *L. matamorensis* but larger than that of *L. Berlandieri*. The white smooth nutlets are 2.5–3 m. long, and as in *L. Berlandieri*, are constricted just above the base. The attachment-scar is concave.

49. *Lithospermum Berlandieri*, sp. nov.

Herba perennis 2–5 dm. alta; caulibus pluribus erectis hispidulis (pilulis minutis 0.2–0.3 mm. longis saepe incurvatis et pilis majoribus 0.7–1.2 mm. longis saepe divaricatis praeditis) supra medium sparse adscendentem ramosis, basim versus 2–3 mm. crassis; foliis basalibus et caulinis inferioribus tempore florendi emarcidis; foliis caulinis numerosis saepissime patentibus oblanceolatis (majoribus 5–7 cm. longis et 10–15 mm. latis) supra medium latioribus deinde deorsum gradatim attenuatis, pilulis 0.2–0.3 mm. longis saepe adpressis et pilis majoribus 0.7–1.2 mm. longis adscendentibus vel adpressis vestitis, apice acutis vel saepissime obtusis, subtus pallidioribus saepe venis lateralibus pauca donatis, supra basibus pallidis discoideis pilorum non rariter ornatis; cymis caules et ramulos terminantibus, maturitate laxe racemosis 5–10 cm. longis bracteis divaricatis oblongis vel lanceolatis ad 3 cm. longis ornatis; corolla alba extus parce strigosa, tubo subcylindraco 2.5–3.5 mm. longo ca. 2 mm. crasso, limbo ad 6 mm. diametro rotato, lobis rotundatis 2 mm. longis et latis, fauce appendiculis intrusis gibbosis ornato, appendiculis invaginati apice sparse velutinis latere abundanter glanduliferis; antheris 0.7–0.8 mm. longis in tertiam partem superiorem tubi corollae gestis; filamentis ca. 2 mm. supra basim tubi affixis basi imo sparse glanduliferis; pollina elongata medie constricta $13 \times 7-10 \mu$; nectario tubi corollae glabro 10-lobulato; stylo altitudinem antherarum attingenti 2–2.5 mm. longo e tubo corollae nullo modo exserto; stigmatibus 2 minutis apice emarginato styli positus; nuculis albis laevibus non rariter sparse punctatis ovoideis 3–3.5 mm. longis supra basim laeviter constrictis, cicatrice basali concava; gynobasi latissime pyramidalis.

MEXICO: TAMAULIPAS: oak forests on Jaumave road about 13 mi. southwest of Ciudad Victoria, 1000 m. alt., abundant, fl. white, May 13, 1949, *R. McVaugh 10517* (TYPE, Gray Herb.); pié la cuesta de Victoria a Tula, Nov. 1830, *Berlandier s.n.* (G); Jaumave, 1932, *Rozynski 567* (Chicago); mountains south of Victoria,

1000 m., scattered, March 1925, *Runyon* 747 (US); foot of mountains near Victoria, 400 m., April 1926, *Runyon* 921 (US).

Closely related to *L. Nelsonii*, from which it differs in its very much smaller corollas with proportionately shorter tube and narrower limb. The present species is known only from the mountains southwest of Victoria, Tamaulipas, whereas *L. Nelsonii* is known only from the mountains west and south of Monterrey, Nuevo Leon.

50. *Lithospermum papillosum* Thunberg, Prodr. Pl. Cap. 34 (1794); Thunberg in Schrad. Neues Jour. Bot. 1³: 44 (1806); Lehm. Asperif. 2: 329 (1818); Wright, Fl. Cap. 4²: 21 (1904).

? *Lithospermum papillosum* β *ambiguum* DC. Prodr. 10: 74 (1846).

A well-marked species endemic to South Africa. It has numerous ascending lanceolate or lance-oblong leaves crowded along erect stems 2–4 dm. tall. In general appearance it much resembles the American *Heliotropium ternatum* Vahl and its close allies. Especially distinctive of *L. papillosum* is the generous development of minute obese hairs on the upper face of the corolla-lobes, giving the latter a granular or somewhat velutinous appearance. The corolla-tube, 2–3 mm. long, may be as long as the calyx or be surpassed by it. The faucal appendages are densely glanduliferous, broad, low-convex invaginations. The throat is usually abundantly glanduliferous below the appendages and sparsely so at the base of the filaments. The nectary is a well-developed thickish collar. The style, 1–2.5 mm. long, bears 2 sessile terminal stigmas, and in some specimens appears to be sparingly and very minutely hairy and glanduliferous below the middle. The pollen is short-cylindric with rounded ends and measures $20\text{--}25 \times 13\text{--}16 \mu$. No fruit has been seen. The nutlets, however, have been repeatedly described as rugose.

51. *Lithospermum diversifolium* DC. Prodr. 10: 77 (1846); Wright, Fl. Cap. 4²: 24 (1904).

A plant of South Africa that somewhat resembles *L. officinale* and was formerly confused with it. From *L. officinale* our plant is readily distinguished by the elevated position of the anthers in the corolla-tube, the broader and petiolate lower cauline leaves, and the very different pollen. The tube of the small white corolla is subcylindric, ca. 2.5 mm. long, and about twice the length of the calyx. The faucal appendages are prominent invaginate gibbosities bearing glands and obese hairs. The throat below the appendages is densely glanduliferous. Other glands are found at the base of the filaments. The nectary is a 5–10-lobulate collar. The style is 1.5–2 mm. long and bears 2 sessile terminal stigmas. The pollen is short-cylindric with rounded ends and measures $20 \times 13 \mu$. The pores distributed about the equator are very obscure.

52. *Lithospermum cinereum* DC. Prodr. 10: 73 (1846); Wright, Fl. Cap. 4²: 23 (1904).

Lithospermum inornatum DC. Prodr. 10: 73 (1846).

A well-marked species from South Africa. Among its notable features are its smooth closely appressed grayish strigose indument, small thickish veinless leaves, very small flowers, and tumulose nutlets. The white corollas are 2.5–3 mm. long. The tube is slightly ampliate, 1.5–2 mm. long, which is shorter than the calyx. The corolla-lobes, 0.5–1 mm. long, are ascending, oblong, and evidently veined. The throat bears 5 slightly invaginate rounded convex areas which are velvety and densely glanduliferous. A few glands are present on the vein directly below the filament-attachment. The nectary is 5–10-lobulate. The style is 1–1.5 mm. long and bears 2 terminal stigmas. The pollen measures $16-18 \times 11-14 \mu$ and varies from distinctly ellipsoidal with rounded sides to cylindric-ellipsoidal with nearly straight sides. The pores are borne at the equator and are very obscure. The nutlets, 2.5–3 mm. long, are half or two thirds the length of the fruiting calyx. Dorsally they have a broad low rounded keel, and towards the sides below the middle are pitted and sparingly but distinctly tumulose.

53. *Lithospermum scabrum* Thunberg, Prodr. Pl. Cap. 34 (1794); Thunb. in Schrad. Neues Jour. Bot. 1³: 44 (1806); Lehm. Asperif. 2: 309 (1818); Wright, Fl. Cap. 4²: 22 (1904).

Lithospermum hirsutum E. Meyer ex DC. Prodr. 10: 77 (1846).

Lithospermum affine DC Prodr. 10: 78 (1846).

A species of South Africa usually readily recognized because of its spreading, short, villose-hispid indument. The white corolla is 8–9 mm. long. Its tube, 5–6 mm. long, is twice as long as the calyx. For most of its length, 4–5 mm., it is cylindric, but towards its summit it becomes ampliate. The corolla-limb becomes 5–6.5 mm. broad. Its ascending lobes are rounded and ca. 2 mm. broad. The throat bears 5 weak gibbosities which are somewhat velvety at the summit and are glanduliferous on the sides. A few glands may also be present at the base of the filaments. The nectary is 10-lobulate. The style reaches at least to the apex of the stamens and may become even slightly exerted from the tube. It has a sterile apex that may be obscurely and weakly prolonged beyond the attachment points of the two stigmas. The pollen, $16-18 \times 14 \mu$, is ellipsoidal. It is broadest at the equator and in lateral profile has rounded sides. The pores are very obscure and borne about the equator or very slightly below it. The small nutlets are ovoid, white, and very smooth.

54. *Lithospermum peruvianum* A. DC. Prodr. 10: 77 (1846).

Lithospermum aequatoriale Brand, Fedde Repert. 28: 14 (1930).

A plant of northern Peru and southern Ecuador which forms prostrate mats. Stems numerous, very slender, very elongate and hispidulous. The leaves are very numerous and small, 15–25 mm. long. The small flowers are borne along the terminal portion of the elongate leafy stems and not in a sharply defined inflorescence. The small white corolla has a stout tube 1.5–2 mm. long, which barely if at all surpasses the calyx. The limb is 3–4 mm. broad. Its broad rounded lobes nearly equal the length of the

corolla-tube. There are 5 circular glanduliferous and minutely hairy areas in the throat. These are convex and only very weakly invaginate. The nectary is villulose. The style is 1–2 mm. long and bears 2 juxtaposed small terminal stigmas. The pollen varies in form from cylindric to ellipsoidal, in lateral profile having the sides more or less parallel or slightly angulate and the body broadest at the equator. It measures $13\text{--}20 \times 10\text{--}14 \mu$. The pores are usually obscure. The nutlet tends to develop a slightly swollen rim at the base.

55. *Lithospermum calcicola* Robinson, Proc. Am. Acad. 27: 182 (1892).

Lithospermum Conzattii Greenm. Bull. Field Mus., Bot. 2: 339 (1912).

Lithospermum calcicola var. *Conzattii* (Greenm.) Johnston, Contr. Gray Herb. 70: 27 (1924).

Lithospermum madreense Brand, Fedde Repert. 28: 14 (1930).

Lithospermum hoyasense Brand, Fedde Repert. 28: 15 (1930).

A species of Mexico, ranging from Coahuila and Nuevo Leon south to Oaxaca. The plant has a distinctive indument that aids in its ready recognition. The leaves on both surfaces bear stiff straight appressed hairs 1–1.5 mm. long. These hairs are loosely spaced (commonly 0.5–1 mm. apart) and, especially on the upper surface, arise from well-developed, evident, usually discoid mineralized bases. The corolla and also the style-length are surprisingly variable as to size and proportions, even among plants from a single locality. This variation may be correlated with the season and general vigor of the plant. The tube of the white corollas is subcylindric, 3–7 mm. long, and may equal the calyx in length or surpass it. The limb is 4–7 mm. broad. The throat bears a congregation of glands below the base of each corolla-lobe and also in the tube above the anthers. There are no definite faucal invaginations. The style, 3–11 mm. long, commonly just surpasses the anthers but is not quite exerted from the throat. In some plants, however, it becomes tardily exerted and protrudes as much as 1–4 mm. In other plants it reaches only to the base of the anthers. Furthermore, some very mature plants have nutlets associated with a style only 1 mm. in length. This latter condition suggests that cleistogamy may be present. Though searched for, no cleistogamic flowers have been recognized in the species. The two stigmas are either juxtaposed and terminal or are slightly subterminal and separated by the sterile tissue of the rounded tip of the style. The latter condition seems to prevail in plants from Puebla and Oaxaca. The nectary in the corolla-tube is a glabrous flange. The pollen is ellipsoidal or, more commonly, slightly but perceptibly broader at one end (fig. 19) and hence somewhat ovoid. The pores are weak or obscure and usually borne at a slight distance below the middle of the grain. Between plants, the grains of *L. calcicola* show more variation in size than is usual in the genus. They measure $16\text{--}25 \times 13\text{--}16 \mu$.

56. *Lithospermum mediale* Johnston, Contr. Gray Herb. 70: 28 (1924).

Lithospermum discolor γ *subviride* Kuntze, Rev. Gen. 2: 439 (1891).

Lithospermum colombianum Brand, Fedde Repert. 28: 16 (1930).

This species is known only from Guatemala, Colombia, and Venezuela. The white corolla has a subcylindric tube 5–8 mm. long and 2–2.5 mm. thick, which surpasses the calyx 1–3 mm. The spreading limb is 4–8 mm. broad. The throat has well-developed invaginate gibbose appendages which are somewhat velutinous at the summit and densely glanduliferous on the sides. Glands are also present, not only on and just beneath the faucal appendages, but also along the vein just beneath the attachment of the filaments. The style reaches to the throat of the corolla. The two stigmas are clearly subterminal, being borne below the prolonged bilobed sterile tip of the style. The nectary is more or less lobulate and villulose. The pollen (fig. 22) is ellipsoidal and measures $23\text{--}27 \times 18\text{--}20 \mu$. The pores are very obscure. In lateral profile the sides are rounded or somewhat angulate. In the South American plants the pollen is clearly broadest at the equator, but not so in all the Guatemalan material. In the latter the grains sometimes become nearly straight-sided. The fruiting calyx in *L. mediale* is usually weakly accrescent. Its lobes are usually only about twice as long as the nutlets.

57. *Lithospermum sordidum* Brand, Fedde Repert. 28: 15 (1930).

Closely related to *L. distichum*, but distinguishable by its short-lived stout fusiform root and the broad, usually clustered basal leaves, the more or less evidently spreading indument, and the subsimple erect stems. It is known only from eastern Mexico (Nuevo Leon, Hidalgo and Puebla), where it appears to frequent lower altitudes and drier situations than its relative. In technical characters it agrees with *L. distichum*.

58. *Lithospermum distichum* Ortega, Hort. Matr. Dec. 1: 8 (1797).

Batschia disticha G. Don, Gen. Syst. 4: 326 (1838).

Myosotis grandiflora HBK. Nov. Gen. et Sp. 3: 90, t. 199 (1818).

Heliotropium scorpioides Willd. ex Lehm. Nov. Act. Acad. Caes. Leop. Nat.

Cur. 9: 140 (1818), nomen; R. & S. Syst. 4: 737 (1819), not HBK. (1818).

Myosotis foliosa Lehm. Asperif. 1: 99 (1818).

Lithospermum spathulatum Mart. & Gal. Bull. Acad. Brux. 11: 337 (1844).

Lithospermum laevigatum Sessé & Moc. Fl. Mex. 32 (1893); Johnston, Jour. Arnold Arb. 30: 109 (1949).

Anchusa mexicana Sessé & Moc. Pl. N. Hisp. 21 (1888); Johnston, Jour. Arnold Arb. 30: 109 (1949).

Lithospermum approximatum Brand, Fedde Repert. 28: 15 (1930).

A perennial with a strong woody taproot and, usually, a shallowly buried, loosely branched caudex. A plant of the mountains of Mexico and Guatemala. The stems are ascending, usually branched at the base, and commonly only 1–2 dm. long. The herbage bears minute appressed hairs and is smooth in appearance. The white corollas have well-developed gibbose invaginations in the throat. They are evidently puberulent and are glanduliferous on the inner side. Glands are most abundant on the faucal appendages. A few, however, are usually present at the base of the filaments. The nectary is a thickish lobed collar. The two stigmas are subterminal

and borne laterally just below the sterile bilobulate tip of the style. The pollen (fig. 24) is cylindric with rounded ends. The pores are equatorial. The grains measure $16-22 \times 10-14 \mu$. The plant is variable in corolla-size and in the relative length of the corolla-tube.

59. *Lithospermum Gayanum* (Wedd.) Johnston, Contr. Gray Herb. 78: 10 (1927).

Eritrichium Gayanum Weddell, Chor. Andina 2: 88 (1859).

Lithospermum andinum Krause, Engler's Jahrb. 37: 636 (1906).

Lithospermum Shepardae Johnston, Contr. Gray Herb. 78: 10 (1927).

An Andean species ranging at high altitudes from central Peru south into northern Bolivia. It is most closely related to the Mexican *L. distichum*, but differs in its smaller stature and in details of floral structure. The faucal appendages are merely puberulent swellings and are not invaginate. Glands are few in the throat and none is present at the base of the filaments. The pollen is short-cylindric with rounded ends and measures $16-20 \times 10-14 \mu$. The style is terminated by the two stigmas. It does not have the bilobate sterile tip developed by the styles of *L. distichum* and *L. sordidum*.

EXPLANATION OF PLATES

PLATE I

Pollen of heterostylic species of *Lithospermum*. In each pair the larger grain (left) from short-styled flower, the smaller (right) from long-styled flower. The arrow indicates the position of a row of pores. Species all Asiatic.

FIG. 2. *L. densiflorum*. FIG. 3. *L. euchromon*. FIG. 4. *L. fimbriatum*. FIG. 5. *L. guttatum*. FIG. 6. *L. Griffithii*. FIG. 7. *L. hispidissimum*.

PLATE II

Pollen of heterostylic species of *Lithospermum*. In each pair the larger grain (left) from short-styled flower, the smaller (right) from long-styled flower. The arrow indicates the position of a row of pores. First species Asiatic, the others American.

FIG. 8. *L. Tournefortii*. FIG. 9. *L. californicum*. FIG. 10. *L. tubuliflorum*. FIG. 11. *L. canescens*. FIG. 12. *L. caroliniense*. FIG. 13. *L. discolor*. FIG. 14. *L. multiflorum*. FIG. 15. *L. cobrense*. FIG. 16. *L. obovatum*.

PLATE III

Pollen of representative non-heterostylic species of *Lithospermum* (American species, figs. 17-26; Eurasian, figs. 27-32). The arrow indicates the position of the row of pores.

FIG. 17. *L. incisum*. FIG. 18. *L. Muelleri*. FIG. 19. *L. calcicola*. FIG. 20. *L. tuberosum*. FIG. 21. *L. Pringlei*. FIG. 22. *L. mediale*. FIG. 23. *L. ruderales*. FIG. 24. *L. distichum*. FIG. 25. *L. latifolium*. FIG. 26. *L. Nelsonii*. FIG. 27. *L. decumbens*. FIG. 28. *L. tetrastigma*. FIG. 29. *L. detonsum*. FIG. 30. *L. tschimganicum*. FIG. 31. *L. Hancockianum*. FIG. 32. *L. officinale*.

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